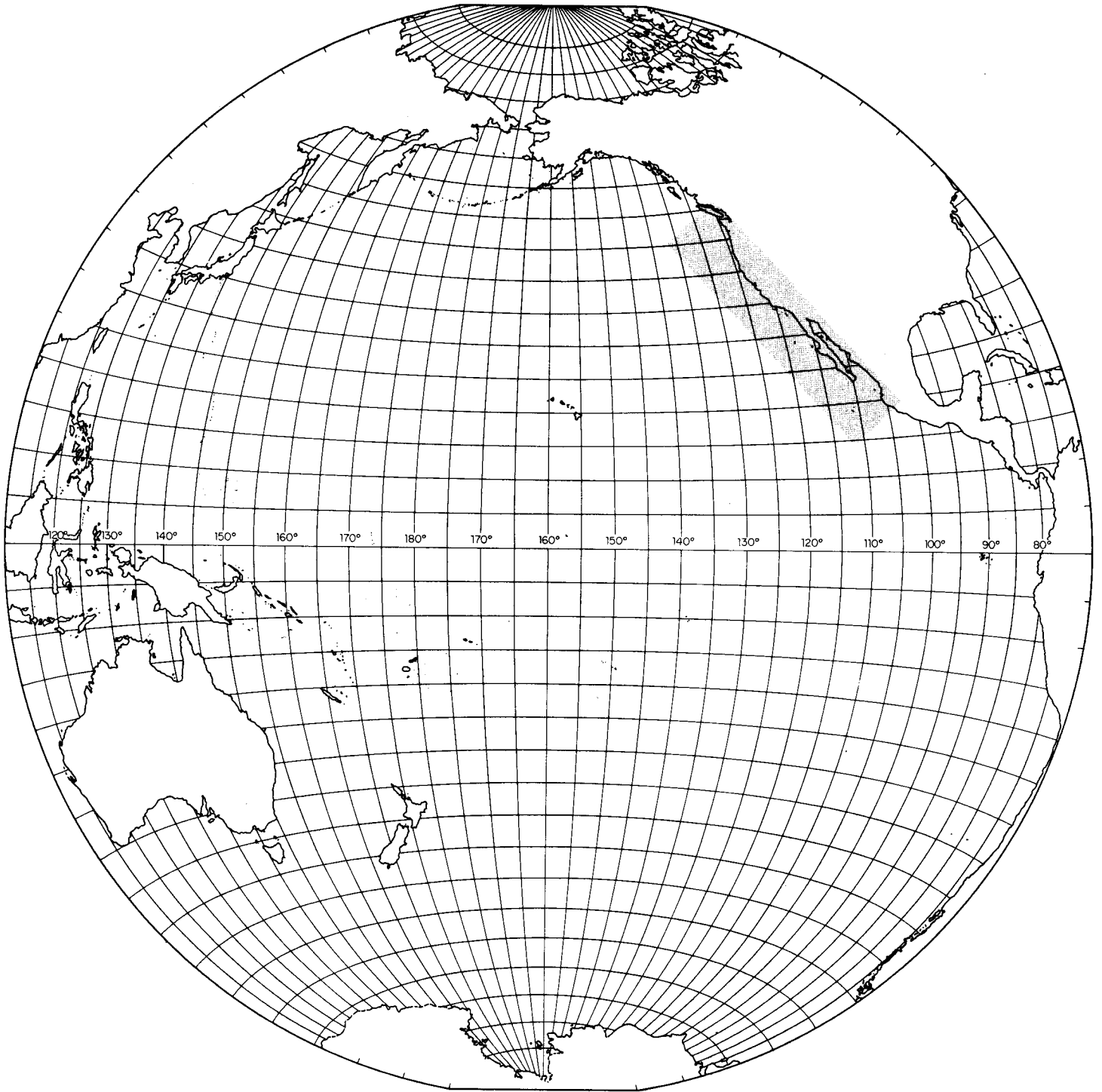


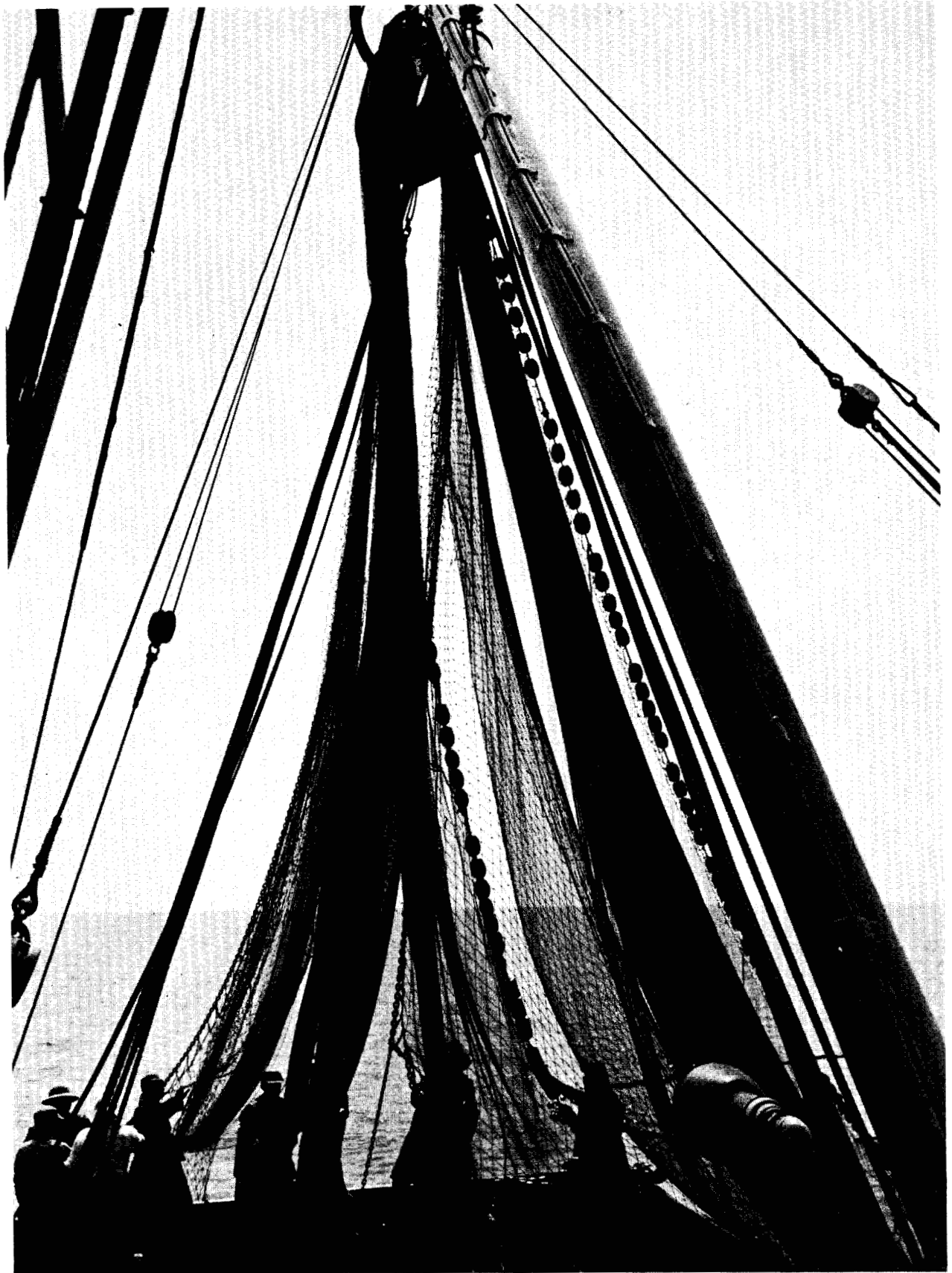
STATE OF CALIFORNIA
MARINE RESEARCH COMMITTEE



CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

VOLUME IX
JANUARY, 1963



Puretic Power Block in operation, pulling a sardine purse seine. *Photograph by G. I. Murphy.*

STATE OF CALIFORNIA
DEPARTMENT OF FISH AND GAME
MARINE RESEARCH COMMITTEE

CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Reports

Volume IX

1 July 1960 to 30 June 1962

Cooperating Agencies:
CALIFORNIA ACADEMY OF SCIENCES
CALIFORNIA DEPARTMENT OF FISH AND GAME
STANFORD UNIVERSITY, HOPKINS MARINE STATION
U. S. FISH AND WILDLIFE SERVICE, BUREAU OF COMMERCIAL FISHERIES
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY

1 January 1963

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LETTER OF TRANSMITTAL

January 1, 1963

EDMUND G. BROWN
Governor of the State of California
Sacramento, California

DEAR SIR: We respectfully submit the ninth report on the work of the California Cooperative Oceanic Fisheries Investigations.

The report consists of two sections. The first contains a brief review of the administrative and research activities during the period July 1, 1960 to June 30, 1962, a description of the fisheries, and a list of publications arising from the program. The second section is comprised of original scientific contributions. These papers are either the direct results of the CalCOFI research programs, or represent research directly pertinent to resource development in the pelagic realm off California.

Respectfully,

THE MARINE RESEARCH COMMITTEE

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PART I
REVIEW OF ACTIVITIES

July 1, 1960 - June 30, 1962

REPORT OF THE CALCOFI COMMITTEE

INTRODUCTION

This series of reports serves as a means of directly publishing some of the scientific results of the CalCOFI research program, especially certain lengthy contributions particularly well served by the format. These occupy the bulk of each issue. In addition, it serves as a general report to the public by indicating the complete scope of the scientific research through an annotated bibliography, including general reports on the status of the fisheries, and describing the activity of the individual laboratories. Finally, especially in this section, an attempt is made to unify the diverse approaches and results of the several laboratories hoping thusly to more nearly approximate the singularity and unity of the natural world.

This last is perhaps the most important function for it strives to achieve cohesiveness and continuity, gives meaning to the total scientific effort by integrating the findings and activities of individual research projects, and presents an intimation of the impact of these findings on the concepts by which the program is guided.

In an equivalent statement in Volume VIII of the Reports, the Committee summarized its objectives and findings and asked a series of critical questions as to the regime of the sardine and other pelagic fishes in the California Current System. Since then much progress has been made in clarifying the conditions under which pelagic fishes live. In particular much is being learned about the interaction of two major species, the sardine and the anchovy. The emerging results are particularly gratifying.

Viewed from the development of marine science the results are a source of encouragement, as they reveal the possibilities for understanding the interplay of various species and their environment—an exciting ecological rapport exceedingly difficult to achieve in the vastness of the ocean. Viewed from the development of marine resources, such understanding opens up the possibility of a more realistic appraisal of the effect of fishing on the ecological system and even of directing man's intervention so that a more useful ecosystem is established.

DEVELOPMENTS

The period July 1, 1960 through June 30, 1962 has seen an accelerated expansion of Marine Sciences. The rapid world-wide development of new fisheries; the power of the seaborne deterrent, Polaris; the interest in sea water conversion; the recognition of vast mineral deposits on the sea floor; the Mohole project;

and many other developments have more clearly focused the attention of scientists and the public upon the significance of the vast ocean resources to meet human needs. The increased requirements of man to dispose of his wastes, atomic and other, and even the increased need for outlets for adventure and recreation have also brought added attention to the marine realm and increased recognition of its challenge.

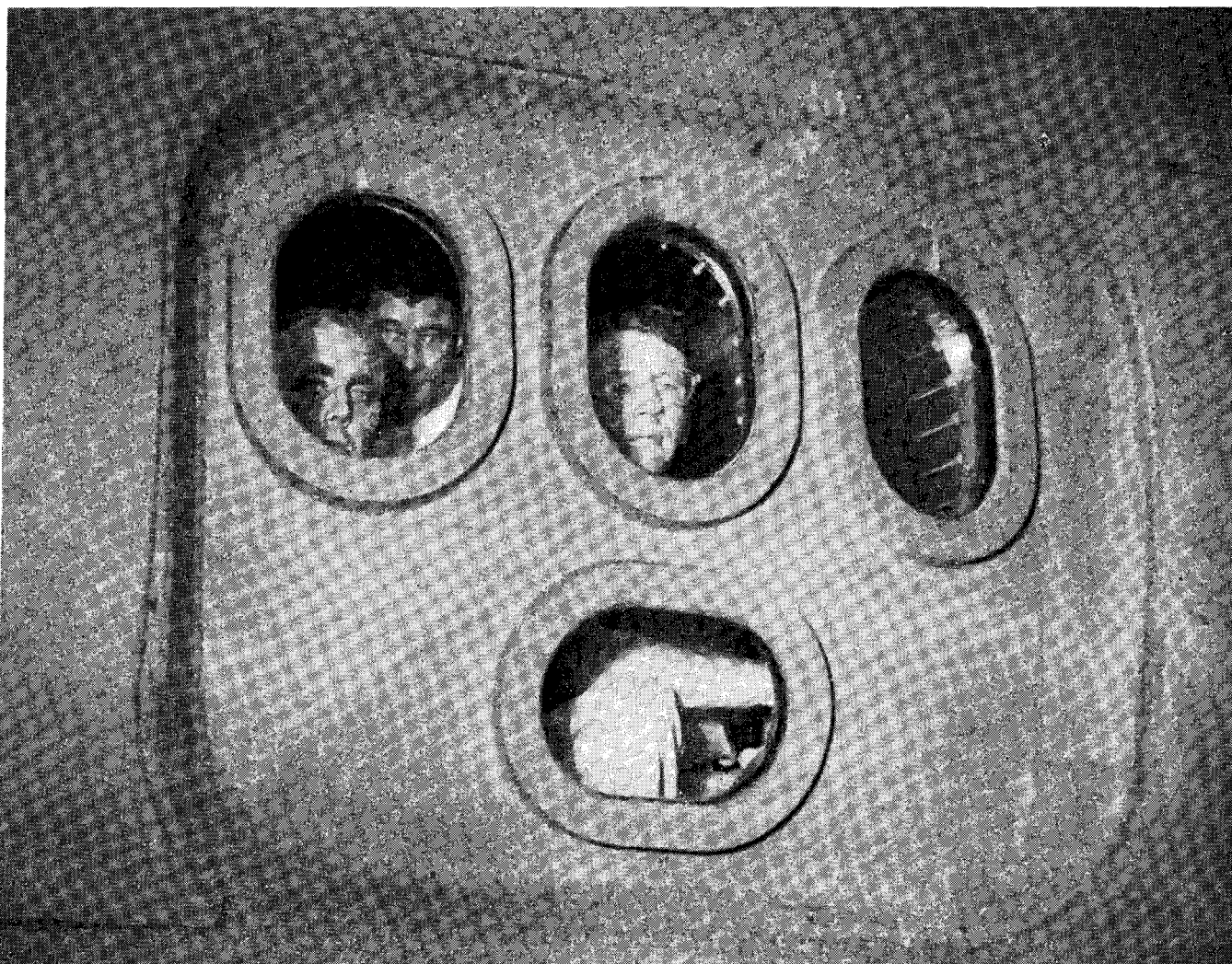
It is not surprising, therefore, to find the CalCOFI Program during this period not only expanding its scope but also intensifying its concentration on the factors influencing the organisms in pelagic waters. Furthermore, additional support has been forthcoming to aid in the expansion and intensification of the research with new facilities becoming available. The M/V ALEXANDER AGASSIZ has been obtained and outfitted especially for the Scripps portion of the CalCOFI Program; a new ship is on the drawing boards for the Bureau of Commercial Fisheries; the Bureau has funds and plans for a new laboratory building. A new hydraulic facility suitable for large scale biological experiments is funded and soon to be constructed by the University of California. Research supported by CalCOFI in other organizations is becoming independently supported. The deep sea research of the Department of Oceanography of Oregon State College, encouraged by CalCOFI support, is now proceeding independently with the new ship, ACONA. Similar work at the Dillon Beach Laboratory of the "University" of the Pacific will probably be independently supported next year.

These developments are further detailed in the separate reports of the individual agencies. The above is a resume of the increasing importance of marine research, the physical facilities, and financial support that CalCOFI is receiving, but research cannot be measured in terms of the level of support that it receives.

FINDINGS

The real substance of this report is the understanding that has been achieved and the illumination that has been shed on the problem of the ecology of the California Current System, the inhabitants and, in particular, on the sardine as a member of a community.

In Volume VIII of the CalCOFI Report the Committee expressed the hypothesis that the niche occupied by the sardine has been largely taken over by the anchovy, perhaps mediated by a long period of colder



The Alaska's underwater viewing ports. Photograph by Charles H. Turner, Department of Fish and Game.

than normal years and abetted by the activity of the fishery in concentrating mainly on the sardine. Subsequent investigations have lent support to this opinion. The sardine plus the anchovy may act as a single population in exploiting the environment and in filling the space that is available. It appears that the sardine-plus-anchovy population of the California Current is now enjoying the success and abundance previously enjoyed by the sardine virtually alone. The two species may act in close concert in utilizing the environment and may exist in widely varied equilibria, with sardines in dominance at one time and a preponderance of anchovies at another.

Much more is being learned about these two species, their associates, and the conditions under which they exist. The existence of separate spawning stocks (sub-populations) of sardines has been established. Community associations of zooplankton species have been related to particular water masses. Research has pointed out mechanisms by which organisms become highly concentrated along coast lines; has expanded into the nature of growth and mortality of larval fish; and has elucidated details of circulation of the Cali-

fornia Current which so profoundly influence its inhabitants. One major discovery has been that preserved samples may be more readily converted into biomass indices than would have been thought possible from fresh samples. This has allowed the beginnings of a program of biomass analysis. Further comments on these and other investigations are included in the sections to follow. *E. H. Ahlstrom, J. D. Isaacs, G. I. Murphy, J. Radovich.*

AGENCY ACTIVITIES

California Department of Fish and Game

The Department conducted investigations on most commercial and sportfishes inhabiting the waters of California. Investigations of the pelagic wet fisheries—sardine, anchovy, Pacific mackerel, jack mackerel, herring, and squid—were conducted by the Department's Pelagic Fish Investigations. A major portion of the effort expended on these species was directed toward collecting basic information, data providing a foundation for more sophisticated studies by all CalCOFI scientists.

Our investigative work included:

- (1) Determining the amounts landed of anchovy, herring, Pacific mackerel, jack mackerel, sardine and squid.
- (2) Measuring the sizes of year-classes of the anchovy, Pacific mackerel, and sardine fisheries. Aging of the sardine and anchovy catches is done in cooperation with the U.S. Bureau of Commercial Fisheries.
- (3) Measuring fishing effort and determining fishing localities. This was done through fishermen interviews and log books.
- (4) Measuring the relative abundance and distribution of fish populations with particular emphasis on the sardine. This work was done at sea, on the fishing grounds and beyond, to cover those portions of the various populations not accessible to the fishing fleet. The survey area extends from central California to the southern tip of Baja California, Mexico, and occasionally into the Gulf of California.
- (5) Measuring abundance and distribution of inshore pelagic fish schools, particularly of the anchovy, by aerial surveys.

In addition to the regular work, special cruises were conducted to improve fish sampling techniques and to obtain live sardines for serological studies conducted by the Bureau of Commercial Fisheries.

One cruise, in early 1962, into the Gulf of California to obtain sardines for blood genetics proved to be of special significance. Sardines were collected throughout most of the Gulf and were serologically tested by U.S. Bureau of Commercial Fisheries personnel. These tests established that Gulf sardines constitute the third known, distinct, non-interbreeding, subpopulation. The other two subpopulations, designated as "northern" and "southern" occur off California and Baja California, Mexico. In conjunction with the serological studies that are designed to distinguish the different stocks of sardines along the coast, the Department continued sardine morphometric studies. This attempts to determine if phenotypic differences can be recognized corresponding with the genetic separation obtained from the serological work.

In order to facilitate fish sampling at sea, the research vessel, ALASKA, was fitted with an underwater viewing chamber. Viewing ports in this chamber will also allow observing fish behavior in a natural environment.

Work was continued on the effect of water temperatures on fish distribution and two papers were published on the subject. A density dependent model describing the relationship between year class size and stock size was developed and the model with its supporting evidence was published.

Hopkins Marine Station

In the period July 1, 1960-June 30, 1962, the Hopkins Marine Station of Stanford University has continued to monitor the marine climate and plank-

ton in the Monterey Bay area. Approximately weekly cruises were made on Monterey Bay, daily shore temperatures were reported from Pacific Grove and Santa Cruz, and once a month shore temperatures were taken at selected stations along the coast between Monterey and Morro Bay. The data collected in these operations have been compiled and distributed to interested agencies and individuals in the form of mimeographed quarterly and annual data reports. The general findings during this period indicate the end of the warm trend, and a return to the general oceanographic conditions prevailing in the first half of the decade 1950-1960.

The information accumulated in the survey of the Monterey Bay area during the years 1954-1960 is summarized and interpreted in a paper appearing elsewhere in this Report (Bolin and Abbott—Studies on the marine climate and phytoplankton of the central coastal area of California). The findings discussed bear out the value of continued monitoring of conditions in selected areas, providing the sort of information on marine conditions that weather stations provide on atmospheric conditions.

Scripps Institution of Oceanography Marine Life Research Program

The Marine Life Research (MLR) Program, Scripps' portion of the CalCOFI Program, has undergone a number of important developments and changes in the last two years. Many of these changes have been the result of new discovery and evolving concepts. Others have stemmed from the quickening tempo of marine research in general. The following is a brief summary of the research and developments of the Marine Life Program. Detailed results have been published elsewhere.

In the early years of the CalCOFI Program, the waters of the California Current region were characterized by surface temperatures somewhat lower than the long-term mean. In 1957, however, the temperature began to rise and in 1958 and part of 1959 the waters were substantially warmer nearly everywhere over the region.¹

In 1960 conditions became more nearly normal, that is, instead of the huge areas of above or below normal temperatures that had characterized the "unusual" years, there were small areas of above or below normal temperature irregularly alternating over the region. Thus the last two years of the California Current region cannot be categorized as either warmer or colder than normal. This period of "normal" temperature has lasted through October, 1962.

These variations of temperature have been shown to be related to the behavior of the wind. The period from 1948 through 1956 was characterized by winds from the north that were somewhat stronger than the mean; 1957 and 1958 showed weaker winds than normal. Since 1959 the winds have varied rapidly and irregularly, and no consistently strong or weak periods have occurred. The first component of an atlas of

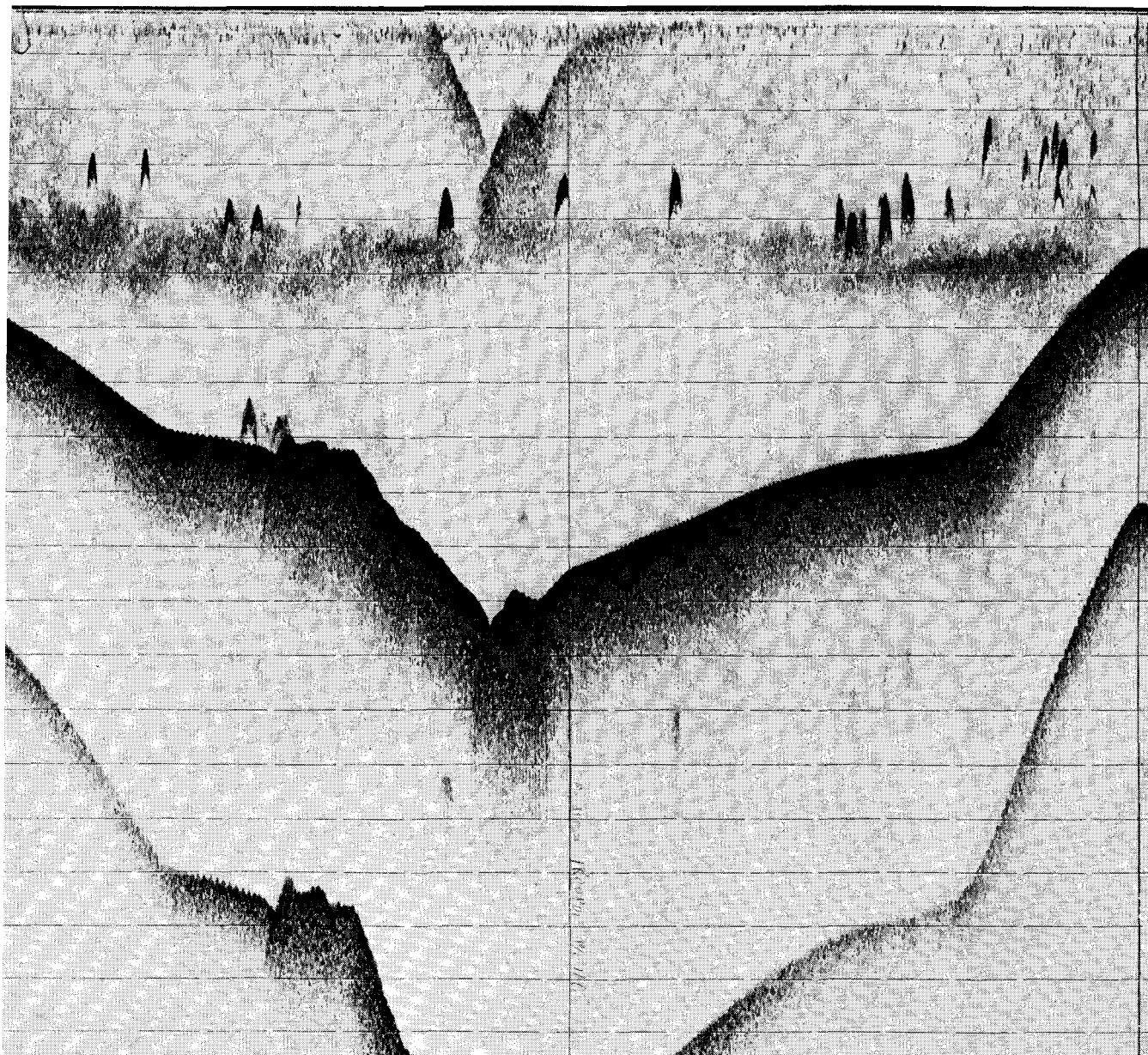
¹ The weather, oceanography, climatology, and biology of the period 1948 to 1958 were extensively reviewed in the CalCOFI Report No. VII.

the California Current (10-meter conditions) has been completed.

Direct current measurements have been continued in critical parts of the California Current. Studies with drogues in the area off central California in autumn have revealed details of the annual beginning of the northward-flowing coastal Davidson Current. Its full development in mid-winter has shown speeds up to 0.4 knot and a width about 50 miles. The existence of the northward flowing undercurrent along the California coast, indicated by the distribution of heat, salt, oxygen, and density has been directly confirmed by studies with drogues 250 meters beneath the sur-

face. These showed that the current had a maximum speed of 0.4 knot and a width of about 40 miles (Reid, 1962). A more detailed study of small-scale eddies has been carried out off northern Baja California, and clearly showing their important role in the process of mixing, and dramatically confirming the efficiency of standard oceanographic methods as a means of describing even small scale features of the currents.

The Cape Lookout Survey revealed strong internal wave activity and a great concentration of zooplankton organisms associated with it. A similar survey of conditions off Cape Colnett also revealed great concentrations of organisms. These were vertical migrat-



Acoustic record of deep scattering organisms and schools of predators concentrated off Cape Colnett. The vertical scale is 20 fathoms per line. The inverted "V" shaped echoes are predator schools which are so dense as to show secondary reflections over the lower of the two false bottoms. The diffuse trace at 100 fathoms is the scattering layer. Two secondary reflections of the bottom are shown, one above and one below the heavy central bottom trace. These are the result of sound bouncing back and forth between the bottom and the ship.

ing zooplankters carried in over the continental shelf by the current that sweeps shoreward in this area. Some phases of this concentration involved intense predation by resident fish in which hake and anchovies were present.

Mutant strains of bacteria for the bio-assay of 19 trace amino acids, vitamins, etc., have been developed. These substances can now be detected in concentrations as small as ten-parts per billion. Development of additional mutants has ceased and we are preparing to carry out synoptic surveys of some of the substances in the California Current System.

The first deep-midwater trawl survey was carried out over the CalCOFI Survey Pattern and the catches were analyzed. A continuation of this work has been supported by the Atomic Energy Commission, and deep collections of organisms and hydrographic data will now extend the MLR Surveys to the bottom of a large portion of the California Current System.

All major groups of zooplankton were under study and their distribution in the eastern North Pacific was collated. The limits of distribution, the changes during the years, and the associations of species of arrow worms, copepods, euphausiids, and pelagic mollusks was brought to a stage of description that has permitted the beginning of a comprehensive atlas of these creatures. The species of zooplankton with which fish larvae are associated are emerging from these studies, and the species of phytoplankton will soon be added to the analysis of associated organisms.

A major task that remains is the analysis of plankton samples in a way that reveals the most information with respect to zooplankton as grazers, as food for larval and adult fish, and as predators on larval fish and other zooplankters. Obviously there are great differences between the significance of different types of organisms. For example, how does one equate a number of jelly-like salps with a similar number of solid, shrimp-like euphausiids? The answer to this problem is probably contained in the recent discovery by the Bureau of Commercial Fisheries, which shows that the measurement of the volume of preserved plankters is a good measure of their original organic content, for they appear to shrink in storage to an almost equal concentration of previously living material. The preserved material is thus more valuable for this understanding than is the fresh catch! These basic qualities of the zooplankton can now be known and related with the changing oceanographic history of the California Current System and the fishes. A Biomass Laboratory is being organized at Scripps to capitalize on this advance.

Most important findings are emerging from the sardine and anchovy larvae data. As introduced in the general CalCOFI statement, investigations have shown that the anchovy and the sardine appear to act as a single population in their utilization of the environment. Apparently various proportions of the two species can exist and essentially fill the ecological space available.

Other very pertinent findings emerge, which will be reported in detail. For example, in years in which the sardine produces better-than-recent year classes, the

anchovy larvae apparently survive better. This only can be explained by a slower relative growth rate of the anchovy in those years. Another finding of this research is that the anchovy and sardine larvae that are caught in the *daytime* plankton hauls are a special category of larvae, and these catches appear to be a measure of the mortality of the population. The best explanation of this is that a large part of the *day* larvae are dead or dying when caught.

Besides its University and MRC funds the Marine Life Research Program received cooperative support during the period on some of its work from the Tuna Oceanography and Office of Naval Research, particularly in instrument development and in the use of special Naval ships. In addition the National Science Foundation provided funds for a quarterly cruise, and the AEC has made funds available to extend the MLR investigations to greater depth, as mentioned above. These other sources of support greatly broaden and enrich the MLR Program.

A major addition to the Marine Life Research Program was the acquisition of a new ship, the ALEXANDER AGASSIZ, for its exclusive use. This 180-foot vessel was outfitted and modified using funds loaned by the Regents of the University. She is the roomiest vessel of the Scripps fleet and perhaps the most seaworthy. She is especially outfitted for biological-oceanography investigations.

The development of unmanned deep-moored stations proceeded. A new station, taut-moored with nylon line, was developed and tested. One of these is now operating off the central California coast in 500 fathoms of water and is expected to continuously record meteorological and oceanographic conditions.

Other developments include a successful free-rising thirty-foot net that descends to 1000 fathoms and fishes to the surface; further perfection of the free fish traps that fish on the bottom in depths up to 3000 fathoms and return; and an electrical bathythermograph.

In summary, the California Current System is now the most thoroughly studied and best understood oceanic region in the world. The CalCOFI Surveys have now covered years embodying essentially all types of physical environmental conditions and change; i.e., warm years, cold years, monotonous years, years with strong countercurrents, years with invasion of tropical waters, etc. Thus, insofar as the oceanography is concerned, the range of conditions and their probability of occurrence is well understood. Since 1960, quarterly monitoring surveys have been substituted for the monthly cruises with the expectation of even a further reduction in the future.

The concomitant biological changes, with their infinitely greater complexity, are, however, by no means as well understood. Yet we will probably never again collect such a volume of biological samples so well integrated with the oceanography.

The effort must now be intensified toward thoughtful studies of the samples and data already obtained during the last twelve or fourteen years and to special investigations to answer the more discriminating

questions that can now be asked. The sardine-anchovy interaction is a case in point where special analyses of the data already have yielded vital findings. The Biomass Laboratory is a development in this direction as is the analysis of zooplankton for associations and the special studies at sea on the currents and the accumulations of organisms.

U.S. Bureau of Commercial Fisheries (BCF)

Research at the U.S. Bureau of Commercial Fisheries Biological Laboratory, La Jolla, comprise 17 projects grouped under the following six programs: 1) population dynamics, 2) sardine spawning and larval survival, 3) subpopulation studies, 4) physiology, 5) behavior, and 6) life history and taxonomy of fishes. Five of the programs center on the Pacific sardine, the other on fishes ecologically associated with the sardine in the California Current System.

One of the major developments in furthering understanding of the population structure of the Pacific sardine has been the establishment of the existence of three genetic subpopulations, two in the area of the California Current, the third in the Gulf of California. The subpopulations were identified by serological techniques, which were employed on samples of fish (preferably 100 or more). No method is yet available for identifying individual fish to subpopulation.

The two subpopulations in the California Current System, termed "northern" and "southern" were more widely separated geographically in 1961 than in earlier years. The "southern" apparently did not enter into the area of the California fishery, and the "northern" stock contributed little or nothing to the Baja California landings. This has afforded the opportunity of studying the age and length composition of the two subpopulations by utilizing samples from the commercial catch. The northern subpopulation in 1961 was made up mostly of older fish, 4- and 5-years of age, the southern group of young fish predominantly 3- and 2-years of age. There were such marked differences in the size of fish of the same ages in the two subpopulations that there was little overlap in length frequency distributions.

The physiology program has been accumulating information on energy and nutritional requirements of the sardine egg and larvae, as well as on the biochemical and nutritional changes related to the reproductive cycle in the adult. It has been shown that larvae

do not have full ability to osmoregulate until two days after hatching, but that energy needed for osmoregulation is insignificant, so that energy derived from yolk is largely available for growth.

Biochemical analysis of the ovaries and some other tissues in the adult sardine has shown that fatty acid composition of the lipids deposited in the ovary does not vary with the stage of ova maturation. It does change, however, with changes in diet and further study on the lipids of crustaceans suggests that dietary fat is deposited largely unchanged in the tissues of the sardine as it is in the tissues of other fishes.

The physiology program advanced its work on early development of fishes by adapting a temperature gradient block for studies of growth in simultaneous ranges of temperatures. Excellent control in this apparatus allowed for rearing of eggs and larvae at 18 different temperatures at the same time. It was possible then to determine the rates of embryonic development of a single species as influenced by temperature in a single experiment.

The behavior program has been attempting to make quantitative estimates of the relations between environmental variables and the distribution and behavior of pelagic marine fishes. Field studies were conducted to determine the extent to which the distribution and movements of sardine schools and school groups are influenced by the distribution of their food organisms. Laboratory studies still in progress are investigating the response of anchovy schools to visual stimuli such as light beams and transparent fence barriers under various conditions of illumination and turbidity.

The distribution and abundance of sardine spawning was determined in quarterly survey cruises in 1961 and 1962. The spawning was small in amount and distributed mostly inshore. There was no evidence of a resurgence of the sardine population. The ecological associate of the sardine, the northern anchovy, continues in high abundance, as evidenced from the distribution and abundance of anchovy eggs and larvae.

The second quarterly cruise of 1962, in addition to the usual oceanographic-biological coverage, focused attention on the sampling of late larval and juvenile stages of pelagic fish by utilizing the Isaacs-Kidd mid-water trawl, a newly designed small beam trawl, and 2.0-meter stramin nets.

REVIEW OF THE PELAGIC WET FISHERIES During the 1960-61 Season

SARDINE

The 27,000 ton sardine catch of the 1960-61 season was approximately 10,000 tons less than the relatively poor preceding season. The catch has been lower in only three other seasons during the 45 year history of the California fishery.¹ These seasons were 1952-53 (5,711 tons), 1953-54 (4,492 tons), and 1957-58 (22,272 tons).

The small catch did not come as a complete surprise to industry members. A pre-season prediction of fewer than 30,000 tons had been given by CalCOFI scientists before the Marine Research Committee on July 26, 1960.

The season officially began on August 1 for central California and September 1 for southern California and closed for both areas on December 31. Sardine and mackerel prices were established at \$35 per ton. This was the same as was paid for sardines the preceding season but was a decrease of \$15 for the mackerels.

Fishing was poor off central California. Although some sardines were caught off Monterey and Cape San Martin in August, the boats shifted operations to southern California in the latter part of September and little scouting effort was expended in central California during the remainder of the season where landings eventually totaled only about 2,000 tons.

Fishing started promptly when the southern season opened but the catches were poor and became progressively poorer during the season. In general, the weather was good, but the exposed location of many of the offshore fishing areas made fishing somewhat difficult. The southern California fleet landed about 25,000 tons of the statewide total of 27,000 tons.

Southern California catches originated farther off shore than has been usual in most previous seasons. Two locales, the Santa Cruz-Anacapa-Santa Rosa Island area and the San Nicolas Island area, produced the bulk of the catch. Lesser amounts were netted in the vicinity of Point Dume, Santa Monica Bay, Santa Catalina Island, San Clemente Island, and Cortez Bank. Landings from the inshore Long Beach-Seal Beach area were small. Throughout the season most individual boat catches were small, but an occasional boat netted 100 tons in one or more sets.

Sardine load limits as low as 40 tons were established early in the season, but these were raised to 100 tons, and at times limits were completely removed. A 20 ton mackerel limit remained in effect throughout the season. Many catches were mixtures of sardines and mackerel.

The number of vessels in the California sardine fleet was the smallest in over 30 years. It consisted

of 108 boats: 58 large purse seiners (60 feet and over) and 50 small purse seine or lampara boats. This was a decrease of 20 vessels from the preceding season. During the season, 12 large and two small purse seiners fished off both central and southern California, 15 lampara boats confined their sardine fishing activity to the Monterey Bay area, and 33 small boats fished only in the southern region.

Fish sampled at San Pedro ranged from 170 to 250 mm in standard length, with a mode at 218 mm. The average weight per fish was 0.27 pounds or approximately four fish to the pound. During recent years sardines have averaged five to the pound. Fifty-five percent of the fish were three-year-olds, 22 percent were two-year-olds, and 20 percent four-year-olds.

ANCHOVY

Cannery and fresh-fish market landings of anchovies continued the downward trend of the last decade, with only 2,500 tons delivered. By comparison, 3,600 tons were landed in 1959 and 5,800 tons in 1958. These low catches have reflected market conditions rather than a shortage of anchovies.

As in other recent years most of the 1960 catch was taken off southern California. About 70 percent of the deliveries were netted in the Long Beach-Los Angeles-Santa Monica area, and 25 percent from the Monterey-Moss Landing area. In addition to the market landings, an estimated 5,000 tons were netted for live bait, making a total of 7,500 tons of anchovies utilized in 1960.

As in 1959, the live bait catch consisted of the small "pinhead" (fish of the year) and fish in their second year of life. No significant live bait catches of juvenile sardines were reported during the year.

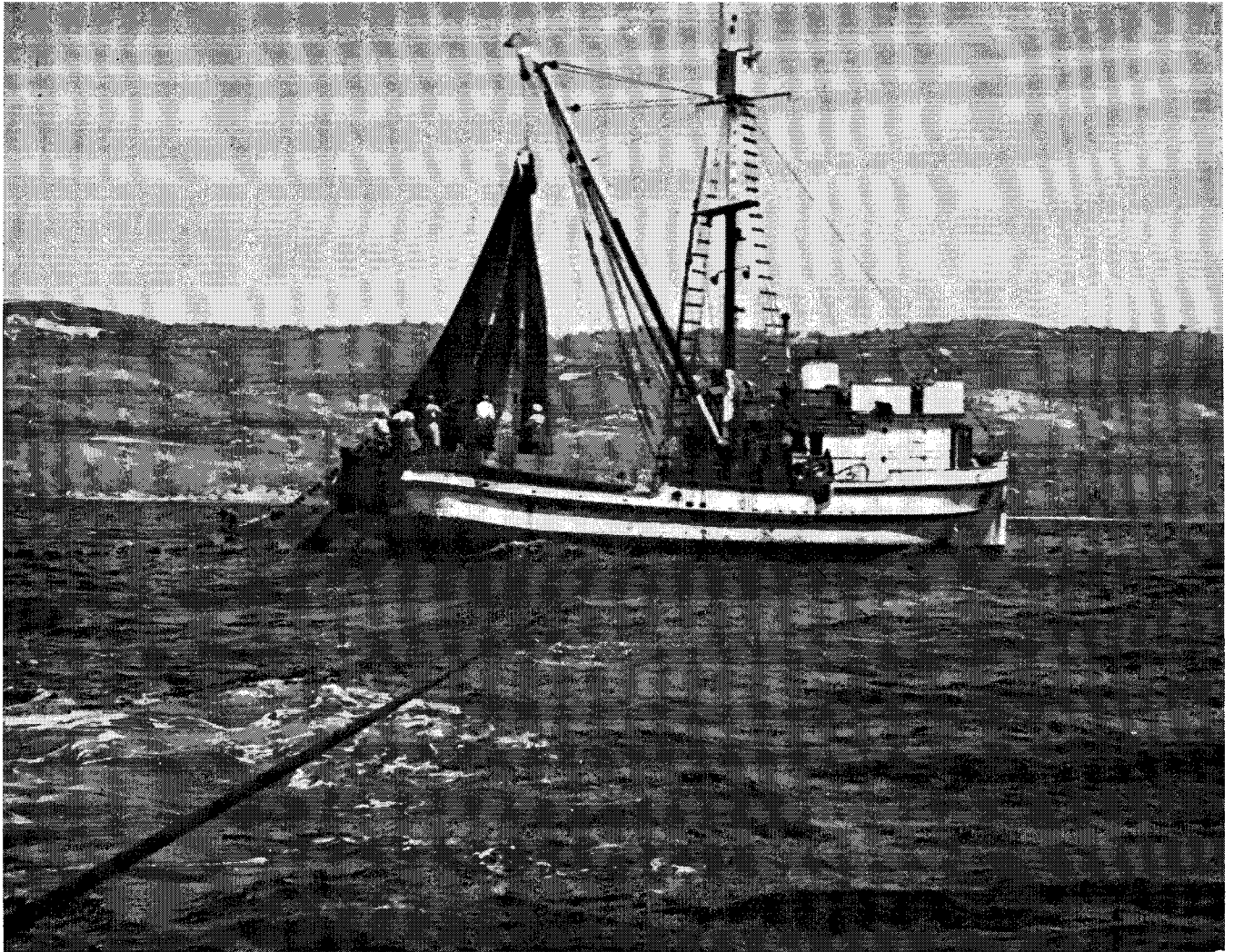
MACKEREL

The 21,000 tons of Pacific mackerel caught during the 1960-61 season closely approximated the preceding season's landings. The 25,000 ton jack mackerel catch was 8,000 tons less than that of the previous season.

During the preceding year, fishermen received \$50 per ton for both species. Most cannery processors lowered the price from \$50 to \$35 per ton in April 1960; however, pet food processors continued to pay \$50 through August 1960. The \$35 per ton price prevailed until March 1961 when it was raised to \$42.50.

Catches originated around the off shore islands with the San Clemente area yielding a major portion; lesser amounts came from around Santa Barbara Island and Santa Cruz Island. The bulk of the catch of both species consisted of fish three years old or younger. *Doyle E. Gates. California Dept. of Fish and Game.*

¹ For a complete catch report, see *California Cooperative Oceanic Fisheries Investigations, Reports*, 8, January, 1961.



Purse Seiner "Maria" washing net, shows power block, nylon sardine net. Photograph by Anita Daugherty.

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1 July 1960 - 30 June 1962

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PART II
SCIENTIFIC CONTRIBUTIONS

**NEARSHORE CURRENTS OF THE WESTERN UNITED STATES AND
BAJA CALIFORNIA AS MEASURED BY DRIFT BOTTLES**

RICHARD A. SCHWARTZLOSE¹

INTRODUCTION

The California Current flows southeast nearly parallel to the Pacific Coast of the United States and Baja California, Mexico, the year round. Along the eastern boundary of the current, near the shoreline, eddies and countercurrents complicate the current pattern. The Atlas of Pilot Charts (U.S.N.H.O., 1950) and Atlas of Surface Currents (U.S.N.H.O., 1947) show the countercurrent to exist in the winter months (November through February) from southern California north to British Columbia. From March through June the current is shown to be flowing southeast along the entire coast. In July the current continues southeast from Washington to central California, but at this time the southern California eddy appears, continuing through February.

In late 1954, Scripps Institution of Oceanography of the University of California began using drift bottles to study these seasonal variations of the eastern edge of the California Current. Drift bottles were released on the California Cooperative Oceanic Fisheries Investigation's (CalCOFI) cruises nearly every month for the following five and one-half years.

Drift bottles or cards had been used before along this coast with some success. Tibby (1939) reports on the results of releases off southern California during the months of March through July 1937. Drift bottles were used in Sebastián Vizcaíno Bay, Baja California, in September, 1952, and drift cards were used during a CalCOFI cruise in July, 1953. The cards in plastic envelopes were released in cooperation with the U.S. Bureau of Commercial Fisheries in Seattle. Other drift bottle data from offshore Canada and Alaska were reported by Dodimead and Hollister (1958) and Fofonoff (1960).

The purpose is to summarize the results of the CalCOFI drift bottle returns from January, 1955 through June, 1960, and other drift bottle data available at Scripps. It is not possible to show charts of all the releases and recoveries, therefore only examples of the different patterns of monthly returns are illustrated.

DRIFT BOTTLES

Four ounce commercial salad dressing bottles of clear, heavy glass were converted to drift bottles by

¹Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

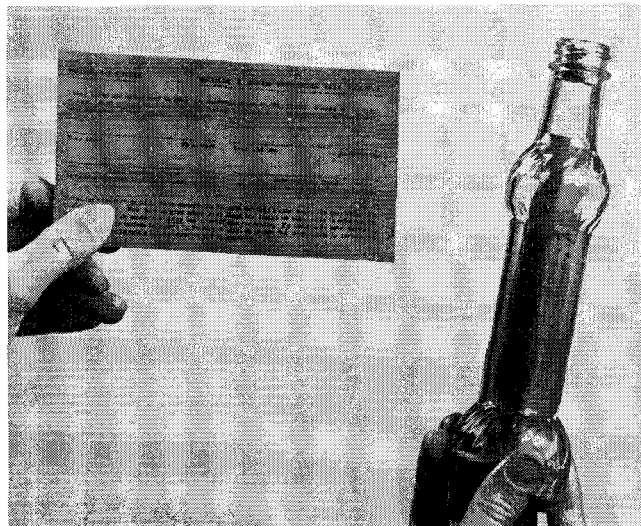


FIGURE 1. Drift bottle and postal card.

inserting red postal cards (Fig. 1) and ballasting them with sand so that nine-tenths of the bottle was underwater. The bottles were then sealed with a cork and wax poured on the cork.

The message on the post-paid (U.S. only) card tells the purpose of the survey in English and Spanish and asks the finder to fill in the place, date, time of finding, and his name and address. Upon receipt of a card, a letter is sent to the finder telling where and when the card was released. When cards from Mexico are received, a letter in Spanish is sent with a peso enclosed to repay the sender for the Mexican stamp.

Normally twelve bottles are released on each regular station of the cruise pattern although there have been some variations of this procedure.

RELEASE AREAS

The areas covered by the cruises have varied somewhat during the five and one-half years and the patterns of releases have varied particularly after it was found that few returns came from bottles released at the western end of the patterns. During 1955 and 1956 bottles were released nearly every month of the year offshore as far as 120 miles and north to about 31° N. latitude. During the cruises in 1955, 1956, and 1957 few were released north of Point Conception (35° 24.4' N.). 1957, 1958, and part of 1959, bottles

were released at nearly every station. In 1958, 1959, and through June, 1960, the northern limit of the majority of the cruises was just south of San Francisco. Only on two cruises during the entire period were drift bottles released as far north as Cape Mendocino (40° N.).

From mid 1959 on, Scripps furnished drift bottles to be released on cruises made by the University of the Pacific and Oregon State University to fifty miles offshore, from Bodega Bay, California (38° N.), and Newport, Oregon (45° N.).

DRIFT BOTTLES RETURNS

From October, 1954 through June, 1960, 52,650 bottles were released and 2,439 were returned; a return of 4.6 percent. The shortest water distance between the release and the landing points has been used to compute speeds. The time used is the period between the release and the recovery. This gives minimum speed because the time the bottle lies on the beach before being found will reduce the apparent speed.

The greatest northward movement of any bottle recovered was from 25 miles south of San Clemente Island, southern California, to Schooner Cove on the west side of Vancouver Island, British Columbia. This was during the countercurrent season in the winter of 1957-58. The minimum distance of its travel was 1140 miles at a minimum speed of 0.26 knot. The greatest southward movement was from just south of Punta Abreojos, Baja California, to just north of Acapulco, Mexico, during the summer and fall of 1959. This was a minimum distance of 1040 miles at a minimum speed of 0.23 knot (Fig. 2).

To study the relation of the distance from shore of the release point and the percentage of returns, lines parallel to the coast were drawn on a chart at 20, 40, 80, 120, and 160 mile intervals from shore. The zones thus delineated were subdivided from north to south (Fig. 3). The number of bottles released was compared to the number returned from each of the areas on the chart using data from January, 1955 through December, 1959, (Table 1). No recoveries have been recorded from farther than 160 miles offshore. Because the southern California region was surveyed most frequently, 51 percent of the bottles were released there.

The significant results from Table 1 are as follows:

1. Eighty-two percent of the total number of returns were from releases in the southern California region;
2. Seventy-five percent of the bottles returned were released within 20 miles of the coast; and
3. There were returns from all distances offshore from releases only in the southern California region. In central and northern California no returns were made beyond the 40 mile line.

In a sample two years of data for the southern California region 41 percent of the bottles were found on Saturdays and Sundays. If only the winter months

were considered, 51 percent of the recoveries were on those days.

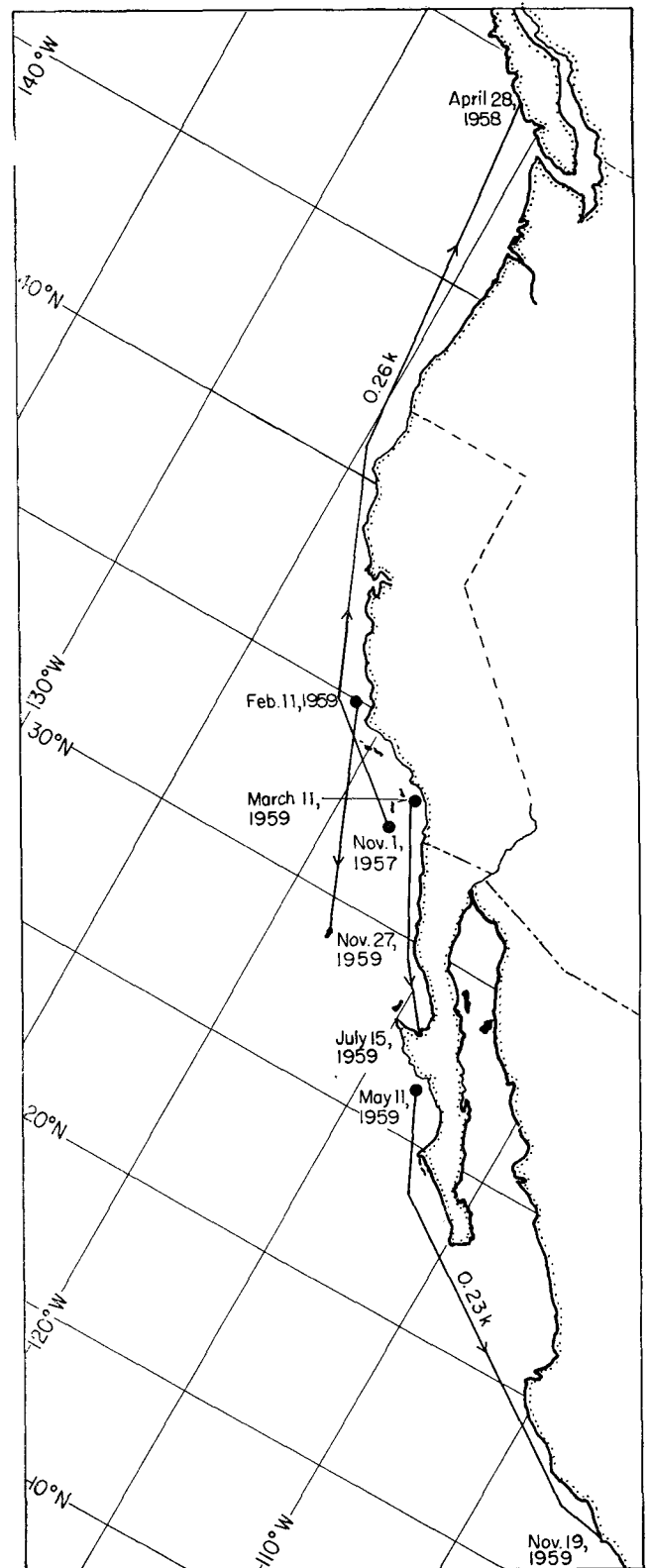


FIGURE 2. Extreme north and south movements of drift bottles.

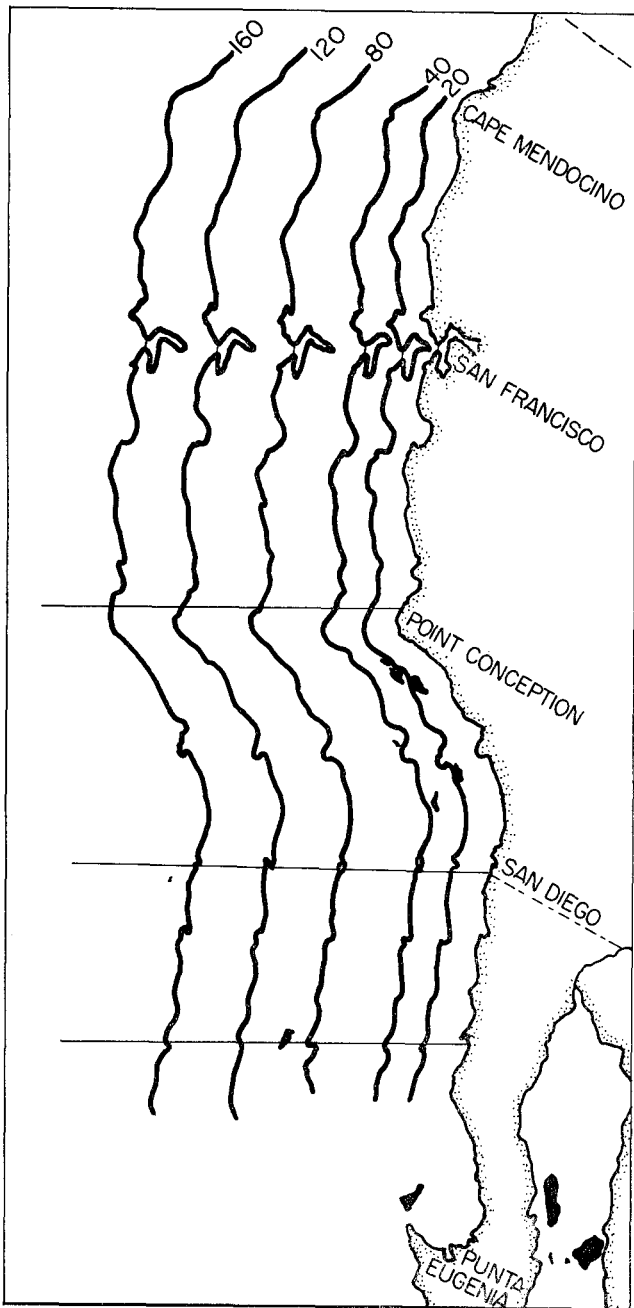


FIGURE 3. Delineation of areas for numbers of drift bottles released and returned. See Table 1 for summary of data.

ANALYSIS OF CURRENTS

In the analysis the returns are divided into six areas: Washington and Oregon, northern California, central California, southern California, northern Baja California, and southern Baja California. When examining these data it should be kept in mind that in most of the areas the returns were from releases no farther than 40 miles offshore and most of these returns were from releases within 20 miles of shore (Table 1).

Each month that drift bottles were released, a chart was prepared showing the position of release and the

TABLE 1
NUMBER OF DRIFT BOTTLES RELEASED AND RECOVERED BY DISTANCE FROM SHORE AND REGION OF RELEASE 1955-1959 IN AREAS SHOWN BY FIGURE 3

	Miles from shore					Total
	160	120	80	40	20-0	
North and Central California						
No. released.....	816	878	2,000	1,990	3,282	8,966
No. returned.....	0	0	0	23	222	245
Percentage returned....	0	0	0	1.2	6.8	2.5
Southern California						
No. released.....	1,296	2,606	4,841	3,744	6,922	19,409
No. returned.....	2	17	181	282	1,305	1,787
Percentage returned....	0.2	0.7	3.7	7.5	18.8	9.2
Northern Baja California						
No. released.....	888	1,296	2,532	2,280	2,552	9,548
No. returned.....	0	0	11	28	112	151
Percentage returned....	0	0	0.4	1.2	4.4	1.6
Total						
No. released.....	3,000	6,780	9,373	8,014	12,756	37,923
No. returned.....	2	17	192	333	1,639	2,183
Percentage returned....	0.1	0.3	2.0	4.2	12.9	5.8

position of recovery. Table 2 summarizes the currents as derived from these plots. In most cases the drift along the coast could be classed as southerly or northerly, but in some cases the data indicated the current was southerly offshore and northerly near shore, as in the California eddy.

Table 2 indicates that for one year (1959) of data along the Washington and Oregon coasts, the countercurrent began as early as August and continued through May. In August, 1959, drift bottles were released at three stations (from near shore to 25 miles offshore) off Newport, Oregon, by personnel of the Department of Oceanography at Oregon State University. The drift bottles went northward, one as far as Grays Harbor, Washington, at a minimum speed of 0.13 knot. Recoveries from the September and October, 1959 cruises indicated that the countercurrent was about 25 miles wide with a speed of 0.25 knot. The current direction was southward beyond 25 miles. Although there were not data from the cruises off Oregon for two of the winter months, the data from along northern and central California indicate that the countercurrent continued. From the March and April returns, the countercurrent was found to be present as far seaward as the farthest releases, nearly 50 miles from shore, with minimum speeds as high as 0.9 knot (Fig. 4). The southward flow near the coast was at least 0.4 knot during 1959 when there was no countercurrent.

Before the latter part of 1959 there had been very few releases of drift bottles off northern California. But in August, 1959 the Pacific Marine Station at Dillon Beach of the University of the Pacific began releasing bottles from ten to twenty miles offshore. The results indicate the flow was southward along the coast from April through August (Table 2). The countercurrent did not appear there until December. But the returns from bottles released off central Cali-

ifornia indicate that the countercurrent began as early as October along the northern and central California coast. The speeds calculated for the southerly current and countercurrent along the northern California coast exceeded 0.4 knot.

TABLE 2
MONTHLY ESTIMATE OF DIRECTION OF CURRENT
FLOW FROM DRIFT BOTTLE RETURNS

Oregon-Washington												
	J	F	M	A	M	J	J	A	S	O	N	D
1959							S	S	N	S/N	S/N	O
1960	O	—	N	N	S/N	—						
Northern California												
	J	F	M	A	M	J	J	A	S	O	N	D
1959									S	O	—	O
1960	N	O	O	S	S	—						
Central California												
	J	F	M	A	M	J	J	A	S	O	N	D
1955	—	S	—	—	O	O	O	O	—	N	N	N
1956	—	—	—	S/N	O	O	—	—	—	—	N	N
1957	—	N	—	—	S	S	X	—	—	N	N	N
1958	N	N	O	O	S	O	X	—	—	O	N	O
1959	N	N	—	S/N	O	O	S	O	—	N	N	N
1960	N	O	O	S	S	S						
Southern California												
	J	F	M	A	M	J	J	A	S	O	N	D
1955	O	S	X	S	E	E	S	S	S	O	E	E
1956	X	X	X	S	S	X	E	—	—	E	E	E
1957	—	S	S	S	S	E	X	—	—	E	E	E
1958	E	X	E	S	S	X	S	—	X	E	E	X
1959	S	E	S	S	E	X	E	E	E	E	E	O
1960	O	S	S	S	X	S						
Northern Baja California												
	J	F	M	A	M	J	J	A	S	O	N	D
1955	—	O	—	O	O	O	S	O	S	—	—	—
1956	—	O	O	—	—	O	—	—	—	—	—	—
1957	—	—	—	O	S	—	—	—	O	—	S	—
1958	—	S	O	S	O	S	O	—	S	S	S	S
1959	S	S	S	O	O	O	S	O	—	O	—	—
1960	O	O	O	O	S	O						

O — No returns or not enough to estimate flow direction.
 X — Ample returns but complex flow pattern, both North and South from same area of release.
 N — North flowing countercurrent.
 S — Southeast flowing current.
 S/N — Transition—Offshore current flowing south, inshore current flowing north.
 E — Southern California eddy present.
 — — No drift bottles released.

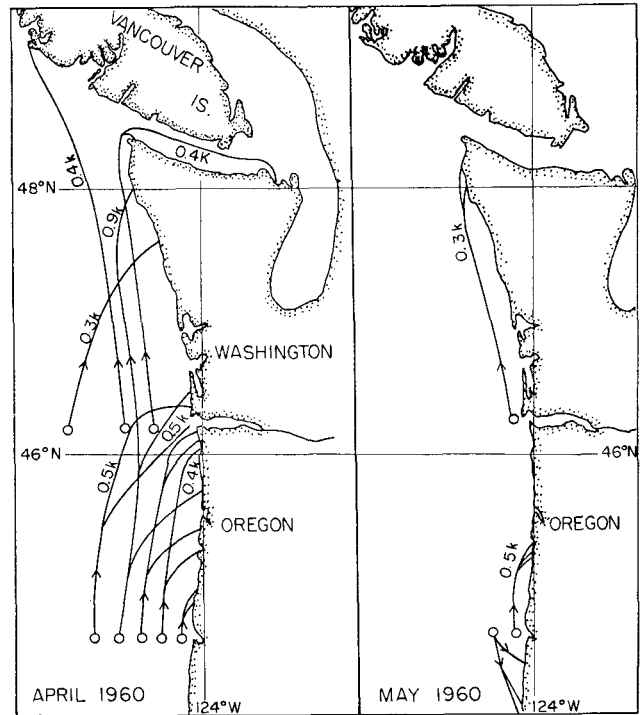


FIGURE 4. Drift bottle returns for April and May, 1960, along the Washington and Oregon Coasts.

There were many more returns from releases off central California. Most of the returns were during the countercurrent period, which began in October and ended between February and April. The strong period of the countercurrent is shown by the number of returns by months when drift bottles traveled more than 150 miles northwest along the central California coast.

J	F	M	A	M	J	J	A	S	O	N	D
33	1	0	0	0	0	0	1	0	5	18	5

Few bottles were returned from May through August. This indicates that the coastal waters were primarily moving offshore or parallel to shore with very little flow toward the coast.

There appears to be a movement toward shore between San Francisco and Monterey Bay and occasionally to the north during the summer (Figs. 5 and 6). The movement inshore as shown in Figure 5 was more than 0.5 knot for five days, from more than 50 miles offshore.

The most variable drift was observed in the channel island area off southern California where the data are most numerous. From Table 2 the southern California counterclockwise eddy was present most of the year. The months it commonly was not present were March, April, and May. In the months where the data are not clear, the confusion may have been caused by the eddy being present for a short period and then disappearing for a while, thus distributing the bottles in a confused pattern along the beaches.

The drift bottle returns do not tell much about the eddy. Figure 7 is an example of the returns when the

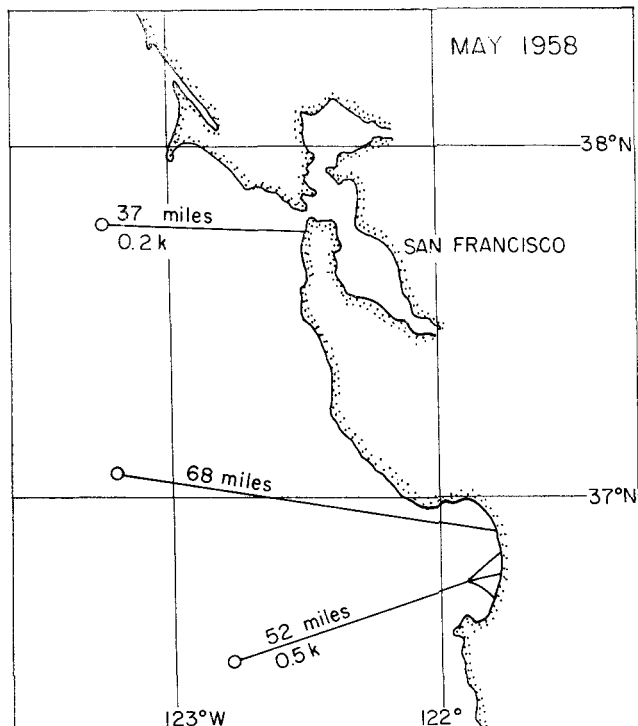


FIGURE 5. Movement of water toward shore off central California in May, 1958.

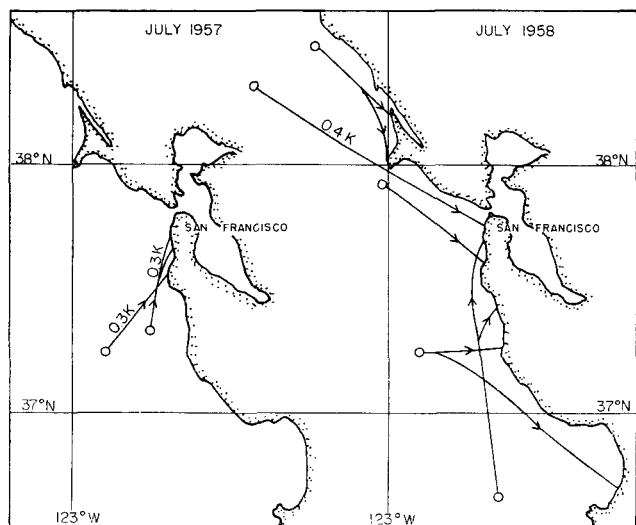


FIGURE 6. Examples to show movement of water to the north off central California during the summer. (July, 1957 and 1958.)

eddy is present. Examination of the returns of many months suggests that there is an eddy between Santa Rosa-Santa Cruz Islands and San Nicolas-Santa Catalina Islands. There may also be an eddy between San Clemente Island and the mainland. The amount of flow to the north from the area between Santa Catalina and the mainland is not known; the returns do indicate that there is movement at times into the northern part of the Channel Islands. The returns

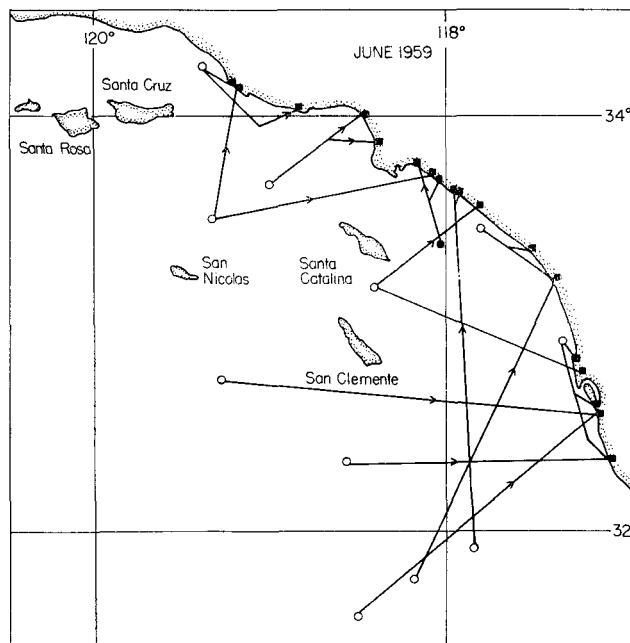


FIGURE 7. Drift bottle returns in June, 1959, indicating the eddies off southern California.

also indicate that there is a flow to the southeast very near shore at times when the eddy is present.

Other data that are available indicate a complex circulation off southern California. From direct current measurements made in October, 1958 (S10 Ref. 1962) there were indications of a counterclockwise eddy between Santa Catalina Island and the mainland, a small clockwise eddy east of San Clemente Island, and a counterclockwise eddy between Santa Cruz and San Nicolas Islands. More current measurements in May, 1961 (S10 Ref. 1962) indicated a counterclockwise eddy between San Nicolas and San Clemente Islands. The large counterclockwise eddy to the east of San Clemente Island is believed to be present at least part of the time as indicated from CalCOFI cruise data which shows a warmer body of water within that area for several months during summer.

Possibly the general circulation in the Channel Island area is a large counterclockwise gyre with some small eddies scattered within it. The data for the Channel Island region do not give a clear picture of the complexity of the eddies nor their duration.

Figure 8 best illustrates the pattern that was seen when the eddies do not exist in the southern California area. The returns are always from releases close to the coast. The months when this type of circulation was the strongest were March, April, and May. As seen in Table 2, there was no indication of the counterclockwise circulation in April during any of the years of drift bottle returns.

Very few of the drift bottles released off southern California moved north of Point Conception during the fall and winter countercurrent period (Reid, Roden and Wyllie, 1959; Reid, 1960; and Berner and Reid, 1961).

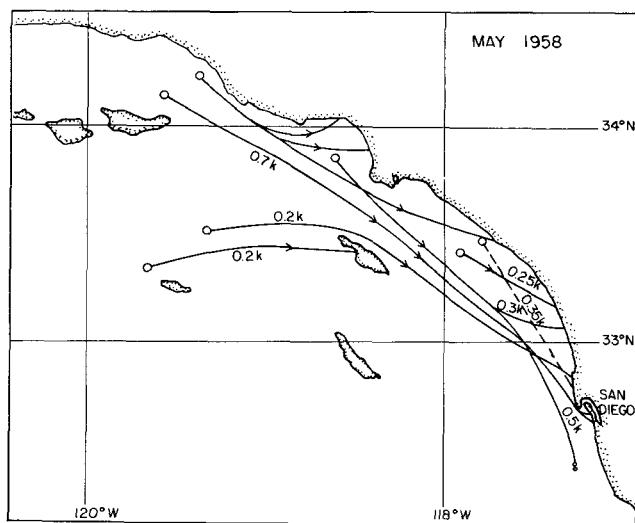


FIGURE 8. May, 1958, drift bottle returns indicating no eddies off southern California.

Figure 9 indicates how far offshore and how far south, surface water enters the southern California circulation. The maximum inshore movement of a drift bottle was from approximately 120 miles westward of the nearest island. The longest movements into the southern California area were primarily during the fall and winter months. Shown below are the number of returns by months when the drift bottles traveled more than 150 miles to reach the southern California coast.

J	F	M	A	M	J	J	A	S	O	N	D
8	3	5	4	3	0	1	1	2	6	3	5

The data from Table 3 indicate that there was a marked increase in the percentage of returns beginning in March and lasting until October when considering the 0-20 miles offshore releases. This same trend may appear from other distances offshore, but is not clear. From the range of 120-160 miles there

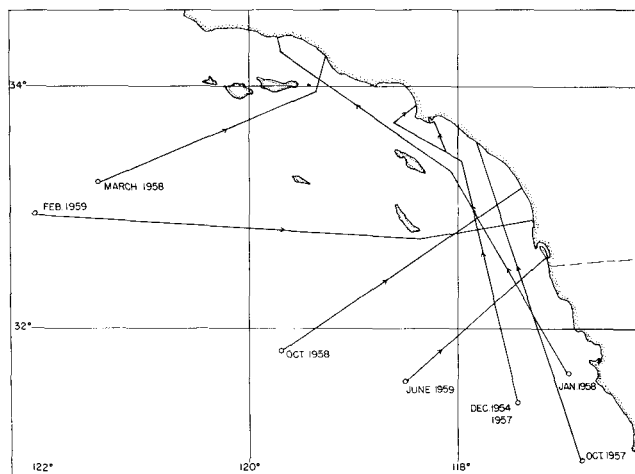


FIGURE 9 Indications from drift bottles as to how far west and south water enters the southern California eddy.

TABLE 3
RATIO OF RETURNS/RELEASES

Distance from shore	J	F	M	A	M	J	J	A	S	O	N	D
0-20	14.1	10.8	22.4	26.5	20.4	28.7	25.2	20.0	23.7	15.8	10.3	8.0
20-40	7.7	8.0	6.2	8.0	10.2	11.1	6.7	6.9	11.6	5.3	5.3	4.7
40-80	3.3	2.8	5.2	1.1	3.1	3.9	2.8	5.2	7.9	4.1	2.5	2.9
80-120	0	0.4	1.0	0	1.6	1.2	2.4	0	0	0	0.7	0.4

were only two returns, one from February and one from October. Some of the increases in returns from March through September may be a consequence of more beach visitors during that period.

Along the northern Baja California coast there are very few recoveries. Most of the coast is sparsely settled and rarely visited. From the small amount of information gleaned from the drift bottles it appears that a southeast current flows along most of the coast all year. The eddy off southern California extends south into the most northern part of Baja California (Figs. 7 and 9). Beyond the southern boundary of the southern California eddy, the data indicate that the current throughout the year is to the southeast. For example, figure 10 shows a southeasterly current in January, 1959, during the period of the countercurrent along the West Coast of the United States. In Sebastián Vizcaíno Bay, the circulation is generally a strong clockwise eddy as shown from current surveys in 1952 and 1960, and the few drift bottles returned from that area.

Along the southern Baja California coast there are so few returns that a pattern cannot be determined clearly from the drift bottles. However it would appear that the flow is southeast along the coast most of the year and that two short countercurrents or counterclockwise eddies appear during the winter between 27° N. and 28° N., just south of Punta Eugenia, and off the southern tip of Baja California, between 23° N. and 24° N.

There was a strong movement of water to the southeast from about 26° N. to 16° N. near the Mexican mainland during the summer of 1959 (Fig. 2). Also a bottle that was recovered from Tres Marias Island, near Cape Corrientes, Mexico, about 20° N., had been released 120 miles offshore from Magdalena Bay, Baja California, about 25° N. A bottle released in January, 1959, about 60 miles offshore from the southern end of Baja California, was recovered just south of Cape Corrientes.

SUMMARY

Drift bottle returns can give some useful indications of the near shore currents, but care must be taken when interpreting the returns since only the points of release and return are known. The unknowns are the route traveled and the amount of time the bottle has lain on a beach before being found.

Eighty two percent of the drift bottles recovered were released within 20 miles of shore, and 90 percent recovered were released within 40 miles of shore. In contrast the total releases were about equally di-

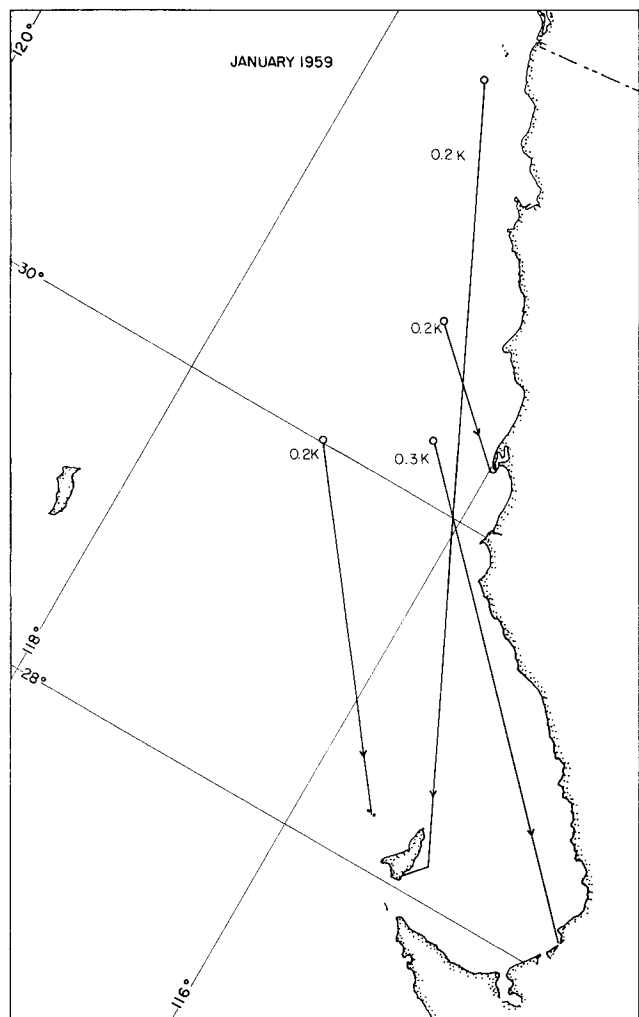


FIGURE 10. Flow to the southeast long the northern Baja California Coast during January, 1959.

vided between the coast to 40 miles and 40 to 160 miles.

The predominate feature exhibited by the drift bottle releases and returns is the countercurrent during the fall, winter, and early spring months from central California north to British Columbia. The countercurrent develops along the Washington and Oregon coasts in August or September, first close to shore, later widening. By October it appears as far south as Point Conception. The countercurrent appears to be at least fifty miles wide and with speeds of at least 0.5 to 0.9 knot for distances of several hundred miles (Fig. 4). For distances of more than seven hundred miles minimum average speeds of at least 0.3 knot have been shown by drift bottle returns (Fig. 11). In the spring the process is reversed. The countercurrent disappears in April off central California and in May off Oregon and Washington.

The important unique features of the countercurrent are its narrowness compared to its length (a ratio of about 1/20) and its ability to carry drift bottles at speeds over 0.5 knot for long distances before

they come ashore. No other data have shown these features as clearly as the drift bottle returns.

South of Point Conception to the southern tip of Baja California there is little evidence of a countercurrent such as exists north of the Point. From southern California only a small amount of surface water passes to the north of Point Conception. The drift bottle returns indicate that when water is moved north of Point Conception there is a very strong countercurrent from central California northward (Fig. 2, 11, and Berner and Reid, 1961).

The Pilot Charts (U.S.N.H.O. 1950) show a northward movement along northern Baja California in November and January while the Atlas of Surface Currents (U.S.N.H.O. 1947) show southerly currents all winter. The few drift bottle returns from this area indicate a drift south along the coast all months of the year.

Off southern Baja California there are so few data that it is difficult to determine whether a counter-

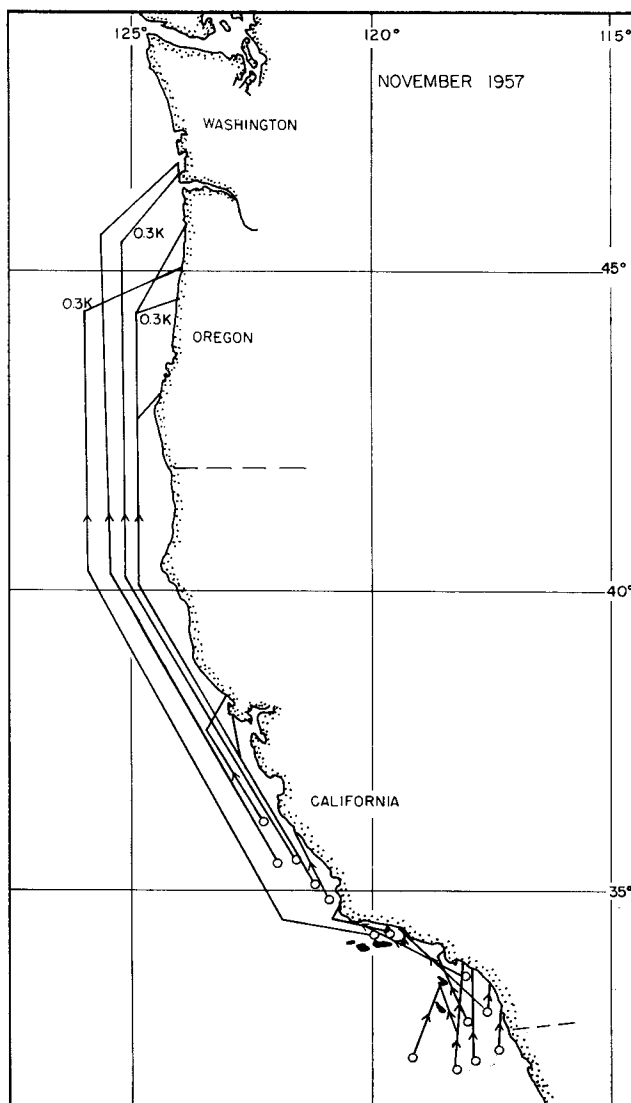


FIGURE 11. The countercurrent during November, 1957.

current exists in the winter. A few returns indicate that there may be several short countercurrents sometimes during the winter.

The current is south to southeast near the coast during the months when there is no countercurrent along the coast from Washington to Point Conception, off central California, and from northern Baja California to its southern tip. The relatively few returns are from near shore. They indicate flow at times of at least 0.4 knot. The few exceptions to the southeast flow have appeared between San Francisco and Monterey as small countercurrents or eddies, with shoreward movements of water from fifty miles offshore in May and July (Figs. 5 and 6).

The southern California circulation is different from the rest of the coast in that eddies predominate. Large and/or small eddies have been observed in every month of the year except April from the five and a half year's returns. Only during April has the current smoothly flowed to the southeast past southern California.

There are some months from which returns were numerically adequate, but the complex patterns of the returns, for example, recoveries both north and south of the release points cannot be resolved into a cohesive circulation. This suggests either a very complex or a changing circulation during these months.

ACKNOWLEDGMENTS

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STUDIES ON THE MARINE CLIMATE AND PHYTOPLANKTON OF THE CENTRAL COASTAL AREA OF CALIFORNIA, 1954-1960

By

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INTRODUCTION

Our knowledge of the behavior of oceans must depend in good part on extensive sampling and collection of data in areas far from shore. However, the survey cruises needed to collect such data are so expensive, and the area to be covered is so large, that sampling intervals are usually enormous in both space and time. Broad survey cruises therefore need to be supplemented by more frequent and concentrated sampling of conditions in more limited areas. Regular monitoring in such areas can provide to oceanography, data analogous to those that weather stations provide to meteorology. Where the area being monitored is strategically placed, the information derived may suggest the conditions prevailing over a much larger region than that actually surveyed, and may facilitate interpretation of results obtained on the open sea.

Our initial studies of the superficial water layers of Monterey Bay, begun in 1951, involved only the collection of hydrographic data, and included more than twice the number of stations now occupied. It became apparent as work went on that a smaller number of stations, properly placed, would provide us with essentially the same hydrographic information we were then obtaining, and that the biological conditions in the bay could be at least crudely sampled in the time saved. The present cruise pattern and program of physical and biological sampling were adopted in March, 1954. Subsidiary parts of the monitoring program include the taking of daily shore temperatures at Pacific Grove and Santa Cruz (the latter provided through the courtesy of personnel at Natural Bridges State Park), and monthly runs down the coast as far as Morro Bay, taking shore temperatures at 26 different locations.

These studies, which are continuing, have been supported almost entirely by funds provided by the State of California Marine Research Committee, as a part of the California Cooperative Oceanic Fisheries Investigations. It is a pleasure to acknowledge this support.

In the program we have been aided by a series of excellent graduate students who have relieved us of most of the routine field and laboratory work, and we gratefully acknowledge the efforts contributed to the program by Eric G. Barham, Jr., Louise McCann, the late Reginald A. Gaines, Bernard D. Fink, Leonard Greenfield, Thomas N. Fast, J. D. Weil, Peter Glynn, Margaret G. Bradbury, Norine Tallmadge Haven, William Chan, William C. Austin, and James H. McLean. It is a further pleasure to extend our special

appreciation to Joseph Balesteri who was entirely responsible for the efficient operation of the research vessel TAGE.

The present paper represents an attempt to use data collected on the weekly cruises to analyze certain aspects of the marine climate and to determine their relation to variations in the abundance and composition of the phytoplankton.

SAMPLING PROGRAM

Since March, 1954, six stations have been occupied by the research vessel TAGE at approximately weekly intervals, in so far as weather conditions and other factors permitted. The location of the stations is shown in figure 1. Stations 1 and 5 are marked by per-

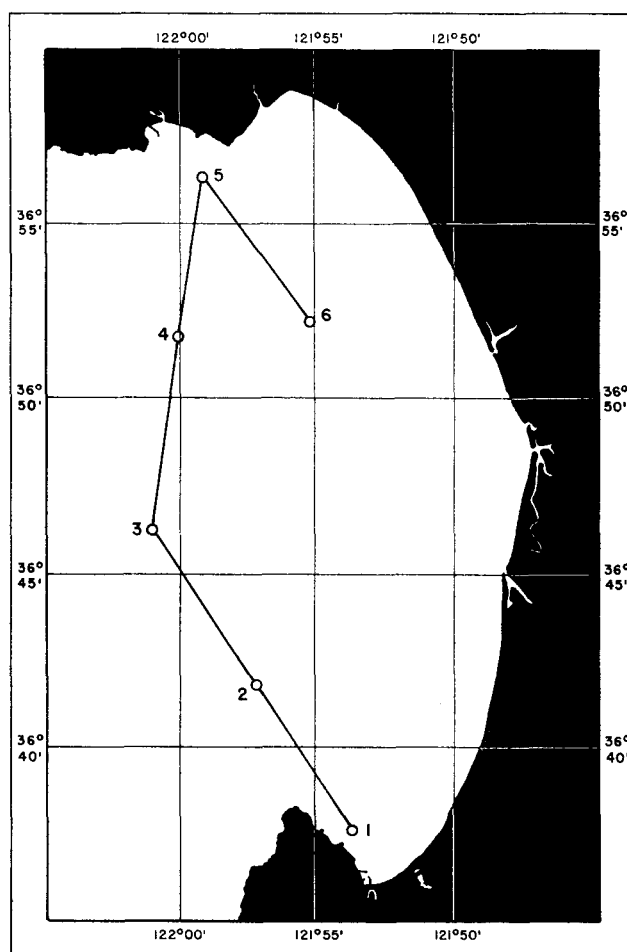


FIGURE 1. Monterey Bay, California, showing cruise pattern and station locations.

manent buoys; each of the four remaining stations is considered to fall within a circular area of approximately $\frac{1}{4}$ mile radius. Stations 1 and 2 are over the sand flats in the southern part of the bay where the water is about 35-75 meters deep; station 3 is near the center of the mouth of the bay and over the Monterey Submarine Canyon in water of about 1650 meters depth; stations 4, 5, and 6 are over the northern sand flats in depths of 90, 20, and 55 meters, respectively.

On each cruise, stations were normally occupied consecutively, starting with station 1. Weather conditions occasionally necessitated skipping a station and occupying it later in the day's cruise. The first station was usually occupied between 0530 and 0930, Pacific Standard Time, and station 6, approximately four hours later. At each station water samples were taken by Nansen bottle at the surface and at 15 meters, and temperatures at these levels were taken by reversing thermometer (prior to 1958, surface temperatures were taken by bucket thermometer calibrated to 0.1°C). A bathythermograph was lowered to a depth of 50 meters at all stations except 1 and 5, where BT drops were limited to 30 and 20 meters respectively. Following this, vertical phytoplankton tows were made from 15 meters to the surface. Phytoplankton was sampled with a truncated Apstein net $\frac{1}{4}$ meter in greatest diameter, mouth ring 18 cm. in diameter, and filtering surface of No. 20 bolting silk. Zooplankton hauls were made with a standard $\frac{1}{2}$ meter net of No. 30XXX Grit gauze, following an oblique path.

TEMPERATURE AND SALINITY

Derivation of monthly average values.

In order to examine and interpret the temperature and salinity characteristics of the superficial water layers of the bay during the period of study, it was deemed desirable to treat the data secured on individual cruises and stations in terms of monthly average figures for the bay as a whole. (See Hopkins Marine Station, 1958-1961). These values are plotted in figure 2, and were derived in the following manner.

In figure 2A, the heavy central curve represents the *monthly average surface temperature of the bay in $^{\circ}\text{C}$* . This was determined by averaging all of the surface temperatures taken at all stations in the bay during all of the cruises made during that particular month. Where four cruises were made during the month, the figure given is the mean of 24 individual temperature readings. The lighter upper curve in figure 2A represents the *average monthly maximum surface temperature*. To obtain this we selected the highest of the six surface temperatures taken during each separate cruise during a given month, and averaged them for the month. Thus where four cruises were made during the month, the average monthly maximum surface temperature is the mean of four temperature measurements. The lighter lower curve in figure 2A represents the *average monthly minimum surface temperature*, similarly obtained by averaging for each month the lowest single surface temperature recorded on each cruise during that month. A portion of this graph has

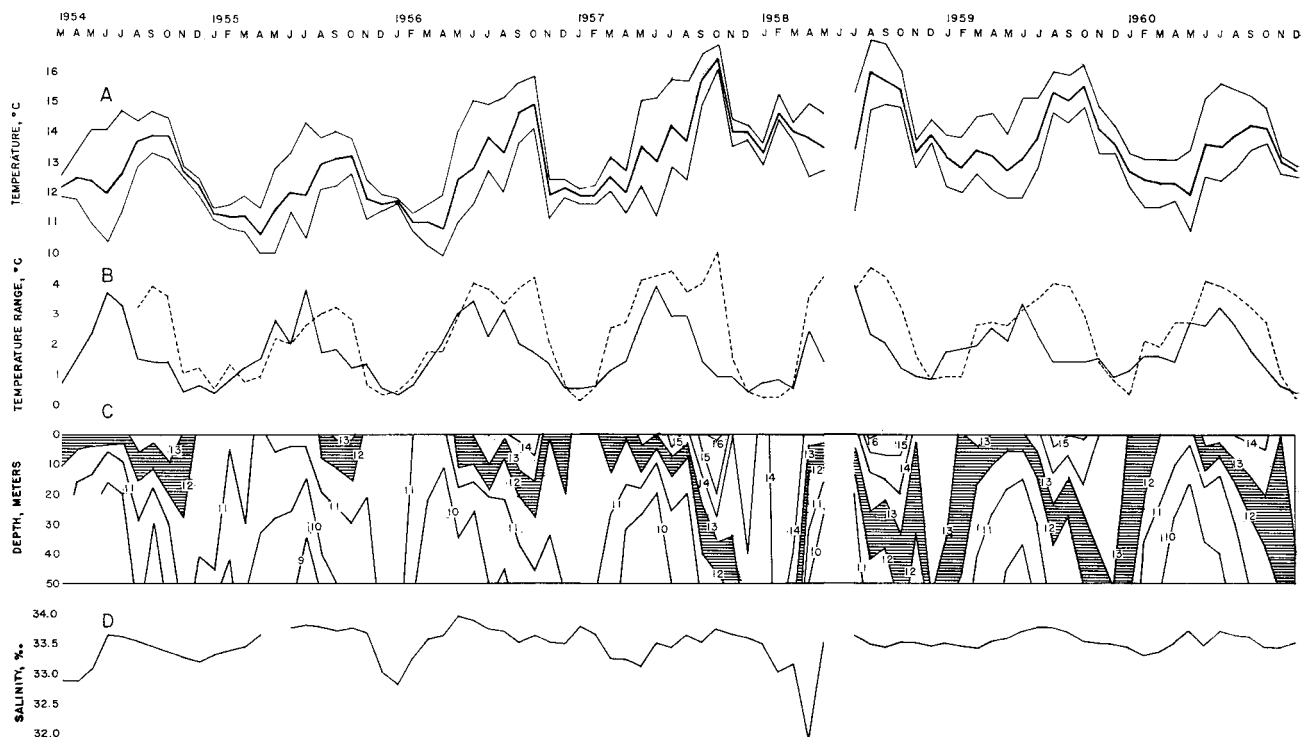


FIGURE 2. Monthly averages of temperature and salinity conditions in Monterey Bay for individual years 1954 through 1960. A. Surface temperatures ($^{\circ}\text{C}$) showing means, average monthly maxima and average monthly minima. B. Temperature spread ($^{\circ}\text{C}$) between average monthly maximum and minimum surface temperatures (solid line) and between monthly averages of surface temperatures and those at 50 meters (broken line). C. Average monthly temperature profile of the upper 50 meters. D. monthly averages of surface salinity in parts per thousand.

been presented previously (Marine Research Committee, 1957 and 1958). The earlier versions included a plotting error for the minimum temperature of December, 1956, which has been corrected in the present report.

It will be noted in figure 2A that the temperature range or spread in degrees centigrade between average monthly maximum and average monthly minimum surface temperatures varies according to a repetitive annual pattern. The increase in the spread between the lines tracing these variables is typically initiated in March or April and is due to upwelling, primarily at station 3. This brings water to the surface, in the center of the bay, that is markedly colder and more saline than the surface waters of the relatively stable eddies at its northern and southern extremities (CalCOFI Prog. Rept. 1955-1956, p. 17, figure 8). Since this temperature spread is one important indicator of upwelling or lack of it, and since it is difficult to compare the spread in different segments of the curve that show markedly different slopes, the temperature difference in degrees centigrade between the average monthly maximum and average monthly minimum surface temperatures on the bay is plotted by the solid line in figure 2B.

Figure 2C shows the seven-year temperature profile of the upper 50m. of the bay, based on the monthly means. These means were obtained for each of the depths sampled by averaging all of the observations made at that depth at all stations on all cruises of that month. Since the 12° C. water may be considered as typical for the bay, the area on figure 2C between the 12° and 13° isotherms has been shaded in order to aid the eye in following the annual rhythm. It is apparent that the magnitude of the difference in temperature between the surface and 50m. fluctuates markedly in a characteristic annual pattern. A somewhat similar but much less marked cycle of increasing and decreasing vertical temperature gradients characterizes the entire northeastern Pacific Ocean (Robinson, 1957, chart 1). However, while over most of this area the increasing spread between the surface and subsurface temperatures during summer is the result of the heating of the superficial layers by incoming radiation, the situation along shore is different. As Robinson points out, "In summer the temperatures along the coast are depressed by upwelling, while they are increasing rapidly west of the California Current . . ." This depression of temperatures affects the subsurface layers to a greater degree than it does the surface which is subject to solar heating. The effect is most pronounced near shore, and as a result the annual temperature cycle in Monterey Bay shows characteristic differences from that of the adjacent offshore area, as depicted in the lower right-hand corner of Robinson's Chart 1. For direct comparison we have converted our temperature data to degrees Fahrenheit and in the left half of figure 3 we present curves depicting our average monthly temperatures at the surface and at 100 feet; the right half of the figure traces the same variables taken directly from Robinson's chart for the area bounded by 35° and 40° N. Lat. and 121° and 125° W. Long., of which Monterey Bay is a part. It will be

noted that the temperature spread between the surface and 100 feet in Monterey Bay is comparable to that of the adjacent open ocean only during the period of November through February. During the rest of the year it is notably greater—more than twice as great during the period of March through June. Furthermore, the increased temperature spread is initiated by a strong depression of the 100-foot temperatures rather than by an elevation of the surface temperatures. We interpret the local appearance of cold water at subsurface levels, and the resulting increased vertical temperature gradient, as due to upwelling. This is in sharp contrast to the offshore regions where the somewhat similar but smaller increase in gradient is the result of incoming radiation. Since the difference between the temperatures of the water at the surface and at deeper levels in the bay is another valuable indicator of upwelling or lack of it, and since the difference is not easily read in figure 2C, it has been depicted separately by the broken line in figure 2B.

Finally, the average monthly values for salinity at the surface are plotted in figure 2D. Like the average monthly surface temperatures, the average monthly salinities were obtained by averaging all of the surface salinities taken at all stations on the bay during all of the cruises made during that particular month.

All of the original figures upon which these averages are based, and the averages themselves, are available in the Hopkins Marine Station annual reports of CalCOFI data (Ann. 1954-1960).

Before examining the individual characteristics of the separate years represented in the survey, it seems desirable to attempt to establish the fundamental features of the annual cycle of temperature and salinity, so that the individual years may be compared to "average" conditions. Since no single year serves by itself as a normal or average year, a composite model has been constructed (Fig. 3). In order that every phase of the changing picture may be considered in clear relation to adjacent phases, each curve in figures 3 A-D depicts two successive and identical average cycles. These curves were derived from those depicted in figure 2 by simply combining and averaging for each individual month, the monthly mean figures for that month from each of the years covered in the present survey. For example, the average monthly mean surface temperature shown for July in figure 3A is simply the mean of all of the July average monthly mean surface temperatures for the years of 1954 through 1960 shown in figure 2A. While the composite curves of figure 3 are therefore artificial, and while this particular sequence of years probably does not provide a "normal" standard (cf. Sette & Isaacs, 1960, p. 215), the curves do indicate very well the general annual cycle of events, discussion of which follows.

Annual hydrographic cycle in Monterey Bay.

The terms used for phases in the cycle are those used by Skogsberg (1936) in his studies of the hydrography of Monterey Bay.

At the beginning of the calendar year the hydrographic climate is in the Davidson Current phase.

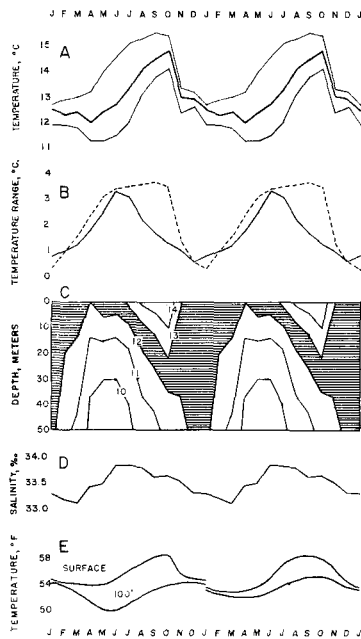


FIGURE 3. Average annual cycles of temperature and salinity, Monterey Bay, based on all the years 1954 through 1960. Figures A-D each show two identical complete cycles. A. Average surface temperatures ($^{\circ}\text{C}$.); the central line traces the general average, the upper and lower lines trace the average monthly maxima and minima. B. Temperature spread ($^{\circ}\text{C}$.) between average monthly maximum and minimum surface temperatures (solid line) and between average surface temperatures and those at 50 meters (broken line). C. Average temperature profile of the upper 50 meters; the space between the 12°C . and 13°C . isotherms shaded as an aid to following the cyclic pattern. D. Average surface salinity in parts per thousand. E. Average temperature cycle ($^{\circ}\text{F}$.) at the surface and at a depth of 100 feet in Monterey Bay (left half) and in the area bounded by 35° and 40° N. Lat. 121° and 125° W. Long. (right half; after Robinson, 1957).

This is normally initiated in November when, concomitant of the cessation of the upwelling a surface countercurrent develops and the superficial waters begin to flow northward along the coast. This current is reinforced by the southerly winds of winter and it persists until February or March when the wind direction changes. The general northwest-southeast trend of the California coast and the divergence of free-moving particles to the right under the influence of Coriolis's force combine to give the surface water an onshore set, and it tends to pile up along the coast. As a result of the slight head thus developed, the water along the coast sinks and is continuously replaced by more surface water from offshore. At the same time the heavy storms of this season effectively churn and mix a system that has become relatively unstable through the sinking of the surface water. More as a result of this admixture with deeper water that is abnormally cold for its depth as a consequence of upwelling than by cooling at the air-water interface, the surface temperatures normally drop 1.8°C . (3.2°F .) in a single month. This drop is much more abrupt than the gradual decline characteristic of the same season in the open ocean as shown by Robinson (Fig. 3) and is a striking change in a region where the average monthly temperatures vary less than 3°C . throughout

the entire year. It marks the beginning of the Davidson Current as by far the sharpest and most easily recognized seasonal limit. In spite of the sharp drop signaling the beginning of the Davidson Current, the average surface temperatures still remain rather high, considering that this period includes the middle of winter. They continue to decline slowly throughout the entire Davidson Current phase and are usually appreciably above the low point for the year. Figure 3A, based on averages, shows the low point in April, but it may occur during almost any month during the first half of the year.

As a result of its derivation from the relatively uniform mass of offshore water, and due to the fact that solar heating is at a minimum, the coastal surface water displays very little variation in temperature at this time of year. Within the spatial limits of Monterey Bay, and throughout any of the months between November and February inclusive, the difference between the observed maximum and minimum temperature averages not more than 1°C . (Figs. 3A and 3B).

As a further consequence of the mixing of surface and deeper water, the temperatures become uniform to considerable depths. The change in the gradient between the surface and 50 meters is just as abrupt and dramatic as the drop in surface temperature. This gradient is reduced from $3.5^{\circ}\text{C}/50\text{m}$. in October to $1.4^{\circ}\text{C}/50\text{m}$. in November, and during the following months of December, January and February the temperature difference remains at 1°C . or less (Figs. 3B and 3C).

While the surface temperature is gradually becoming lower during the Davidson Current period, the temperatures at deeper levels are slowly rising. At a depth of 50 meters, December and January are normally the warmest months of the year. During the winter the water at this depth differs very little in temperature from that at the surface (Figs. 3B and 3C); it is in fact largely surface water from offshore areas to the south and west that has become mixed with some of the deeper water. Since the Davidson Current period coincides with the period during which almost all of the annual rainfall occurs, the surface salinities are low and irregular at this time of year. The runoff from land takes some time to reach the sea, and the declining salinity values normally reach their low point in March, slightly after the termination of the Davidson Current (Fig. 3D).

In late winter intermittent shifts in the direction of the wind tend to lessen or reverse the flow of the surface water. The change is not as sharp as the one that initiated the northward flow of the coastal water, and the end of the Davidson Current period is usually diffuse and difficult to pinpoint. By about the time of the vernal equinox the winds have become steady from the northwest, and during spring and summer the direction of the current induced by the prevailing winds is toward the south. At this time the deflection of the free-moving particles to the right of the direction of the wind by Coriolis's force carries the surface water offshore. The water moving outward must be

replaced from somewhere, and the only possible source is the deeper layers below. Initially the upwelling of cold deep water is of primary importance as a thermal factor, and the temperature of the surface water continues to decline, reaching its minimum in April a full month later than occurs offshore (Fig. 3). By May, however, solar radiation is so great that the average surface temperatures begin a steady rise that continues for several months (Fig. 3A).

As the cold deep water rises to replace that continuously being moved outward from the coastal region, it tends to follow certain pathways. The Monterey Submarine Canyon is the major one of these, and the strong upwelling along the upper reaches of this prominent geological feature consistently lowers the surface temperature over or adjacent to the canyon during the spring and summer. While the average surface temperatures and the minima are depressed by the impingement of upwelling water on the surface in certain places, previously upwelled water may remain in local areas close to shore as circular eddies on the surface, particularly at the northern and southern extremities of the bay, and under these circumstances its temperature is raised by solar heating. The rising line of monthly maxima in figure 3A during the early part of the year, at the same time that the line of minima is falling, reflects this phenomenon. The marked divergence of the maximum and minimum curves, due primarily to lowered minimum values, is the first and clearest indication of the onset of upwelling. By July the strong northwest winds of spring have usually begun to slacken or to become intermittent. As their influence decreases, less of the cold water reaches the surface and, as a consequence, the minimum temperatures are not as strongly depressed as previously. The spread between the maximum and minimum curves, which were separated by values of slightly over 3°C . in June and July, thus becomes reduced to about 2.2°C . in August (Fig. 3A and 3B).

As the cold water wells upward from below its influence is felt much sooner and more strongly in the deeper layers than at the surface. This is the natural effect of the great volume of uniform water that must be moved outward before it can be replaced from below. By May the simple uniform thermal structure of January has been completely changed by the elevation of the deep water; the temperature at 50 meters has been lowered almost 3°C ., while that at the surface has declined only slightly and is rising again. A vertical gradient of more than $3^{\circ}\text{C}/50\text{ m}$. is thus established (Fig. 3B and 3C), and the temperature of the entire water column is relatively low. This is in marked contrast to the changes occurring in offshore waters (Fig. 3E). The cold water that was induced to rise by the action of the wind on the surface, first pauses and then, reversing its trend as the effect of the wind diminishes, begins to sink once more. The rise, the temporary equilibrium, and the subsequent decline of this great surge of deep water is roughly traced by the 12°C . isotherm in figure 3C. It should be mentioned that, since there is considerable variation in the force and steadiness of the wind,

the progression of this part of the cycle is seldom uniform. The upwelling and subsequent sinking of the deep water typically occurs in pulses, and whenever the cold water sinks in response to a slackening of the wind, be it early or late in the season, an onshore flow of surface water normally ensues.

During the first half of the upwelling period the salinity at the surface increases. This is in part due to the progressive dispersal of the low-salinity surface water that results from the winter precipitation, and in part to the rise of high-salinity water to the surface from the deeper layers. The salinity values are highest in June and July, just at the time when the effect of upwelling, as indicated by the spread of the maximum and minimum curves, is greatest. Thereafter the salinity decreases slightly as upwelling diminishes and the deep water is diluted by mixing with surface water.

September and October normally bring a period of calm intervening between the northerly winds of summer and the southerly winds of winter. With wind stress practically lacking, the previously elevated mass of cold water continues to sink downward toward equilibrium. The reversal in the trend of the deeper isotherms in figure 2C gives the impression that in some years the water even sinks beyond the level of equilibrium, and then appears to rebound. However, in other years equilibrium is not quite reached before the influence of the Davidson Current is felt, and in such years the deeper isotherms continue their downward course throughout the autumn. The evidence of the "rebound" is minimized by averaging, but the approach to equilibrium is shown in figure 3C by the flattening in the trend of the 12°C . isotherm during the October to November period.

As the cold water sinks, warm surface water from offshore flows toward the land to replace it. This is the same phenomenon noted earlier as occurring sometimes for brief periods during the upwelling period. Now, however, the flow is persistent, and clear blue oceanic water, with a characteristic open-water zooplankton, commonly replaces the opaque greenish coastal water of other seasons. During this oceanic period, the surface temperatures rise to the highest values of the entire year, while those at a depth of 50 meters continue to become lower. The stratification that was established during upwelling is thus preserved, or even strengthened somewhat (Figs. 3B and 3C), but the temperatures at all levels are some 2 or 3°C . above those prevailing about three months previously. Further evidence that the increase in temperature is due to the invasion of the area by warm relatively high-salinity water from offshore rather than to continued solar heating of the local surface water is provided by the salinity curve (Fig. 3D). This shows a small but unmistakable rise in October that interrupts the normal decrease in the surface salinity from midsummer to early spring. Since all of the isotherms are, by their downward trends, indicating sinking of the water (undoubtedly accompanied by some surface warming), the increased salinity cannot be due to upwelling. It must be the result of either evaporation or an invasion of the area by water of different char-

acteristics. The transparency, color and zooplankton all indicate that the latter phenomenon is the main cause.

As indicated in the foregoing discussion, the marine climate of the central California coastal area may be divided into three seasons, characterized as follows:

A. The Davidson Current period (November-February) marked by: 1) surface temperatures abruptly lower than in the preceding months but not at the low point of the year, slowly declining; 2) surface temperatures varying very little, normally not more than 1°C. difference between the maxima and minima of each month; 3) temperatures uniform to considerable depths, the difference between those at the surface and 50 meters usually less than 1°C.; 4) the temperature at 50 meters at its high point for the year; 5) surface salinity low.

B. The upwelling period (February-September) with: 1) surface temperatures reaching the low point of the annual cycle and then rising steadily to approach the annual high; 2) surface temperatures variable, the spread between the monthly maximum and minimum values reaching 3°C. or more, but considerably less during the late stages of the period; 3) a strong temperature gradient developing with differences of more than 3°C. between the surface and 50 meters; 4) temperatures at 50 meters reaching the low point of the year; 5) surface salinities rising to the high point of the year and beginning a decline.

C. The oceanic period (September-October) showing: 1) surface temperatures at the high point of the year; 2) the spread between the maximum and minimum surface temperatures moderately great, but less than 2°C. and diminishing; 3) the strong vertical temperature gradient persisting; 4) temperature values at all levels 2 or 3°C. higher than during the peak of the previous upwelling period; 5) salinities at the surface reversing their previous trend, rising slightly.

The only really sharp and consistent climatic change is the one that, almost invariably in November, ushers in the Davidson Current period. Early or late surges of upwelling render the beginning and termination of the upwelling period obscure, or the suppression of upwelling during the middle of the summer by the vagaries of the wind can even introduce short phases of other periods into its middle portion. This picture of the annual cycle in Monterey Bay is in agreement with, and amplifies, that established by Skogsberg (1936) and Skogsberg and Phelps (1946).

It should be clearly understood that many of the features that characterize the marine seasons in the Monterey Bay area are not unique to the coastal region of central California. The cyclic changes outlined above permit an investigator to determine the particular phase of the annual cycle that is active at a particular time in the local area, but similar cyclic changes are taking place over the entire northeastern Pacific, and in a similar temporal sequence. An examination of chart 1 in Robinson's analysis of sea temperatures (1957) shows that a very wide region is subject to an annual spring and summer increase and

a fall and winter decrease in surface temperatures, and that the increase is concomitant with an increasing differential between the temperatures at the surface and subsurface levels. This is exactly what occurs in Monterey Bay. However, regardless of the similarities, the vertical components imposed upon the direction of water flow by the adamant barrier of the shoreline modifies the details of the basic pattern in the immediate coastal waters in a manner that is readily recognized and explained. The forced elevation of the deep water during upwelling causes the decline in the temperature of the superficial layers to continue longer into the spring and forces a more abrupt and more extensive drop in subsurface temperatures (with the consequent establishment of a larger vertical gradient) than occurs in truly oceanic areas where upwelling does not take place. Also, irregularities in the upwelling, induced by features of the bottom topography, cause surface temperatures to be much more variable within short distances near shore than they are in the deep ocean where topography has little or no effect. During the Davidson Current period the sinking of the surface water, forced by the impingement of the surface flow on shore, renders the vertical mixing, the establishment of a deep layer of homogeneous water, and the depression of the surface temperatures much more abrupt than in the open ocean where the downwelling is not induced.

Perhaps the oceanic period deserves special mention since, in general, oceanographers have not recognized this season as a distinct phase of the marine climate. It is strictly a coastal phenomenon with no counterpart in the open ocean. It is only in the relatively narrow band where upwelling occurs during the summer that it has any validity. When the upwelling ceases and the relatively cold coastal water begins to sink, a comparatively thin film of warm surface water from off shore flows in to take its place. It may be argued that off-shore surface water also flows toward the coast during the Davidson Current period and that, therefore, there is no essential difference between the two. However, the Davidson Current flow is immeasurably more massive, and the source of its water is appreciably different. That brought in by the flow of the oceanic period is summer oceanic water from the north; the Davidson Current brings in winter oceanic water from the south. Each differs from the other in its temperature characteristics and in the kind of plankters that it transports. Primarily because of its biological importance in determining the kind of plankton populations that are present during late summer and early fall, we recognize and retain Skogsberg's designation of this rather limited phase of the marine climate as the oceanic period.

Descriptive analysis and interpretation of annual cycles, 1954-1960.

By comparing the curves in figure 2 to those presented in figure 3 it is possible to evaluate the deviation, from the average pattern, of the conditions as they actually occurred during the period of 1954-60.

In 1954 no data are available for January and February, nor at depths greater than 20 meters until

August, but the Davidson Current evidently persisted into March, as indicated by the narrow maximum-minimum spread of that month (Fig. 2A and B). Upwelling seems to have been strong and normal. It faltered for the first time in July and declined abruptly in August as is shown by the sharp rise of the minimum line in figure 2A, the reduction in the spread between maximum and minimum values (Fig. 2B), and the downward trend of all isotherms in figure 2C. However, another rather strong surge of upwelling occurred in September; the flattening or reversal in trend of all of the curves in figures 2A to 2C is clear evidence of this. The oceanic period of this year may thus be considered to have occurred in two phases, one in August and the other in October, with a brief period of upwelling intervening between them. The two pulses of open surface water impinging on the coast are represented by the dips in the W-shaped pattern traced by the 13°C. isotherm in figure 2C. The fact that the surface temperatures rose very little, and that the salinity curve (Fig. 2D) continued its even decline, points to a relatively weak surface inflow.

The following Davidson Current period began on schedule in November, was fairly typical, and persisted through January of 1955. The subsequent upwelling began to affect the surface layers in February, slackened in March, as shown by the reduced vertical gradient (Fig. 2B) and the descending isotherms (Fig. 2C), and then increased again to reach its peak in July, about a month later than usual. The general low levels of the curves in figure 2B and the flattening of the isotherms during the period of April to June indicate that upwelling was relatively weak, except during July. The shallow V-shape of the 11°C isotherm in May (Fig. 2C) indicates a slight and very early influx of offshore surface water, an adumbration of the oceanic period that later followed its normal course in September and October, but which seems to have been poorly developed. The low surface temperatures and the weak vertical gradient indicate that surface inflow during the oceanic period was comparatively weak.

The temperature drop during the Davidson Current period of November, 1955, to February, 1956, was small; this may have been due to unusual weakness of the current, but the horizontal and vertical uniformity of the temperatures shown in figure 2B suggest that it was due to other broader-scale factors initiating a general warming of the waters that is evident for the following three years. The upwelling of 1956 started with the strongest surge of the year in March and April. These months show an abrupt spread of the maximum-minimum curves and a sharp increase in the vertical gradient (Fig. 2A and 2B), as well as a strong pulse of cold water from below (Fig. 2C), together with the highest surface salinity recorded during the entire period of the study (Fig. 2D). Although upwelling continued throughout August, its strength abated somewhat irregularly as shown by the jagged nature of all of the curves, particularly those depicting the isotherms in figure 2C. As upwelling slackened, a minor influx of surface

water occurred in July. This was interrupted in August, but in September and October it was repeated in greater strength so that a typical oceanic period was developed.

The subsequent Davidson Current started with an extremely abrupt fall in the surface temperatures, and it persisted through February with a very small spread between the maximum and minimum curves. The period was somewhat atypical in that the surface temperatures reached their low point for the subsequent annual cycle on the initial drop; thereafter they remained about level and did not continue their usual slow decline. The upwelling of 1957 was very irregular. The jagged pattern traced by the 12° and 13°C. isotherms during the spring and summer show that the upwelling water reached the surface in a series of pulses and that between them small surges of outside water invaded the area. These latter surges, actually early abortive stages of the oceanic phase, were replaced in September and October by a much more massive inflow; the average surface temperatures rose to the highest point of the entire investigation, the difference between the surface temperature and that at 50 meters reached 5°C., the upper isotherms developed a very deep V-shape with 14°C. water extending to below 25 meters, while salinity values rose from 33.51 o/oo in September to 33.73 o/oo in October, an unusually sharp climb for this season.

The Davidson Current period of 1957-58 was similar to the previous one but was marked by unusual strength; it developed abruptly and showed very little spread between the maximum and minimum temperatures of any month, and temperatures at 50 meters were not more than 0.6°C. below those at the surface at any time. The actual northward flow during this Davidson Current cycle was beautifully demonstrated by drift-bottle experiments carried out by the Scripps Institution of Oceanography (Reid, 1960, pp. 86-87). As in the previous year, the surface temperature at the end of the Davidson Current was the same as it had been at the end of the initial drop, but the intervening months showed a very irregular pattern. It is noteworthy that the entire season was very warm; for the four-month period, December-March, the entire water column above 50 meters was characterized by water of more than 13°C. and February averaged more than 14°C., almost 3°C. above normal. The period persisted for about a month longer than usual, and the effects of upwelling first became clear in April. The crowded isotherms and their almost vertical trend (Fig. 2C), as well as the steep rise of the curves in figure 2B, show that the first surge of the upwelling water was sudden and intense. It is unfortunate that necessary repairs placed the research vessel on the ways for an extended period and as a result no data were collected in June. This leaves a gap in the middle of an upwelling period that was probably a most unusual one. The following oceanic period began in August and was more extended and brought in a heavier flow of warm surface water than usual.

The subsequent Davidson Current period, evidently began in October, and was in full swing by November.

It was of short duration and was terminated by or shortly after the end of the year. As early as January, 1959, the increasing spread of the maximum-minimum curves heralded the beginning of upwelling. This is corroborated by a fall of 0.5°C . in the temperature at 50 meters, as compared to a normal 0.1°C . decrease. The upwelling displayed an extremely regular pattern as is shown by the smoothness of the arching isotherms in figure 2C and the unusual regularity of the salinity curve (Fig. 2D). The steady flow of rising water kept the average surface temperatures at a relatively constant level until June, a month or more longer than usual, and flattened the curves in figure 2B to a marked degree. The 13°C . water present in March indicates a very minor inflow of surface water, probably a last eddy from the Davidson Current. The following oceanic period was similar to that of 1954. Evidently the initial influx of surface water in August was interrupted briefly by a minor pulse of upwelling in September, but it was followed by a similar influx in October. The effect of the warm water appears to have been felt into November, and as a consequence, the drop in temperature at the beginning of the Davidson Current period and the convergence of the maximum-minimum curves was markedly less than usual. However, the continued decline of the surface temperatures during December and January was steeper than normal and at the end of the Davidson Current period the average temperature was about 2.8°C . below its previous high point, somewhat more than average.

The upwelling of 1960 was similar to that of 1959, but it began about a month later (still a month earlier than normal). By February the spread of the maximum-minimum curves was 1.6°C . and a fairly strong vertical gradient had already been established. It is curious that this gradient reached its maximum development in June, two full months earlier than usual (Fig. 2B), and that thereafter, even during September and October, the water column became more uniform in temperature. This was the only year in which the vertical gradient was less sharp during the oceanic period than during the peak of upwelling. While the descending slope of the isotherms from May onward is approximately as steep as in other years, it appears that the effect of the sinking cold water was not as strong as usual; at any rate the degree to which the superficial layers were warmed by surface inflow was markedly less than in any year since 1955. An initial influx of warm surface water is noticeable in June but this was terminated by a final weak surge of upwelling in July. Thereafter the oceanic period developed steadily, but while it was of longer duration than normal it is probable that the total volume of the invading surface water was somewhat less than usual. The curves for the final two months of the year show the onset of the Davidson Current period to have been typical in all respects.

The long-term trend.

An examination of the surface temperatures as depicted in figure 3A reveals a readily discernable long-

term trend. The early years are noticeably colder than the succeeding ones, and the last two years seem to indicate a reversal of the earlier temperature rise. Further evidence of this trend appears in figure 2C where, during the early years, the 12°C . water represented by the shaded band is restricted to the superficial layers. Later, it penetrates deeper and deeper, even extending well below the 50 meter level for a four-month period during the winter of 1957-58. The final years are marked by cooling again and the band of 12°C . water occurs at higher levels, but not as high as during the initial years of investigation. Each month of the period from May, 1954, through April, 1956, was colder than the average for that particular month during the seven-year period of investigation. The depression of the surface temperatures averaged 0.8°C . and reached an extreme of 2.0°C . in July, 1955. The months from March, 1957 to January, 1960, inclusive, showed an uninterrupted warm sequence, with the temperatures averaging 1.0°C . above normal. In February, 1958, the surface temperature was 2.5°C ., and that at 50 meters 3.2°C . above the seven-year average. Shore temperature data taken at Pacific Grove show that 1958 was the warmest year here in 40 years (Robinson, 1961, Fig. 4).

The annual temperature cycle, which reflects the seasonal sequence of water from different sources, is paralleled by cycles of relative abundance of various phytoplankters carried in by the fluctuating currents or enjoying a brief period of success under the special conditions prevailing during mixing of different water masses. This phenomenon is discussed in the next section, but it may be well to point out here that the long-term trend also has marked biological effects.

During the warm years plankton organisms characteristic of low latitudes are more prominent than during colder years. Berner (1960) has noted the unusual northward extension of the pelagic tunicate *Doliolum denticulatum* in April, 1958, and Brinton (1960) has presented similar observations on large populations of the euphausiid *Nyctiphanes simplex* off northern California during the same month. These northward extensions were noted at the end of, or immediately following a Davidson Current period of unusual strength. Occasionally fairly large and conspicuous organisms are involved, and from reports on the occurrence of these the actual population shifts can sometimes be roughly traced. For example, the pelagic red crab *Pleroncodes planipes*, normally resident along the coast of Lower California, invaded the waters of southern California in late 1957 and became common there during that winter (Radovich, 1961). One year later large populations had migrated as far as Monterey Bay and thousands were cast up on the beach (Glynn, 1961). This particular organism evidently moved northward during the winter in the Davidson Current when the general temperature (and other?) conditions became favorable.

Many larger forms, certainly not dependent on current drift, were also reported north of their normal range during the warm sequence of years. These appeared at various times of the year, often when the

Davidson Current was not running. Several southern fishes such as *Mobula japonica*, *Hemiramphus saltator*, *Trachinotus rhodopus*, *T. paitensis*, *Vomer declivifrons*, *Nematistius pectoralis* and *Kathetostoma averuncus* were added to the fauna of California (Radovich, 1961), but more important was the northern shift in mass of such sport fishes or commercially significant forms as the yellow-fin and blue-fin tunas (*Neothunnus macropterus* and *Thunnus saliens*), skipjack (*Katsuwonus pelamis*), bonito (*Sarda chilensis*), swordfish (*Xiphias gladius*) and white seabass (*Cynoscion nobilis*), which supported fisheries in areas previously barren.

PHYTOPLANKTON AND NUTRIENTS

Methods

The material referred to herein as phytoplankton represents that portion of the total phytoplankton occurring in the uppermost 15 m. of the bay water, which is sampled by vertical hauls and retained by a net of 173 meshes/inch. It thus includes the larger diatoms and dinoflagellates, but not nanoplankton. Phytoplankton hauls taken at each station on each cruise were preserved by addition of formalin. Any large or conspicuous animals accidentally captured in the haul were then removed. Preserved samples were poured into 100 ml. glass graduated cylinders and allowed to settle for 24 hours. A crude wet settled volume was then read directly to the nearest ml. Samples of less than one ml. were recorded as traces.

For further analysis, the concentrated collection from each station was agitated and a sample withdrawn by pipette and placed on a slide for differential counting. At this time the technician made a visual estimate of the volume percent of solid material other than phytoplankton (e.g., detritus, small animals, eggs, etc.) in the sample. This estimate was used to adjust the crude settled phytoplankton volume to a corrected volume for phytoplankton only. Only these corrected phytoplankton volumes were used in subsequent calculations. A differential count was then made of 200 phytoplankters, identification being carried only to genus. The relative abundance of each genus was then calculated as a percent of the total phytoplankters counted for the sample. Where composition of the haul was complex, with many genera represented, a second sample was often counted. For some of the winter hauls, where samples taken by the phytoplankton net were small and consisted very largely of detritus, counts sometimes had to be based on fewer than 200 organisms.

Generic identifications are, of course, of less value than specific identifications in any biological work, and our decision to carry determinations no further than to genus represents a compromise. A technician can easily learn to recognize to genus most of the larger common phytoplankters, whereas specific identification is much more difficult, time-consuming, and uncertain for the non-specialist. Since it was not our objective to contribute to the knowledge of the ecology and distribution of specific phytoplankters, but instead to look for variations in the quantity and gen-

eral character of the larger phytoplankton which might be related to seasonal and other changes in the waters of the bay, generic identification is all we have attempted. Vials of concentrated material from all hauls made in the course of the present study have been retained in the hope that quantitative analysis by species may be feasible at some future date.

Derivation of the monthly average values used in figures 4 to 8 is explained in the paragraphs below. The curve in figure 5A shows monthly averages of the phytoplankton catch, expressed as ml. of wet settled phytoplankton captured per haul, corrected to eliminate animal material and detritus. Each point on

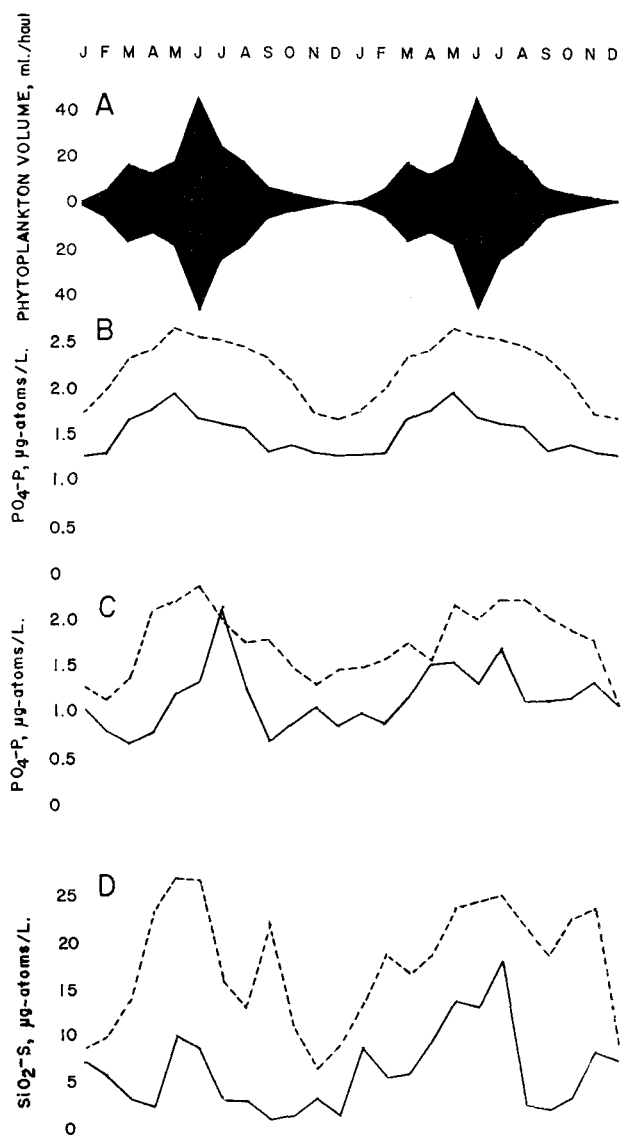


FIGURE 4. A. Average annual cyclic variation in phytoplankton standing crop (ml. per haul), based on all tows made during the years 1954-1960; two identical complete cycles are shown. B. Average annual cycle of phosphate-phosphorus, based on the period 1951-1955; two identical complete cycles are shown. C. Monthly averages of phosphate-phosphorus, 1954-1955. D. Monthly averages of silicate-silicon, 1954-1955. In Figs. 4B to 4D the values are expressed as $\mu\text{g-atoms/L.}$; nutrients at the surface are shown by the solid lines, those at 50 meters by the broken lines.

the curve thus represents the average of the total corrected volumes taken on hauls at all stations on all cruises during the month. Where four cruises were made during the month, the monthly average volume per haul is based on 24 hauls.

The composite or "average" picture of variation in phytoplankton volumes in the bay is depicted in figure 4A (repeated for two years). This was made simply by combining and averaging for each individual month of the year, all of the different monthly mean figures for that particular month from all of the years covered in the present survey.

The accordion graphs showing relative abundance of different genera in the bay (Figs. 6, 7, and 8) represent monthly averages of the number of times each particular genus appeared in the plankton counts for every 100 phytoplankters counted. Where 200 organisms per haul were counted, and four cruises per month were made, the averages are based on counts of approximately 4800 organisms taken in 24 different hauls.

A graphic representation of the relative complexity of the phytoplankton population is presented in figure 5B. The lowermost curve traces the percentage contribution of the most abundant genus, whatever it may be, to the total catch for each month. The next curve adds the percentage of the next most abundant genus, whatever that by may be, and so on until 95 percent is reached. The final 5 percent is commonly composed of several different genera present only as traces; these have been ignored so that the picture will not be unnecessarily complicated and confusing. The percentages are monthly averages of the percentage composition of all hauls taken during the month. Note that the spaces between the various curves sim-

ply represent genera in the sequence of their relative abundance, and that therefore the space between any pair of curves may represent different genera in succeeding months. For example, in June, 1954, the following genera are depicted from bottom to top as contributing the following percentages to the total population: *Chaetoceros*, 71.9; *Asterionella*, 10.2; *Nitzschia*, 6.4; *Rhizosolenia*, 5.9; *Skeletonema*, 2.5. In July the sequence of genera is: *Chaetoceros*, 67.7; *Rhizosolenia*, 20.3; *Nitzschia*, 4.1; *Peridinium*, 2.6; *Thalassiothrix*, 1.1.

No data on plant nutrients were taken as part of the present study, but information concerning the amount of phosphate and silicate present at a point about three miles south of station 3 (and like the latter, over the Monterey Submarine Canyon) was collected at approximately weekly intervals from 1951 through 1955 during the course of another investigation.* Since we lack more pertinent information, we assume that the sequence of years and the geographic position of this earlier study approximate those of the present investigation closely enough that a comparison of the records from the two studies is not without some meaning. It is recognized that concentrations of these particular nutrients may not be limiting in this situation (cf. Reid, Roden, and Wyllie, 1958), but it is presumed that the seasonal cycles shown reflect the seasonal pattern of fluctuations of other nutrients (e.g., nitrates) which may be critical. Figure 4C shows monthly averages for phosphate phosphorus in $\mu\text{g-atoms/liter}$ during the years 1954 and 1955. Each point at each depth represents an average of four

* Unpublished data, from a study supported by funds from the Office of Naval Research (Contract N6-onr-25127) and the National Science Foundation (Grants NSF-G911 and NSF-G1780).

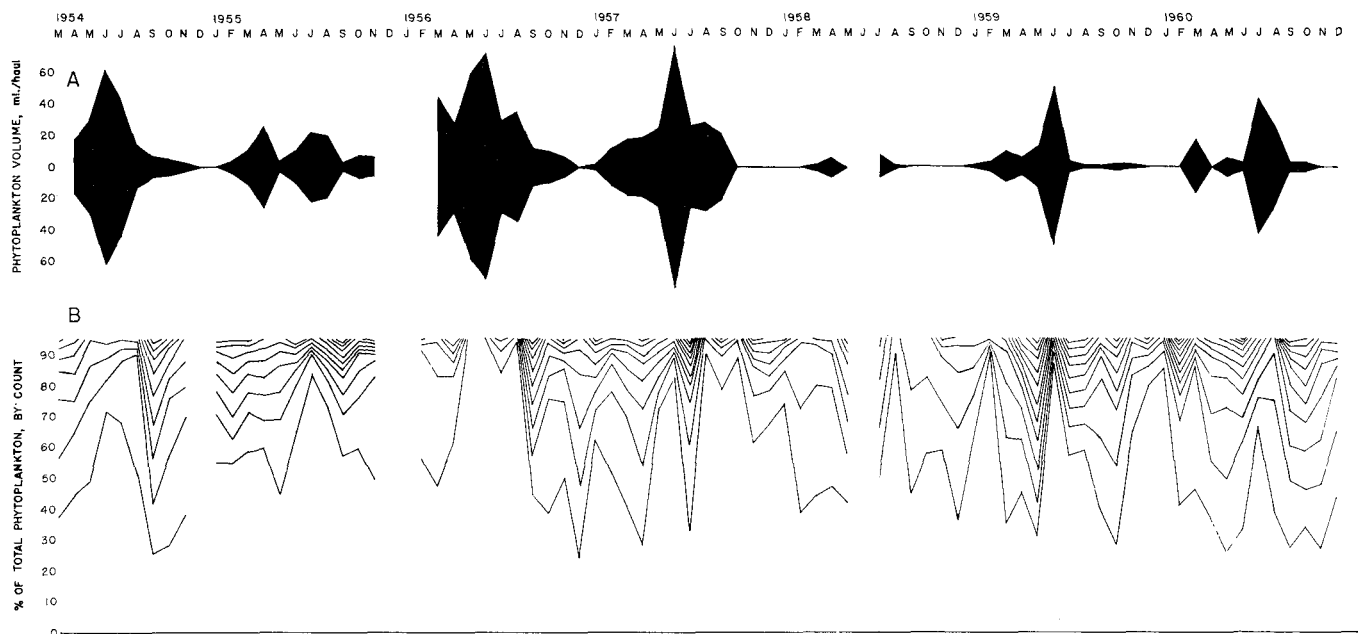


FIGURE 5. A. Monthly averages of the volume of the phytoplankton standing crop (ml. per haul), 1954 through 1960. B. Taxonomic composition of the phytoplankton, based on monthly averages of counts made on all hauls. The lowermost curve traces the percentage of the total phytoplankton contributed by the genus which was most abundant during the month, the next curve adds the percentage of the next most abundant genus, etc. (See text for further discussion.)

samples, taken at the same spot at weekly intervals. Figure 4D shows similar monthly averages of silicate-silicon in $\mu\text{g-atoms/liter}$. The composite or "average" chart of phosphate-phosphorus distribution is shown in Figure 4B. This was made by combining and averaging for each particular depth and month of the year, all of the different monthly mean figures obtained for that particular depth and month from all of the years for which data were available (1951-1955).

Annual variation of phytoplankton volumes and nutrients in Monterey Bay.

The production of phytoplankton depends primarily upon two variables: 1) the amount of radiant energy of sunlight, and 2) the amount of nutrient chemical substances available in assimilable form. In June the solar energy reaching the latitudes of California is greatest. In June also, upwelling along the California coast is typically at or near its height, and plant nutrients from the dark deep layers are being introduced into the sunlight photosynthetic zone at a maximum rate. It is therefore to be expected that the greatest production of pelagic plants would occur in June. In December sunlight is at a minimum; furthermore, at this time of year the Davidson Current is bringing depleted surface water toward shore and the nutrients in the upper layers are at their low point. In December, therefore, phytoplankton production could scarcely be anything but minimal.

We have no direct measures of phytoplankton production or mortality, the present studies having been limited to volumetric determinations of the standing crop of larger phytoplankters. While repeated determinations of the size of the standing crop do not provide any real measure of turnover rates in the present situation, nevertheless they may be in some degree suggestive of production and mortality. At least a low level of primary production will not ordinarily result in massive populations in the sea, nor will heavy concentrations of phytoplankters persist long if production proceeds at a reduced rate.

The average annual cycle of phytoplankton abundance, repeated for two years, is shown in figure 4A. The rather conspicuous bulge in the population in March is a distortion of the normal pattern induced by the very heavy samples of March, 1956. The effect of this abnormal month appears significant only because the averages are based on a limited number of years. If this aberration is ignored, the curve depicting the average rise and fall of the phytoplankton assumes a very symmetrical form. From December, in which month the phytoplankton is at a low ebb, the population increases, at first slowly and then at an accelerating rate to reach a sharp peak in June; thereafter it diminishes, at first abruptly and then more slowly until in December the tows again yield only traces of phytoplankton.

A corresponding average annual cycle of nutrients in the bay, as represented by phosphates, is depicted in figure 4B. While drawn from a previous investigation, the broad general features are applicable here, and the correlation between events in the annual phos-

phate cycle and the phytoplankton standing crop (Fig. 4A) are evident. Plant nutrients, as represented by the phosphate, are present in much greater quantities at 50 meters (broken line) than at the surface (solid line). This is due to the fact that they are introduced from below and begin to be removed by the phytoplankton as they enter the photosynthetic zone. The steady rise of both curves from February to May in figure 4B depicts the enrichment of the superficial layers by upwelling. The beginning of the rise in the 50-meter curve a full month earlier is probably the result of deep mixing induced by winter storms. The beginning of the decline in the nutrients a month before the phytoplankton begins to decrease reflects the rapid utilization of the resource by the burgeoning population. The subsequent decrease in the amount of nutrients is the result of the continued use of these substances by the declining but still fair-sized population of phytoplankton, and of the diminishing replenishment as upwelling slackens.

Annual cyclic change in character and complexity of the phytoplankton.

The preliminary picture of the average general relationship between phytoplankton volumes and concentrations of nutrients seems clear enough as far as it goes, but the situation in the bay is much more complex than would appear from figures 4A and 4B. The bay is not an enclosed body of water like a lake, but a part of the open sea, and any understanding of changes here must be interpreted in terms of the flow and interchange of water at different seasons. Further, the standing crop of phytoplankton changes during the year not only in its size but also in its qualitative character, and this, too, needs to be brought into the picture.

We have already discussed the division of the year into three marine seasons, each characterized by a flow of water in a particular direction. During the upwelling season water rises from the depths along the coast and flows southward and away from shore on the surface. This water, as it rises, is rich in stored nutrients. With the end of upwelling the relatively cold and heavy water along the shore sinks of its own weight, and warm surface water from the open ocean flows toward shore to take its place. The inflowing water of the oceanic period has probably been on the surface and supported a growth of floating plants for a considerable period. At any rate, it is low in dissolved nutrients. However, it forms a comparatively thin superficial layer and through slight mixing with the richer subsurface water nearer shore it is able to support a moderate growth of phytoplankton. The Davidson Current brings about a much more massive onshore flow of depleted surface water from offshore regions to the south. The continuing pressure forces the water to sink and a thick uniform layer of low nutrient content is soon developed along the coast. This constitutes a virtual marine desert until upwelling begins again in late winter.

As the upwelling brings nutrients into the photosynthetic zone, the plankton begins its annual increase. The conditions present at this time favor the

growth of some forms more than others. Those best adapted to the prevailing situation increase in numbers very rapidly, and form ever increasing proportions of the plankton. The number of different forms represented by appreciable quantities is, as a consequence, reduced. At about the peak of upwelling, or somewhat thereafter, one genus, *Chaetoceros*, typically forms about 80 percent of the population, and four or five other genera make up another 15 percent. Sometimes the dominant genus may occur almost without competition, as in May and June, 1956 (Fig. 5B).

As upwelling slackens, and as nutrient levels drop and surface temperatures rise, the dominant phytoplankters of the June bloom begin to decline. At the same time inflows of oceanic surface water carry a number of forms characteristic of the open sea into the coastal area. Mixing of offshore surface water with water recently risen from the depths establishes a milieu which is richer in nutrients than that of the open sea, but not so rich as the upwelled coastal water. The phytoplankton inoculated into this new environment by the influx of surface water finds conditions more favorable than normal, and several species begin to multiply rapidly, unhampered by effective competition of the resident forms. The abrupt decrease in the dominance of the most abundant genus, and the entrance of several new genera into the population as important elements, is depicted in figure 5B by the downward slope of the lines and their increase in number. This pattern occurs first in fairly typical form during the fall of 1954, when the number of genera forming 95 percent of the phytoplankton increased from five in August to ten in September. Thereafter it is repeated annually sometime between July and September. After the initial rapid growth of several different genera in the new environment, a few of them that are better adjusted to the particular conditions prevailing at this time increase in numbers at the expense of the others. This phenomenon, similar to the one noted in the case of the successful organisms of the upwelling period, is indicated by the upward trend and decrease in number of the lines in figure 5B. The history of the representatives of the phytoplankton during the oceanic period is thus traced by a V-shaped pattern of rather short duration, normally extending from about August to October or November, which forms the most prominent recurring feature of the figure.

With the further reduction of nutrients and decline in temperatures during the Davidson Current period, the picture changes once more. Again the phytoplankton takes on a mixed character as several genera show increases in relative numbers in the samples counted. Soon a few of the forms, apparently able to multiply at very low concentrations of nutrients and to compete successfully under the prevailing conditions, display increasing degrees of dominance over others. The result is another V-shaped pattern in the lines of figure 5B, extending from about November to February or March, but usually less deep and clear-cut than that marking the oceanic period.

Finally, the beginning of upwelling promotes the development of other forms, presumably those that require, among other things, a rather high level of nutrients. Their initial increase, while the forms characteristic of the Davidson Current are still present, raises once more the number of genera represented in the plankton by significant numbers of individuals. Since the development of upwelling is usually not abrupt, the left hand side of the V-shaped pattern marking this period in figure 5B often has a more gentle slope than the right hand side which typically traces the achievement of massive dominance by *Chaetoceros*, as already noted.

While the annual cyclic change in the character of the phytoplankton is ideally traced by three annual V-shaped patterns in figure 5B, each indicating increasing population complexity as the character of the water changes and subsequent decreasing complexity as one or a few forms gain dominance during a particular season, the picture is seldom simple. For example, while the V-shaped pattern of the oceanic period can be distinguished during the autumns of 1959 and 1960, more prominent configurations of the same type occurred in May of the former year and February of the latter one. The increased complexity of the population in May, 1959, may be due to a complex inoculum in the slight and very early influx of oceanic water indicated by the dip of the 13° isotherm in March (Fig. 3C), which introduced a number of warm-water types and mixed them with the cold-water populations characteristic of the third month of upwelling. No similar evidence can explain the pattern of February, 1960. However, it may be pointed out that indications of influxes of surface water or surges of upwelling can readily be averaged out if they are of short duration or span parts of two months. Indeed, surface temperatures on January 18, 1960, were abruptly lower than those encountered on the preceding and succeeding cruises, and these temperatures indicate a short and sharp pulse of upwelling between two influxes of surface water. The latter may have brought in numerous oceanic types which prospered during the following month to give the plankton a relatively mixed character. Such disruptions of the ideal pattern occur in every year, and it must be stressed that practically never does a season run an uninterrupted course between a sharp beginning and end.

It is not possible to say, on the basis of the data presented in figure 5, to what extent changes in the character of the phytoplankton are due to import and export, or to what extent they result from changes in reproductive and mortality rates of forms already within the bay and environs. Shifting water masses doubtless do carry numbers of assorted phytoplankters in and out of the bay, particularly during the oceanic and Davidson Current periods, and this may contribute toward the formation of mixed populations. On the other hand, scattered individuals of most genera occur in the bay throughout the year, forming part of that 5 percent of the phytoplankton not represented in figure 5B. It seems very likely that some of the changes in the character of the phytoplankton

result from the increase or decline of forms continuously present as seed populations, in response to subtle changes in complexes of environmental variables.

Analysis and interpretation of variations in phytoplankton volumes, 1954-1960.

It is clear from a perusal of figure 5A, which traces fluctuations in the size of the standing crop during the seven years from 1954 to 1960, inclusive, that in general the standing crop of phytoplankton varies according to the general annual cycle outlined earlier. It is also clear, however, that in individual years there have been conspicuous departures from the average situation depicted in figure 4A.

For the year 1954, the data on phosphates and silicates (Figs. 4C and D) correspond well with those on phytoplankton volumes (Fig. 5A). As these and other nutrients became available in relatively large amounts in the spring of 1954, the phytoplankton increased and reached a strong peak in June. The heavy population of minute floating plants began to remove the nutrients at a greater rate than they were being supplied. As a result both silicate curves showed a slight decline in June, the phosphate at 50 meters turned downward a month later, and that at the surface followed after reaching a sharp peak in July. The decline of the silicate a month earlier than the phosphate is probably due to the heavy concentration of diatoms. In June, which is quite typical of the months from March to August, five genera of diatoms constituted 96.9 percent of the phytoplankton, and several other genera were present in smaller proportions. Since these organisms build silicious skeletons, differential withdrawal of silica may be expected when diatoms are heavily dominant in strong plankton blooms. The peak of phosphate at the surface in July was evidently due to an enriching pulse of upwelling water reaching the most superficial layers, while the subsurface water had already begun to sink (compare the trend of the 12° isotherm with those of the 10° and 11° isotherms in figure 2C). The subsequent decline of the nutrients was interrupted only briefly, and only at the deeper levels, in September. This month shows a reversal in the trend of the nutrient curves at 50 meters (Figs. 4C and 4D) which is matched by a reversal in the isotherms (Fig. 2C), but enrichment by this late pulse of upwelling did not affect the surface and retarded the decline of the population very little, if at all.

While the various curves of this first year form a logical series of interrelated patterns, those of the following year are confusing. During the early part of 1955, the spring increase in nutrients was at first accompanied by the even increase in the phytoplankton that it was logical to expect. In May, however, although the nutrient levels were comparable to those of the preceding year and rising, and although the available light was increasing, the phytoplankton fell off sharply (Fig. 5A). It does not appear that the nutrients were utilized at an excessive rate, for phosphate and silicate remained throughout the summer and most of the fall at levels comparable to or above those that had existed during the heavy bloom in the

spring of 1954 (Figs. 4C and 4D). In spite of the apparently favorable conditions, recovery from the population sag of May was slow, and the second peak reached in July was even lower than the level attained three months earlier. It is possible that, after being ineffective during the summer for some unknown reason, the high nutrient level finally did influence phytoplankton in the fall. At any rate, the standing crop during October and November was greater than in the same months of any other year, with the exception of 1956.

If the relative failure of the phytoplankton crop of 1955 was not due to lowered nutrients or to diminished light, it appears probable that biological agencies were responsible. The zooplankton was abundant during 1955, and it might be argued that in that year the standing crop of phytoplankton was reduced by overgrazing. However, the zooplankton volumes were also high during 1956, a year of very heavy phytoplankton populations, and they were very low in 1959 when phytoplankton volumes were small. Our analyses of the zooplankton samples are at present too incomplete to permit any detailed conclusions to be drawn as to effect of the pelagic animals on the size of the standing crop of phytoplankton.

Skipping now to the year 1958, although no data are available for the critical month of June, the extremely low phytoplankton volumes of the preceding and succeeding months (Fig. 5A) render it practically certain that this was the poorest year of the entire period of study. The extremely steep slope and close spacing of the isotherms between March and May (Fig. 2C), as well as the curves in figures 2A and 2B, leave no doubt that upwelling during this period was extremely strong and that enrichment of the surface layers was much greater than normal. Why then were plankton volumes low? A logical possibility is that the upwelling water flushed most of the plankton out of the area. If upwelling is gradual phytoplankters will flourish as the fertilizing stream reaches the sunlit layers, and the population will be maintained and increased by growth and by re-inoculation through horizontal eddies; if upwelling is too strong and steady, the continuous outward flow of the water, which itself carries no phytoplankton from its source, will disperse the organisms of the surface layers and prohibit buildup of large populations.

Some support for this hypothesis is provided by the data for 1959 and 1960, both years of relatively low plankton volumes. Although the upwelling was not very strong, as is shown by the comparatively small spread between the maximum and minimum curves and the low vertical temperature gradients (Figs. 2A and 2B), it was unusually regular, with little evidence of interruption (Fig. 2C). It seems possible that the steady flow of rising water was sufficient to carry the developing phytoplankton offshore rapidly enough to limit the size of the population within the bay.

The very productive years of 1956 and 1957 provide an illuminating contrast. Upwelling in both of these years was strong, but it was also intermittent. The isotherms present jagged or flattened profiles well

before the peak plankton volumes are reached. This indicates alternating surges of upwelling and inflows of surface water from outside. At least some of the enriched water flowing offshore is returned, together with its rapidly multiplying organisms. Each inflow brings with it a rich flora, each pulse of upwelling provides added nutrients for further growth, and the transport back and forth in flows of alternating direction provides time for the development of heavy blooms in the coastal region.

The data of the early part of 1954 are inadequate to offer a satisfactory explanation of the excellent plankton crop of that year. In 1955 the beginning of what promised to be a good bloom is correlated with a markedly jagged pattern of the isotherms during the early part of the year. Interestingly enough, the bloom was aborted in May just when the upwelling, although apparently somewhat reduced in force, became steady. It seems quite possible that unidirectional flow during the following months dispersed the bloom, and prevented plankton volumes from reaching a high peak within the area investigated.

There is no indication that the phases of the long-term temperature cycle influence the size of plankton populations; both warm and cold periods include years of both high and low volumes. Neither does there appear to be any clear and simple correlation between the relative strength or duration of particular marine seasons and the size of the plankton crop in different years.

The data available from the present investigation fall far short of what would be required to explain fully the differences in phytoplankton volumes obtained within the bay. Nevertheless, these data do appear to support the suggestion that coastal plankton blooms are promoted by irregularities in the upwelling stream.

Relative abundance of different genera in the phytoplankton.

In addition to consideration of the phytoplankton as a whole, it is of some interest to attempt to analyse the relative importance of the various genera comprising it. To this end we present figures 6 and 7, which depict the commoner genera of diatoms arranged in sequence according to their abundance, i.e., according to the height of their greatest peaks, and figure 8 which shows the commoner dinoflagellate genera arranged in the same way. These curves are based on phytoplankton counts made very largely by Mr. Bernard D. Fink, whose contribution to the present program has been an outstanding one. Specific determinations of a large number of diatoms occurring in the samples from May, 1958, through April, 1959, were made by Dr. Enrique Balech of Argentina (Balech, 1959), and we are very much indebted to him for permission to make use of these determinations in connection with the discussions below.

By far the most important genus in the local phytoplankton is *Chaetoceros*. This genus of diatoms aver-

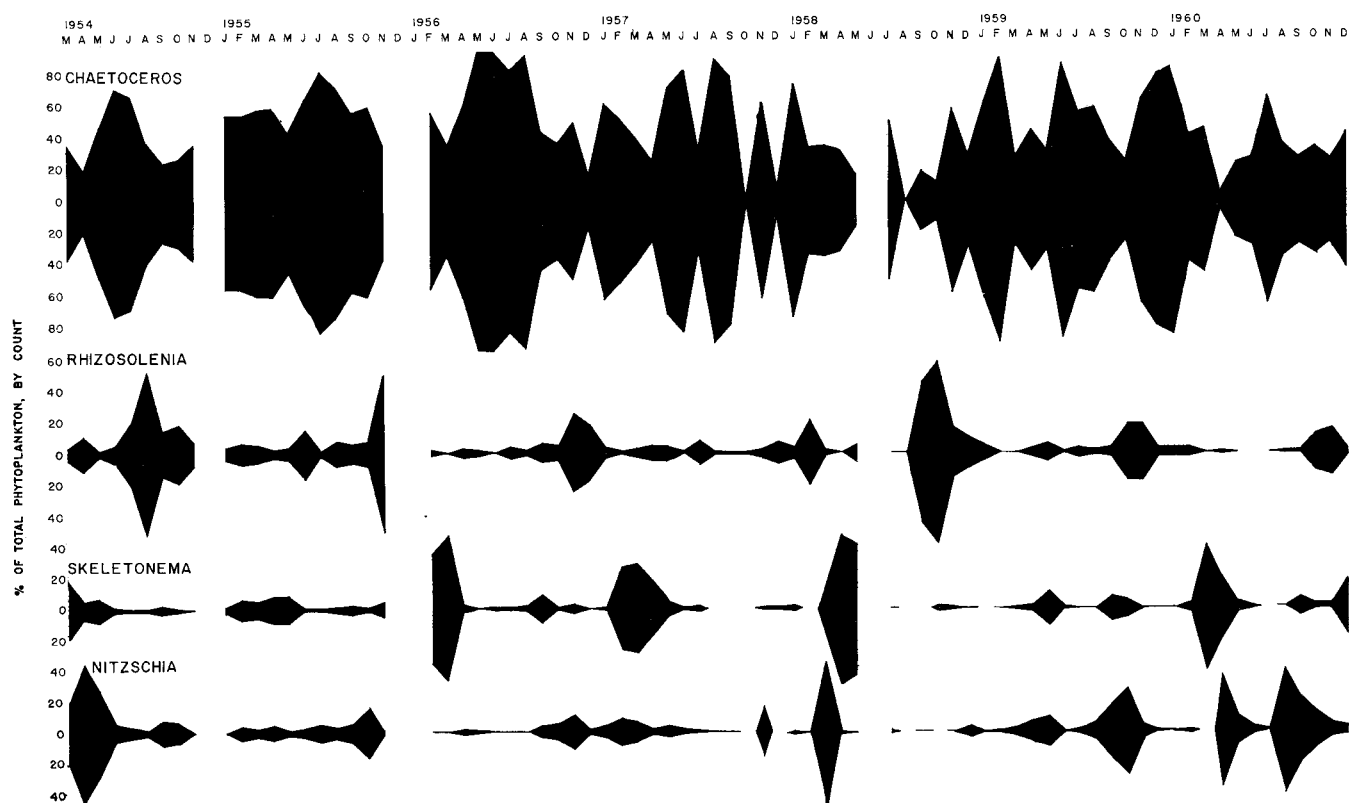


FIGURE 6. Relative abundance of the four commonest genera of diatoms, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

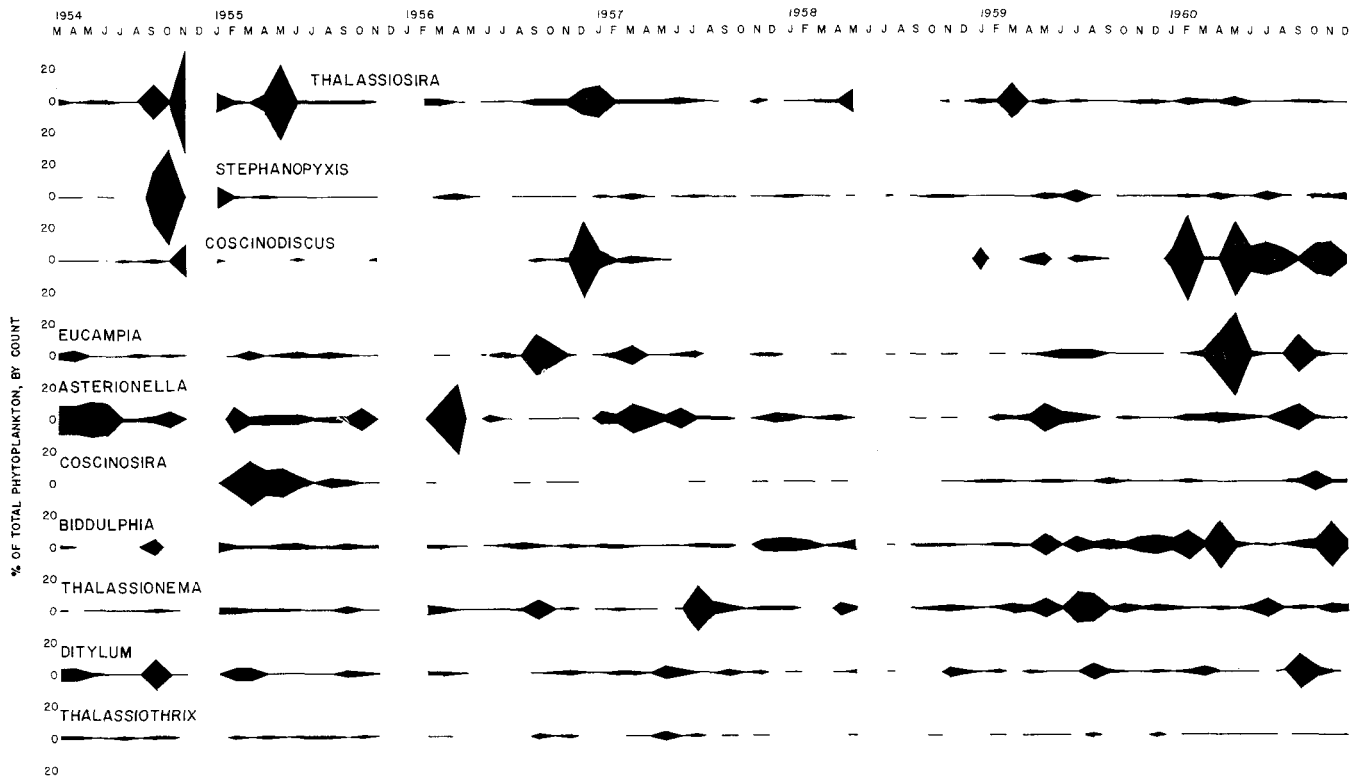


FIGURE 7. Relative abundance of ten genera of diatoms, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

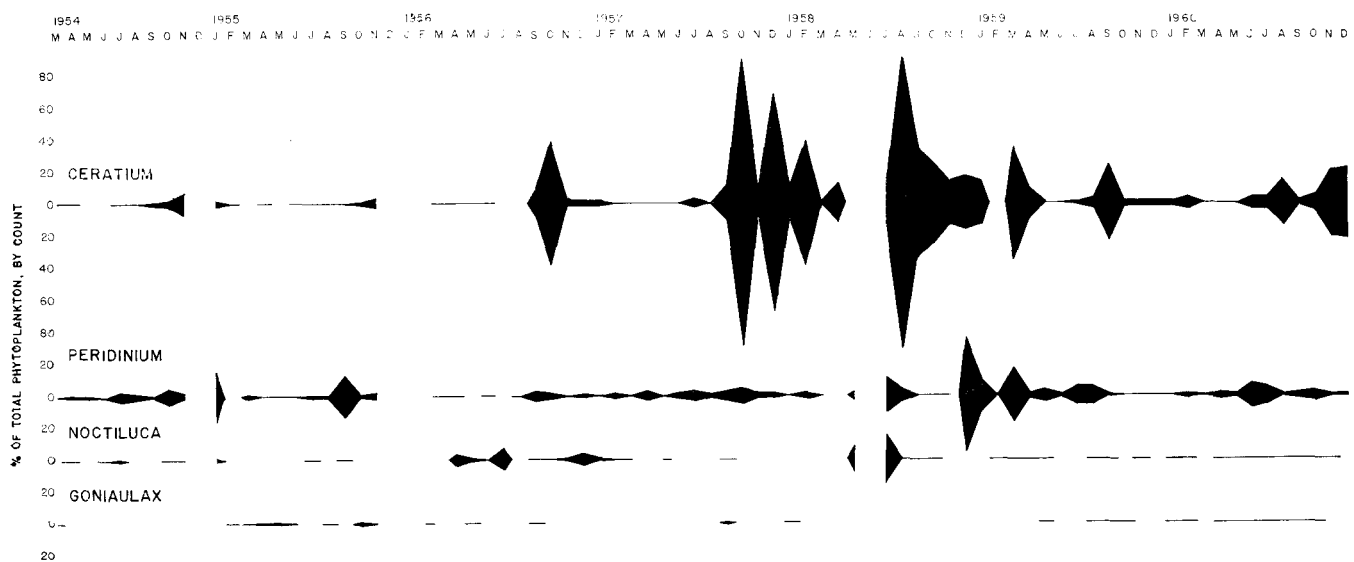


FIGURE 8. Relative abundance of the four commonest genera of dinoflagellates, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

ages about 50 percent of the catch throughout the years, and always dominates during the periods of peak volumes in June and July, when it typically constitutes more than 80 percent of the catch (Fig. 6). During the months of low plankton volumes *Chaetoceros* normally constitutes less than 50 percent of the catch, but occasionally it may account for three-fourths of the count even when the total plankton

volumes are very low (January, 1958; February, 1959; January, 1960). During only 10 percent of the months did this genus make up less than 20 percent of the plankton, and on only one occasion (August, 1958) did *Chaetoceros* species form less than 4 percent of the catch; the genus was never totally absent. While figure 6 shows a degree of dominance that is high in summer and lower in winter, the average values are so

high and the progression of the curves so irregular that the trend is somewhat obscure, particularly in 1959 and 1960.

The dominance of *Chaetoceros* in Monterey Bay reflects very well the importance of this genus in the whole temperate and subtropical eastern Pacific. Cupp (1943) lists 54 species and varieties of *Chaetoceros* from the west coast of North America, and notes that the genus outnumbers all others in the area in terms of number of species and number of cells present. In a partial analysis of the Hopkins Marine Station CalCOFI samples for the period May, 1958 through April, 1959, Dr. Enrique Balech noted 15 species of *Chaetoceros*. These are tabulated below, arranged according to temperature tolerance. In each column the species are listed in order of decreasing importance in the plankton; those listed below the horizontal lines were noted only once or twice during the year. The species list is very probably not exhaustive.

Cold-water species	Widespread eurythermic species	Warm-water species
<i>C. debilis</i>	<i>C. didymus</i>	<i>C. lorenzianus</i>
<i>C. decipiens</i>	<i>C. affinis</i>	<i>C. costatum</i>
<i>C. constrictus</i>	<i>C. eibeni</i>	<i>C. messanensis</i>
<i>C. radicans</i>		<i>C. peruvianus</i>
<i>C. convolutus</i>		<i>C. daydi</i>
<i>C. concavicornis</i>		
<i>C. socialis</i>		

The complexity of the *Chaetoceros* curve in figure 6 reflects the fact that we are dealing with a large and varying mixture of species. Since warm-water, cold-water, and tolerant forms occur in the area, the genus may be represented by respectable numbers of individuals at any season of the year. Notwithstanding this, the dominance of this genus is strongest during the upwelling period, the coldest season, and the species of *Chaetoceros* which are most abundantly represented are all cold-water forms: *Chaetoceros debilis*, *C. decipiens*, *C. constrictus*, and *C. radicans*. *Chaetoceros debilis* is probably the most abundant diatom species in Pacific waters off California (Allen, 1928; Cupp, 1943).

It is obvious that the fluctuations in the relative abundance of such a regularly dominant genus as *Chaetoceros* will play an extremely important role in determining the pattern of similar charts for other representatives of the phytoplankton. These can constitute a relatively important part of the population only when *Chaetoceros* is present in rather small proportion. However, we are dealing not with a simple reciprocal but one that is composed of 17 other genera, and the varying abundance of some of these in relation to one another is significant and of interest.

The remaining common genera of diatoms fall into three major groups on the basis of their seasonal occurrence. The first of these groups consists of genera whose locally occurring species appear to have requirements which are somewhat similar to those of *Chaetoceros*, but which tend to occur in larger relative numbers before and after the main *Chaetoceros* peaks. Among these genera are the following.

Skeletonema (Fig. 6). This is represented in our material by the single cosmopolitan species *S. costatum*. The species is most prominent in the plankton during the early stages of upwelling, and forms 10-25 percent of the catch for a one-to-three-month period between February and May (Fig. 6). This season of abundance agrees well with the February through April period reported by Cupp (1943), and with the findings of Bigelow and Leslie (1930) who found *S. costatum* a prominent element in the phytoplankton of Monterey Bay in March, 1923 and 1925, and April, 1924. In five of the seven years of our collections (the warm years 1957 and 1958 are the exceptions), there was a minor increase in the importance of this species during September, with the population averaging about 5 percent of the entire phytoplankton. It appears that *Skeletonema* is able to thrive on the modest amounts of nutrients present just as upwelling begins and shortly thereafter, but that it is soon overshadowed by the rapid multiplication of *Chaetoceros* when the waters become really rich. As the *Chaetoceros* population declines in the fall, *Skeletonema* once more increases in relative numbers, but only to a limited extent and for a brief period before the Davidson Current period sets in and nutrients drop to a low level once more. Thus the pattern of relative abundance for *S. costatum* is one in which peaks in the spring and fall are separated by depressions in summer and winter.

Nitzschia (Fig. 6). This genus, represented by one to several species, also tends to display peaks of relative abundance during the spring and fall, but these are less regular than those which characterize the populations of *Skeletonema*, both in the relative magnitude from year to year and in the comparative prominence of the spring and fall populations. Sometimes the spring peak is the major one (1954), sometimes that of fall is greater (1959); sometimes both are insignificant (1956) and sometimes both reach considerable proportions (1960).

Eucampia (Fig. 7). The only species determined in our material by Dr. Balech is *E. zoodiacus*. Although its contribution to the total population is always small, recognizable increases occurred at the beginning of upwelling in April, 1954, March, 1955, and March, 1957, while somewhat greater expansions developed during the oceanic periods interrupted by a brief surge of upwelling in September, 1956 and 1960. Curiously, the greatest relative development took place in May, 1960, toward the end of an apparently uninterrupted period of upwelling. In spite of the latter phenomenon and the generally low level of the population, *Eucampia* appears to behave in a manner somewhat similar to that of *Skeletonema*. Bigelow and Leslie (1930) found *Eucampia zoodiacus* an important element in the phytoplankton of Monterey Bay in March, 1924, and Cupp (1943) notes that this widely distributed species is often abundant off southern California, especially from March through July.

Thalassionema (Fig. 7). Dr. Balech has identified our local form as *T. nitzschoides*, the only species of the genus listed in Cupp (1943). Four of the five occasions when it comprised 6 percent or more of the total phytoplankton catch (Sept., 1956, and July, 1957, 1959, and 1960) coincided with periods of surface inflow alternating with upwelling. On the fifth occasion (May, 1959), it appears that upwelling was progressing steadily. However, there is a possibility that this peak may bear some relation to a minor pulse of surface water from the open ocean that intruded in March and increased the population at that time.

Ditylum (Fig. 7). This genus appears to be represented solely by *D. brightwellii*, the only *Ditylum* listed in Cupp (1943). The species was taken at 83 percent of the stations occupied on Monterey Bay by Bigelow and Leslie (1930), but was nowhere common. In our present samples *Ditylum* normally displays an increase each spring and another in the fall, but the levels are usually so low that the pattern is none too clear. The species reached a maximum development of 11 percent of the phytoplankton in September, 1960, during a period of rather low phytoplankton volumes.

Asterionella (Fig. 7). *Asterionella japonica*, determined by Dr. Balech, appears to be the only species represented in our material. Bigelow and Leslie (1930) found it at 72 percent of their stations in Monterey Bay, where it formed an important element in the plankton in March, 1924. In the present period of investigation, it displayed each year an increasing importance in the plankton during early upwelling, and there was often a similar increase in the fall. *Asterionella*, however, differs from the other genera listed above in that it appears better able to compete with *Chaetoceros* species when nutrients are high. It usually persists in appreciable quantities during the entire upwelling period.

A second group of diatoms presents a strong contrast to those already discussed. These are the species of the genus *Rhizosolenia*. Members of this genus characteristically appear in numbers with the beginning of the Davidson Current, and gain their maximum importance in the plankton during the middle or even near the end of that period. Consequently, the peaks of *Rhizosolenia* do not coincide with those of any other genus, though members of the genus do occur in appreciable numbers throughout the year. Exceptions to the general rule that *Rhizosolenia* occurs in greatest relative numbers during the period of the Davidson Current were provided in August, 1954, and in September and October, 1958. These peaks coincide with influxes of oceanic water.

Cupp (1943) lists 20 species, varieties, and forms of *Rhizosolenia* from the west coast, and Bigelow and Leslie (1930) list four species in their collections from Monterey Bay. Dr. Balech has noted the following in our collections, though no attempt was made to provide a complete listing of all species occurring.

Cold water species	Widespread eurythermic species	Warm water species
<i>R. styliformis</i>	<i>R. stolterfothii</i>	<i>R. robusta</i> (tolerant species)
		<i>R. calcar-avis</i>
		<i>R. acuminata</i>
		<i>R. bergonii</i>
		<i>R. temperei</i>

The high relative numbers of *Rhizosolenia* occurring in September, 1958, are attributable primarily to populations of *R. robusta* and *R. styliformis*, and in October, 1958 to *R. styliformis*. In December, 1958 and January, 1959, however, the *Rhizosolenia* species of the Davidson Current period were all warm water forms (*R. robusta*, *R. calcar-avis*, *R. bergonii*, and *R. temperei*), undoubtedly brought in from the west or south by the Davidson Current. All of the species listed in the table above, with the exception of *R. stolterfothii*, are oceanic species. It appears these are able to form an important element in the coastal plankton only when other genera are present in low numbers.

The remaining genera of diatoms are relegated to a third group only because we have been able to discern no regular recognizable pattern in their occurrence. The peaks come too irregularly, are too few, occur in too limited a number of years, or the general level of occurrence is too low for interpretation. These genera, also charted in figure 7, include the following.

Thalassiosira. The only common form noted by Dr. Balech in the 1958-1959 samples was *T. rotula* though several species are reported from Monterey Bay (Bigelow and Leslie, 1930).

Stephanopyxis. The only species noted Dr. Balech in our 1958-1959 collections was *S. turris*. Bigelow and Leslie (1930) found this at 11 percent of their stations in Monterey Bay.

Coscinodiscus. Very likely a mixture of species is involved here.

Coscinosira. *Coscinosira polychorda* is the only species listed by Cupp (1943), and the only species found in Monterey Bay by Bigelow and Leslie (1930). The latter investigators found it in samples from 28 percent of the stations occupied in the bay. The scarcity of this widespread north temperate species in the plankton of the warm years of the present study is suggestive.

Biddulphia. The only form especially noted by Dr. Balech in the 1958-1959 plankton from our collections was *B. longicruris* var. *hyalina*, though other species may have been present in this and other years. It was noted (under the name *B. extensa*) in 94 percent of the stations collected by Bigelow and Leslie (1930) in Monterey Bay.

Thalassiothrix. *Thalassiothrix frauenfeldii* and *T. longissima* are reported from Monterey Bay by Bigelow and Leslie (1930), and it seems likely that at least these are represented in the present samples.

The dinoflagellates ordinarily form a less conspicuous element in the plankton than do the diatoms. Nevertheless, there are times when the phytoplankton

catch consists of up to 90 percent dinoflagellates. The following account includes discussion of our own results, but incorporates and draws heavily on the findings of Dr. Balech, who surveyed the dinoflagellates in samples taken in the year May, 1958 through April, 1959.

The genus *Ceratium* is represented in our hauls by a greater number of species and individuals than any other dinoflagellate genus, and the curve showing its relative prominence in the phytoplankton traces a most interesting pattern (Fig. 8). As can be seen, the genus is usually present as a few scattered individuals throughout the year, but it frequently rises to 20 percent or more, and may even constitute 90 percent of the phytoplankton. Since the increases in the relative abundance of *Ceratium* always coincide with, or follow immediately after, the influx of surface water from outside the bay, it is of particular interest to follow the local history of the genus, as traced in figure 8, against a background of the hydrographic conditions.

During the upwelling period of 1954 *Ceratium* was present only as scattered individuals. In August there was a slight inflow of surface water, as indicated by the depression of the isotherms in figure 2C and the decline of the nutrients in figures 4C and 4D. As this water was enriched by mixture with deep water, as a result of the late surge of upwelling in September (note the reversal of the trend of the isotherms and the surface nutrient curves), the dinoflagellates began to increase in relative numbers. The trend continued at least through November, possibly due to reproduction, possibly as a result of continued inoculations from offshore. However, by February, 1955, the initial strong upwelling pulse was probably forcing an offshore flow, and the population appears to have been flushed out. Representatives of the genus were present only as scattered individuals during the entire upwelling period of 1955, but when the late summer calms arrived and the resulting oceanic period was initiated in August, this was followed by an increase in the *Ceratium* population similar to that of the previous year. In 1956 the minor surface inflows that might have occurred in May and July were overshadowed by the intervening upwellings. The oceanic period really got started in September, however, and *Ceratium* reached the respectable peak of 39 percent of the phytoplankton in October. This soon declined as the deeper water rebounded toward the surface (Fig. 2C), but the genus was present in appreciable amounts throughout all of the Davidson Current period. Again in 1957 it was present only as traces during the upwelling. The short early influx of surface water in June produced an unseasonable increase of *Ceratium* to 3 percent of the phytoplankton, but this was reduced during the upwelling of the following month. However, *Ceratium* increased in relative abundance during the subsequent strong Davidson Current period, and reached 89 percent of the phytoplankton population in October. The unusual irregularity of the surface-temperature curves (Fig. 2A) and the isotherms (Fig. 2C) during the normally very stable Davidson Current period indicates the ebb and

flow of different water masses, with possibly some upwelling in November and January. This is reflected also in the prominence of the *Ceratium* population, which persisted in declining but rather high and very irregular quantities into April, during which month a very strong surge of upwelling occurred. *Ceratium* was totally lacking from the catches of May. Lack of data for June, 1958, makes it impossible to pinpoint the beginning of the oceanic period in this year. Since *Ceratium* constituted 15 percent of the individuals in the phytoplankton during July, it is possible that the oceanic period had already begun in this month. In August, when it was in full swing, *Ceratium* reached a peak of 91 percent and continued at relatively high levels through January, 1959, which marked the start of upwelling. The rise in all of the surface temperatures in March (Fig. 2A) and the V-shaped 13° isotherm (Fig. 2C) indicate a brief inflow of surface water from offshore. This appears to have brought with it a heavy inoculum of *Ceratium*, the residue of which persisted for another month. In July the first slight inflow of warm surface water typical of the oceanic period may have occurred, and in August this inflow had reached sizable proportions. Along with this there occurred another relative increase in the *Ceratium* population, which reached a fair peak of 24 percent when a short burst of upwelling enriched the water in September. The genus persisted at levels of two to four percent during the subsequent Davidson Current period, but during the upwelling of March, April, and May, 1960, it occurred only as traces. The weak influx of surface water in June was accompanied by the usual relative increase in *Ceratium*, which persisted through the late surge of upwelling in July and continued to be present in appreciable amounts through the rest of the oceanic and Davidson Current periods of the year. One could scarcely ask for a better correlation between the relative abundance of a plankton genus and the fluctuating hydrographic conditions.

Dr. Balech's studies of the May, 1958-April, 1959 dinoflagellates indicates that the situation is considerably more complex than might be judged from the relations indicated above. The species and varieties he noted in our samples are tabulated below, according to their general distribution in the sea (Graham, 1941; Graham and Bronikovsky, 1944; Balech, 1959). In each column species listed below the line were noted only in one or two samples during the year.

Cold-water species	Cosmopolitan species and very tolerant warm-water species	Warm-water species
<i>C. lineatum</i>	<i>C. dens</i>	<i>C. candelabrum</i>
<i>C. azoricum</i> (north- ern form)	<i>C. azoricum</i>	<i>C. horridum molle</i>
<i>C. horridum</i> var. <i>genuinum</i>	<i>C. extensum</i>	<i>C. macroceros gallicum</i>
<i>C. arcticum</i> var. <i>longipes</i>	<i>C. furca</i>	<i>C. platycorne</i>
<i>C. macroceros</i> mac- roceros	<i>C. hexacanthum</i>	* <i>C. vultur pavillardii</i>
<i>C. fusus</i>	<i>C. massiliense</i>	* <i>C. belone</i>
<i>C. tripos</i>	<i>C. arietinum</i>	* <i>C. limulus</i>
		<i>C. gibberum</i>

Warm-water
species

**C. axiale*
C. coarctatum
C. contrarium
 **C. falcatifforme*
 **C. inflatum*
 **C. paradoxides*
C. pentagonum
C. subrobustum
C. semipulchellum
C. strictum
C. tenue
 **C. longirostrum*
C. kofoidii
C. karsteni

Species in the right hand column marked with an asterisk (*) are strictly tropical species intolerant of colder waters (below 19°C). The placement of *C. dens* in the center column is tentative, since its distribution is not very well known.

It is not possible with the data now available to assign particular *Ceratium* peaks to particular species in any quantitative manner. Nevertheless, Dr. Balech's survey, covering the period from May, 1958 to April, 1959, indicates that the cosmopolitan and somewhat more tolerant warm-water species dominated the *Ceratium* catch from August, 1958 to the end of the year, the highest peaks being due primarily to *Ceratium dens* and *C. candelabrum*. The strictly tropical species showed up in largest numbers particularly in December, 1958 and January, 1959 (no less than seven of those marked with an asterisk in the table were present during the latter month). This strongly suggests transport by the Davidson Current. The *Ceratium* peak in March, 1959, apparently accompanying an inflow of oceanic surface water, was made up of cold-water species.

The other dinoflagellate genera normally taken in the catches provide very little additional information.

Peridinium. Individuals of this genus are usually present in greatest proportion during the period when upwelling is not occurring and when influxes of surface water occur. Dr. Balech's studies indicate that at least 22 species are involved. The highest peak reached was that of December, 1959, and was due primarily to the warm-water species *Peridinium pentagonum*.

Noctiluca scintillans, the only representative of a monotypic genus, was seldom present in more than traces. On the few occasions when it contributed as much as 5 percent of the phytoplankton population, upwelling was in progress or had just yielded to a surface inflow.

Goniaulax, the final genus, was represented in the plankton during scarcely more than one-third of the months surveyed in the seven-year program. It never constituted more than 1 percent of the phytoplankton, and no discernable pattern is traced by its occurrence and relative abundance.

Any discussion of the variation of phytoplankton in relation to hydrographic conditions raises a question noted earlier: to what extent are population shifts due to import and export, and to what extent are they to be explained by local natality and mortality? Data upon which an unequivocal answer could be based are seldom available.

The point has been stressed (cf. Haxo in Balech, 1960, p. 131) that phytoplankters cannot be regarded as drift bottles, since resident or transported seed

populations of forms not normally present in significant numbers may undergo rapid increases if conditions become suitable. Nevertheless, as noted by Balech (1960), such seed populations require time to produce blooms, and increases in numbers of tropical forms during periods when temperatures are not only below the normal range for those species but are actually declining, are almost certainly referable to transport of these forms from warmer areas rather than to local multiplication.

While no conclusive answers are provided by the present investigation, Dr. Balech's studies of our May, 1958 through April, 1959 samples appear to throw some light on the probable origin of the water at different seasons. The following discussion is based upon Dr. Balech's determinations and his characterizations of the various species as warm-water forms, cold-water forms, or eurythermic forms of wide distribution. However, he is in no way responsible for the conclusions we have drawn as to the origin of water entering Monterey Bay and carrying with it organisms either in the form of seed populations or of fully developed planktonic communities.

In the early stages of upwelling in 1958 the phytoplankton was dominated by *Skeletonema costatum* and some other species of wide distribution (*Thalassiosira rotula*, *Asterionella japonica* and several *Coscinodiscus*), but these were mixed with a number of forms more or less typical of cold water, such as *Chaetoceros debilis*, *C. decipiens*, *C. constrictus*, *C. radicans*, and *Biddulphia longieruris* var. *hyalina*. These are largely neritic forms and probably represent a population of resident species. By the end of July the cosmopolitan forms were still present, but the cold-water species of *Chaetoceros* dominated the plankton completely.

With the first surface inflow of oceanic water in August, *Ceratium candelabrum*, a definitely warm-water form, appeared, as did also *C. dens*, a species that is more eurythermic but seems to prefer warm water. The latter form was by far the dominant species, and the two together constituted more than 90 percent of the sparse population. The indication of mixing of warm offshore water with the colder upwelled water mass was fortified in September by the appearance of a number of other warm-water species of *Ceratium*: *C. macroceros gallicum*, *C. pentagonum subrobustum*, *C. gibberum*, and *C. horridum molle*, and of the diatom *Chaetoceros lorenzianus*. However, the dominant forms were *Rhizosolenia styliformis*, *Ceratium dens*, *Chaetoceros debilis*, and *C. concavicornis*, all cold-water or eurythermic types.

Plankton samples of October, although collected from relatively warm water, were still composed largely of species typical of high latitudes. *Rhizosolenia styliformis* comprised more than 50 percent of the phytoplankton: *Ceratium*, largely *C. azoricum* (northern form), contributed another 25 percent; and *Chaetoceros*, represented by several cosmopolitan and cold-water species, was present in considerable quantities.

Although November marked the very abrupt beginning of the Davidson Current period, the plankton situation did not change drastically. The only significant difference was the relative increase in abundance

of *Chaetoceros* at the expense of the other two genera. The plankton was definitely of a cold-water type with *Chaetoceros concavicornis* dominant. The probable explanation is that plankton typical of the central California coast in October had first drifted southwestward and was then returned by the reversal of the water flow, and the difference noted was due either to normal temporal changes in the population of the same water mass or to normal spatial variation in water returned from a slightly different area.

Early December was similar to November, with cold-water *Chaetoceros* predominating. Then came a fluctuating period in which warm-water types became more abundant only to decline again, but by the end of the month the plankton was definitely of a warm-water type, consisting almost entirely of *Peridinium*, primarily *P. pentagonum*, and 13 species of *Ceratium* of which, except for three cosmopolitan forms, all are to be classed as warm-water types. In addition there were small numbers of such southern species of diatoms as *Rhizosolenia robusta*, *R. calcar-avis*, *R. acuminata*, *Chaetoceros lorenzianus*, and *Planktoniella sol*. No cold-water phytoplankters were noted.

The plankton retained its southern character throughout the entire Davidson Current period and in early January some rare and typically tropical forms, intolerant of cold water, were noted: *Ceratium belone*, *C. falcatiforme*, and *C. paradoxides*. It seems evident therefore, that by the end of December and early January the Davidson Current, which had been running for some six weeks or more, was bringing into the Monterey Bay area water from a considerable distance to the south. In this connection it is worth remembering that many drift bottles released along the central California coast in January travelled northward for several hundred miles with velocities as great as 0.5 knots (Reid, 1960).

With the first hint of a slackening of the Davidson Current, late in January, there was a notable decrease in the warm-water types and an increase in cold-water species of *Chaetoceros* such as *C. debilis*, *C. decipiens*, *C. concavicornis*, and *C. radicans*. However, the dominant species was *C. didymus*, a eurythemic form, and the numerous warm-water diatoms and dinoflagellates still present gave the plankton a southern character. At the end of the month the cold-water forms were becoming more prominent and the warm-water species less abundant. By early February the plankton was dominated by several cold-water species of diatoms, of which *Chaetoceros debilis* was the most abundant, and the residual southern forms were all dead and represented only by scattered empty thecae. Evidently the cessation of the Davidson Current and the beginning of upwelling was irregular and intermittent instead of sharp and abrupt, since the latter part of the month the cold-water diatoms disappeared, the cosmopolitan *Chaetoceros didymus* became dominant, and several warm-water types returned, among them *C. peruvianus*, *Planktoniella sol*, *Ceratium platycorne*, *C. strictum*, etc.

March and April, as one might expect from the indication of slight surface inflow provided by the dip in the 13°C. isotherm in figure 2C, presented a fluctuating

pattern of alternating prominence by northern and southern forms, but by the middle of April the eurythermic cosmopolitan species were dominant and toward the end of the period these were being replaced by the neritic cold-water species *Chaetoceros radicans*, *C. concavicornis*, *C. decipiens*, and *Rhizosolenia styliformis*, while the warm-water species had almost disappeared. The situation thus approximated that of the previous May.

It seems clear from the above that there is indeed a significant transport of water from other areas into Monterey Bay, and that the general area of origin of this water may sometimes be indicated by the phytoplankton accompanying it. This is particularly the case during the Davidson Current period, but there is also clear evidence of surface inflows of oceanic water during the summer and fall, and occasionally at other times of the year.

The long-term trend.

While there appears to be no correlation between the long-term temperature trend and total plankton volumes, a few of the genera contributing to the phytoplankton do appear to fluctuate consistently with thermal factors. By far the best correlation is provided by *Ceratium*. During the colder years the relative numbers of the genus rose to comparatively modest peaks. Unfortunate interruptions in the winter data make it impossible to determine the prevalence of *Ceratium* in December, 1954, December, 1955, and January, 1956. However, there is no evidence in the preceding and succeeding months that any high degree of dominance was attained at those times. On the other hand, the warm years of 1957 and 1958 showed *Ceratium* attaining peaks in relative numbers which were greater and of longer duration. Whether this marked relative increase is a simple consequence of temperature is open to some question. It may possibly have been due to abnormally massive inoculations of organisms into a suitable environment, since the fall influx of oceanic surface water during 1957 and 1958 appears to have been greater than normal.

The response of other genera is not so clearly indicated. A perusal of figures 6 to 8 suggests that *Thalassionema*, *peridinium*, and *Noctiluca* may tend to develop more high peaks in relative abundance in warm years than in cold ones. Conversely, cold years appear to have been somewhat more favorable than warm ones for the development of *Thalassiosira*, *Stephanopyxis*, and *Coscinosira*.

COMMENT ON MONTEREY BAY AS A LOCATION FOR OCEANOGRAPHIC MONITORING

If the monitoring of the hydrographic features of the Monterey Bay area is of more than local significance, the results obtained should reflect in a broad way the oceanographic conditions and events occurring over an extensive segment of the eastern North Pacific. In fact they do. For example, evidence of upwelling in Monterey Bay is normally paralleled by evidence of upwelling along most of the coast of the

United States north of Point Conception. The extent of the phenomenon, and the possibility of using conditions in one central area as a rough indication of events in a wide region, is shown by the pattern of the isotherms in the Sea Surface Temperature Charts, Eastern Pacific Ocean, issued monthly by the U.S. Bureau of Commercial Fisheries' Biological Laboratory, San Diego, California. During the upwelling period at Monterey the isotherms typically enclose one or more cold upwelled water masses along shore, which extend from somewhere between Vancouver Island and Cape Blanco, Oregon, to the region of Point Conception; this shows that subsurface water is rising along a coastal stretch comprising some 15° of latitude. Particularly interesting is the situation depicted on the chart of February, 1960. During this month the appearance of two small patches of cold water indicated that the Davidson Current period was over. One, along shore and enclosed by the 52°F. isotherm, was centered on Cape Blanco; the other, circumscribed by the 54°F. isotherm, lay somewhat off shore and just south of Monterey Bay. Our records show the beginning of upwelling in January; the practically simultaneous appearance during the following month of similar temperature patterns in areas separated by almost 400 miles of coastline suggests that the time of onset of upwelling in Monterey Bay can be used to determine roughly the time at which upwelling begins along an extensive stretch of the coast north of Point Conception.

The Davidson Current is clearly indicated in the present study by the changing characteristics of the water. The drift bottle experiments performed by Scripps Institution of Oceanography have demonstrated, among other things, clearly that this current also is much more than a local phenomenon. In addition, the Sea Surface Temperature Charts, Eastern Pacific Ocean, show that the disappearance of completely circumscribed masses of cold water along shore and the shift of the isotherms to approach the coast at greater angles than during the summer, take place almost simultaneously along most of the coast north of Point Conception, and indicate the sudden reversal of the direction of water flow over a wide area.

Finally, it is gratifying to note that the observations in the Monterey Bay area, of the progressive elevation of the annual average surface temperatures culminating in the very warm year of 1958, corroborated very closely the results gained by the very much more extensive investigations that were reported in detail in the CalCOFI Report, VII, 1960.

Unfortunately, detailed data on the quantitative and qualitative fluctuations of phytoplankton populations over extended periods of time and in different areas are not available, and it is therefore impossible to assess the applicability of biological results gained in our area to a broader region. However, it may be worth while to point out the interesting parallels that are to be found in a comparison of the results reported by Balech (1960) on the phytoplankton of La Jolla during the period August, 1957 to May, 1958, with those gained by the same worker in his study of the Monterey Bay plankton during May, 1958 to

April, 1959 (Balech, 1959). While direct comparison between the conditions in one area with those prevailing in another area one year later can scarcely be claimed to have much validity, it may be pointed out that the entire time encompassed by both investigations fell within the limits of the unusually warm period of the long-term trend, and that the temperature patterns of the two years were similar. If, then, there is a repeated annual qualitative biological cycle, and if the character of the cyclic changes is similar along a wide stretch of coastline, one might expect the biological pattern at a given season of one year in one area to show some similarity to that of the same season in the subsequent year in another area. We actually find this to be the case.

Ignoring the difference of twelve months in time and considering only the seasons, we find the following situations prevailing at both La Jolla and Monterey Bay. The plankton was definitely of a warm-water type in December. In January the plankton became sparse and consisted of a mixture of warm- and cold-water organisms, the latter becoming more prominent in February and March. In April the plankton had a cold-water cast, but during May cosmopolitan types dominated, although there was a mixture of both warm- and cold-water forms. The data for June and July are not detailed enough at one or the other of the localities to permit a satisfactory comparison, but August brought an appreciable difference. At La Jolla the plankton was definitely of a warm-water type while the Monterey Bay plankton was dominated by cosmopolitan forms mixed with warm-water elements. The difference persisted and was even augmented through most of the autumn; the plankton at La Jolla retained its tropical character while cold-water forms became dominant in Monterey Bay in November. Considering the tenuous nature of a comparison between the marine populations of two different areas in two different years, the parallel occurrence of a characteristic warm-water flora in December and its subsequent progression through mixed plankton to dominance by cosmopolitan types with northern and southern admixture in May is worthy of note. It suggests that as more comparative information accumulates it may be possible to make a rough estimate of the probable character of the plankton in one area on the basis of detailed data collected at a distant monitoring station, at least during certain seasons.

SUMMARY

1. The marine climate along the coast of central California is characterized by three more or less well-defined seasons. These are the result of the alternating water flow induced largely by the prevailing winds. During the period of northwesterlies the surface water is driven to the south and offshore, and upwelling deep water replaces it. The subsequent period of calms is marked by a superficial inflow of oceanic surface water. In winter the southerly winds induce the Davidson Current which flows northward and impinges on the coast.

- The water during each of these seasons differs from that characteristic of other seasons by recognizable features of temperature and salinity.
2. The Davidson Current period (November to February) is marked by (1) an abrupt decrease followed by a continuing decline in surface temperatures, (2) homogeneous surface temperatures over Monterey Bay, (3) a thermal gradient of usually less than 1°C. between the surface and a depth of 50 m. throughout the bay, (4) temperatures at 50 m. at the high point of the year, and (5) surface salinities at the low point of the year.
 3. The upwelling period (February to September) is marked by (1) surface temperatures reaching the low point of the year, then rising to approach the annual high, (2) surface temperatures showing a spread of 1 to 3°C. or more in different parts of the bay, (3) a thermal gradient of 3°C. or more between the surface and 50 m., (4) temperatures at 50 m. reaching the low point of the year, and (5) surface salinities rising to the high point of the year and beginning to decline.
 4. The oceanic period (September and October) is marked by (1) surface temperatures at the high point of the year, and exhibiting a range of 2°C. or less in different parts of the bay, (2) persistence of a strong thermal gradient between the surface and 50 m., often with a clear thermocline, (3) temperature values at all levels from surface to 50 m. 2-3°C. higher than during the peak of upwelling, and (5) salinities tending to rise slightly.
 5. While the general pattern of seasons is repeated annually, marked differences do occur from year to year. These differences are discussed for each individual year during the period 1954-1960.
 6. In addition to a clear annual temperature cycle a much longer temperature trend is recognizable, which reached its warmest point in 1958.
 7. The phytoplankton undergoes an annual cycle of increase and decrease in standing-crop volume, with peak volumes tending to occur in June. The relationship between plankton volumes and such variables as nutrients, and direction and intensity of water flow are discussed. In general, high plankton volumes occur during periods of upwelling. It appears that steadiness of upwelling is a major factor influencing the magnitude of coastal plankton blooms: if upwelling is intermittent, coastal plankton volumes are high; if it is steady, volumes are lower, probably as a result of horizontal divergence of coastal surface waters rather than low production.
 8. The beginning of each marine season is marked by a rather abrupt increase in the taxonomic complexity of the phytoplankton, with many genera and species represented simultaneously in the catches. As the season develops, certain forms achieve dominance over the others, and the plankton becomes more homogeneous until the next season is ushered in.
 9. Different genera of phytoplankters reach peaks of relative abundance at different times of year (e.g., *Chaetoceros* during the upwelling period, *Rhizosolenia* during the Davidson Current period), and it appears that some genera may be indicators of the initial stages of upwelling or of influxes of oceanic surface water. During the Davidson Current period of 1958-59 the predominance of tropical forms indicates considerable transport of offshore southern water into Monterey Bay.
 10. There is no clear indication that total plankton volumes were influenced by the long-term temperature trend, but some of the individual genera, especially *Ceratium*, show a greater predominance during the warm years.
 11. The results obtained in the present studies of Monterey Bay and environs coincide with findings in other areas of the coast well enough to indicate the site is suitable for continued monitoring of oceanographic conditions.

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ESTIMATING THE SIZE OF A FISH POPULATION USING VESSEL SURVEY DATA

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INTRODUCTION

The methods described in this paper were developed to enable personnel of the Department of Fish and Game to estimate the population numbers of the Pacific sardine. The basic data required are the results of research surveys, e.g., those described in Radovich (1952), and standard age frequency data from the commercial fishery. A major prerequisite is that the species in question be vulnerable to the survey technique one year prior to the time it is recruited to the fishery. The technique has been presented orally to several research groups subsequent to its development in 1952, and the interest generated was the stimulus for the present brief report.

Originally, the symbols used for mortality and survival rates and for rates of exploitation were the same as those of Ricker (1948). However, since then, Ricker (1958) revised his symbols and, in addition, an international standard terminology for fishery dynamics has been proposed (Holt *et al.*, 1959). Because most fisheries biologists on the west coast of North America are familiar with Ricker's notation, I have used his revised notation (Ricker, 1958) whenever practicable. For those who prefer the standard terminology of Holt *et al.* (1959), I have placed a glossary of the terms I have used at the end of this paper and have compared them with the other two systems (Table 4).

REASON FOR SURVEYS

The size or availability of a population of pelagic fish is most difficult, if not impossible, to determine from catch data alone when the species is not distributed uniformly throughout its range, when the proportion of fish in different parts of its range varies greatly in different years, and when a fishery exists in only a small part of the species' range. Under these conditions, it is necessary to extend sampling for population density estimates beyond the range of the fishery to include the whole range of the fish.

METHOD

In most types of fish surveys designed to estimate relative abundance or population size, the statistic most readily obtained is the average catch-per-effort of the sampling gear used. The average catch-per-effort value from a given region is a relative density value and can be expressed as

$$\frac{\sum c_s}{\sum E} = D$$

where

c_s = catch by sampling gear,

E = sampling effort,

and

D = relative density.

This relative density value applies only to the region covered and sampled during the survey. One may think of this density value as being directly proportional to numbers of fish per square mile.

If D were the true density, represented by numbers of fish per square mile, the product of D and the area in square miles would be the total population size. However, in this case the product of the relative density D and the area (of the region sampled) is proportional to the true density and may be regarded as relative abundance when compared to similar values for other areas or to values of the same area at different times. This may be expressed as

$$DA = R$$

where

A = area,

and

R = relative abundance.

The relative abundance of a greater region is simply the sum of the relative abundances of the smaller regions. The relative abundance of the population is the sum of the relative abundances of all regions making up the range of the fish.

The relative abundance of the total population at a given time, t , divided into the relative abundance one year later, $t+1$, excluding additions to the population between the time intervals, gives the annual survival rate of the same combined year-classes, or

$$\frac{R_{t+1}}{R_t} = s$$

where

s = annual survival rate.

Within any given area, if the area is constant, the relative densities at two given times are proportional to relative abundance, and the survival rate is the ratio of the density at $t+1$ to the density at t , or

$$\frac{R_{t+1}}{R_t} = \frac{(D_{t+1})A_t}{D_t A_t} = \frac{D_{t+1}}{D_t} = s.$$

The survival rate thus calculated is some fraction that is less than unity, and the total mortality rate equals the difference between the survival rate and unity, or

$$a = 1 - s$$

where

a = total annual mortality rate from all causes.

The following relationships and definitions are after Ricker (*op. cit.*):

$$a = m + n - mn$$

where

m = annual fishing mortality rate if no natural mortality occurred,

n = annual natural mortality rate if no fishing mortality occurred,

and

a = total annual mortality rate.

By transposition of the above equation

$$m = \frac{a - n}{1 - n}$$

In addition, Ricker (*op. cit.*) gives the following relationships:

$$a = u + v,$$

$$i = p + q,$$

and

$$\frac{i}{a} = \frac{p}{u}$$

or

$$u = \frac{ap}{i}$$

where

u = rate of exploitation (fishing mortality rate when natural mortality occurs),

v = expectation of natural death (natural mortality rate when there is fishing mortality),

p = instantaneous rate of fishing mortality ($p = -\log_e(1 - m)$),

q = instantaneous rate of natural mortality ($q = -\log_e(1 - n)$),

and

i = instantaneous rate of total mortality ($i = -\log_e(1 - a)$).

The rate of exploitation u is the fraction of the total population N that is actually caught, or

$$u = \frac{C}{N}$$

where

C = commercial catch in numbers.

A HYPOTHETICAL EXAMPLE

Let us assume two hypothetical populations, as shown in Figure 1, in which the range of a fish population is divided into three regions: A, B, and C. In each situation the entire range of the population is surveyed, yielding 2,000 fish per standard-effort-

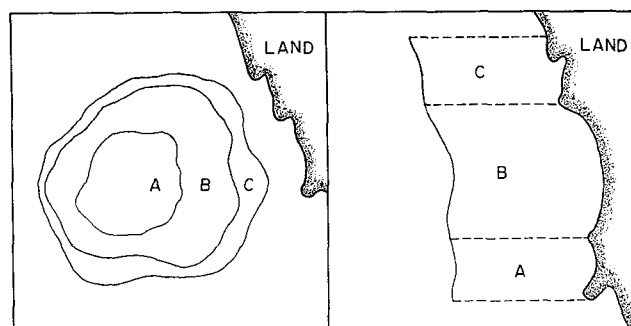


FIGURE 1. Two hypothetical fish populations, each divided into three regions: A, B and C. The population on the left is associated with an offshore bank; the one on the right is distributed along the coast. The method described in the text is applicable to either situation.

unit in region A, broken down by ages as 1,000 two-year-olds, 500 three-year-olds, 300 four-year-olds, 150 five-year-olds, and 50 six-year-olds. Region B yielded 400 twos, 200 threes, 125 fours, 75 fives and 25 sixes, for a total of 825 fish per unit of effort. Region C yielded 100 twos, 50 threes, and 20 fours and older, for a 170 fish total. The data may be summarized as in Table 1.

Let us assume that region A encompassed 300 square miles of habitat for the species being considered, region B encompassed 650 square miles, and region C, 325 square miles. Since catch-per-effort values of Table 1 are relative densities, when multiplied by square miles they become relative abundance values ($DA=R$). Thus, a comparable table of relative abundance may be constructed (Table 2).

TABLE 1
Hypothetical Catch-per-effort from Survey by Age

Region	Twos	Threes	Fours and Older	Total
A.....	1,000	500	500	2,000
B.....	400	200	225	825
C.....	100	50	20	170

From Table 2, total (x) shows the relative abundance of fish of each age with respect to the others and total (y) shows the relative abundance of fish of all ages in each region. Let us assume that this

TABLE 2

Relative Abundance by Age (Hypothetical Example)

Region	Twos	Threes	Fours and Older	Total (y)
A.....	300,000	150,000	150,000	600,000
B.....	260,000	130,000	144,250	534,250
C.....	32,500	16,250	6,500	55,250
Total (x).....	592,500	296,250	300,750	1,189,500

TABLE 3

Relative Abundance by Age (Hypothetical Example)

Year	Twos	Threes	Fours and Older	Total
1st (Total (x) from Table 2).....	592,500	296,250	300,750	1,189,500
2nd.....	473,000	362,000	240,000	1,255,000

survey is repeated at the same time in the same manner during the next year; the results are as indicated in Table 3. We can then calculate the survival rate of fish between ages two and three as follows:

$$\frac{362,000}{592,500}$$

The annual survival rate of fish older than age two is

$$\frac{240,000}{296,250 + 300,750}$$

or

$$\frac{R_{t+1}}{R_t} = s.$$

The survival rates thus calculated are 0.611 between ages two and three, and 0.402 for the older fish. Since $a = 1 - s$, the total annual mortality rate for fish between ages two and three is $a = 1 - 0.611 = 0.389$, and for fish older than two years is $a = 1 - 0.402 = 0.598$.

If for some reason (gear selection, fish habits, or other factors) the fish are not available to the fishery before they are three years old, and provided that we can assume the natural mortality rate between ages two and three represents the annual natural mortality rate of older fish,

then

$$n = 0.389$$

and

$$a = 0.598,$$

and since

$$m = \frac{a - n}{1 - n},$$

then

$$m = \frac{0.598 - 0.389}{1 - 0.389} = \frac{0.209}{0.611}$$

or

$$m = 0.342.$$

From Ricker's tables (1958), $i = 0.91125$ corresponds to $a = 0.598$, and since p bears the same relationship to m as i does to a , one can find a p value corresponding to $m = 0.342$ by locating 0.342 on the a column and reading $p = 0.4185$ from the i column. The rate of exploitation of u is then calculated as follows:

$$u = \frac{ap}{i} = \frac{(0.598)(0.4185)}{0.91125},$$

or

$$u = 0.2746,$$

and since

$$N = \frac{C}{u}$$

the population can be calculated if the catch data (numbers of fish taken by the commercial catch) are available. If, for example, the catch was 500,000 fish in the season between surveys, then

$$N = \frac{C}{u} = \frac{500,000}{0.2746}$$

or

$N = 1,820,000$ fish that were three years old and older. The total population of fish three years old and older would be 1,820,000 (or 1.82 million) at the beginning of the first year. The total population at t of fish two years old and older, N_{2+} , bears the same relationship to the population of fish three years old and older, N_{3+} , as the relative abundance of fish two and older, R_{2+} , does to the relative abundance of fish three and older, R_{3+} , or at t

$$\frac{N_{2+}}{N_{3+}} = \frac{R_{2+}}{R_{3+}}$$

or

$$N_{2+} = \frac{(R_{2+})(N_{3+})}{R_{3+}}$$

The population in the first year t , including two-year-old fish, N_{2+} , would then be

$$N_{2+} = \frac{(1,189,500)(1,820,000)}{296,250 + 300,750}$$

or

$$N_{2+} = 3,626,281$$

or 3.63 million fish are past their second year of life. The population of age two and older fish in the second year, $t+1$, may be calculated by the equation

$$N_{t+1} = \frac{(R_{t+1})(N_t)}{R_t}$$

where

N_t = total population in the first year (N_{2+} at t),

N_{t+1} = total population in the second year,

R_t = total relative abundance in the first year,
and

R_{t+1} = total relative abundance in the second
year.

Substituting into the equation we get

$$N_{t+1} = \frac{(1,255,000)(3,626,281)}{1,189,500}$$

and

N_{t+1} = 3.83 million fish two years old and older
in the population at time $t + 1$.

ALTERNATE METHOD

An alternate formula for calculating population size more directly, by using common logarithms, can be derived in the following manner:

since

$$s = e^{-i} = e^{-(p+q)},$$

the survival rate of younger fish that are not vulnerable to the fishery s_y can be expressed as

$$s_y = e^{-q}.$$

It then follows that

$$q = -\log_e s_y$$

and

$$p = \log_e s_y - \log_e s.$$

By combining the equations

$$N = \frac{C}{u}$$

and

$$u = \frac{ap}{i}$$

and substituting for i , a and p , we get

$$N = \frac{C(-\log_e s)}{(1-s)(\log_e s_y - \log_e s)}$$

or

$$N = \frac{C(\log_e s)}{(s-1)\log_e (s_y/s)}.$$

Finally, since the natural or Napierian logarithm of a number is equal to that number's common logarithm times a constant, we may substitute the equivalent common logarithms and their constants into the equation. The constants cancel out and we end up with

$$N = \frac{C(\log_{10} s)}{(s-1)\log_{10} (s_y/s)}.$$

In the hypothetical example given previously, the survival rate for the younger (non-vulnerable) fish was 0.611, and for the older (vulnerable) fish, it was 0.402. By substituting these values, and the value for the number of fish in the catch (500,000), into the formula, we may solve for the population size directly:

$$N = \frac{500,000 \log_{10} 0.402}{(0.402 - 1) \log_{10} \left(\frac{0.611}{0.402}\right)}.$$

We need only to substitute the values for the common logarithms and complete the calculations to find

$$N = 1.82 \text{ million fish,}$$

which is the same value we previously obtained, for the population size at the beginning of the first year.

ASSUMPTIONS

The accuracy of this method in approximating a real population is dependent upon the degree to which the equations describe actual phenomena. A perfect fit of this method into a real situation implies that a number of assumptions will be met. Following are some of the more apparent ones:

1. The entire population is an entity that will not change by movement out of or into the range of the survey, *i.e.* the survey encompasses the range of the population.
2. Natural mortality is distributed evenly throughout the year.
3. Fishing mortality is distributed evenly throughout the year. This condition may not be met in an actual fishery. However, if the "fishing year" is adjusted so that the fishing period is in the middle of that year, the error will be minimized.

4. The survey randomly samples the population and its catch-per-effort is proportional to the true population density.
5. The observed natural mortality rate of the young fish is approximately the same for older fish in the population.
6. Other mortality caused by fishing, in addition to the amount landed, is negligible.
7. Age reading is accurate.
8. Catch figures are reliable and the conversion from weight to numbers is valid.

TABLE 4

GLOSSARY OF SYMBOLS AND DEFINITIONS
Compared with those of Ricker (1958) and Holt *et al.* (1959)

Symbols Used	Definition	Ricker (1958)	Holt <i>et al.</i> (1959)
c_s	Catch by sampling gear		
E	Sampling effort		
D	Relative density $(D = \frac{\sum c_s}{\sum E})$		
A	Area sampled or covered by survey		
R	Relative abundance in area covered ($R = DA$)		
t	Time (a subscript indicating a specific time)	t	t
m	Annual fishing mortality rate if no natural mortality occurred ($m = 1 - e^{-p}$)	m	$1 - e^{-F}$
n	Annual natural mortality rate if no fishing mortality occurred ($n = 1 - e^{-q}$)	n	$1 - e^{-M}$
u	Annual rate of exploitation (fishing mortality rate when natural mortality occurs; $u = ap/i$)	u	$E; (1 - S) \frac{F}{Z}$; unconditional fishing mortality rate
v	Annual expectation of natural death (natural mortality rate when there is fishing mortality; $v = aq/i$)	v	$D; (1 - S) \frac{M}{Z}$; unconditional natural mortality rate
a	Total annual mortality rate from all causes ($a = 1 - s$; $a = u + v$; $a = m + n - mn$)	a	$(1 - S); 1 - e^{-Z}$
p	Instantaneous rate of fishing mortality ($p = -\log_e (1 - m)$)	p	F ; fishing mortality coefficient
q	Instantaneous rate of natural mortality ($q = -\log_e (1 - n)$)	q	M ; natural mortality coefficient
i	Instantaneous rate of total mortality ($i = -\log_e (1 - a)$; $i = p + q$)	i	Z ; $-dN/Ndt = F + M$; total mortality coefficient
s	Annual survival rate ($s = e^{-i}$)	s	$S; e^{-Z}$; fraction surviving
s_y	Annual survival rate for fish which are not yet vulnerable to the fishery		
C	Total catch by the fishery in numbers	C	C
N	Number of fish in the population	N	N

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CONTRIBUTION TO THE BIOLOGY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS* (AYRES)¹

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INTRODUCTION

Although Pacific hake give promise of being one of the most abundant fishes indigenous to the continental shelf of western North America, little or nothing has been published on their biology, although their taxonomy has been fully covered (Ginsburg, 1954). In the course of investigating bottomfish, personnel of the California Department of Fish and Game have made routine observations on all fish sampled. A recent compilation of these accumulated facts, plus examination of the literature on Pacific hake are the basis of this paper.

To the present time, only limited use has been made of the Pacific coast hake. In contrast, most, if not all other species of *Merluccius* in the world, are harvested on a far larger scale. Fritz (1960, p. 2) reports 170 million pounds of silver hake (*M. bilinearis*) landed at the ports of eastern United States. California landings have been about one million pounds annually (Paul, 1961, p. 31); most of these were unloaded at northern California ports and used for animal food. However, when more desirable fish have been scarce, hake have been prepared for the fresh-fish markets in limited amounts. North of California hake are present but become increasingly scarce in the landings.

RANGE

The recorded range for Pacific hake is from the Gulf of Alaska (Wilimovsky, 1954, p. 283) south to the Gulf of California (Starks & Morris, 1907, p. 241). This is roughly the limit of the south boreal region of the eastern Pacific Ocean described by Rass (1959). From sampling the adult population by the commercial fishing fleet, their indicated center of abundance is in northern California. The lack of a fishery that would harvest them off southern California may have biased this location to a considerable degree. This is pointed out by the Nissan Fisheries Institute (1937, p. 57) who stated that hake were abundant and a common food fish in Mexican waters. Their report was based upon fishing trials conducted by Japanese trawlers off the Pacific coast of Mexico during 1935 and 1936. Juvenile hake have been collected by the California Department of Fish and Game in the vicinity of Cedros Island, Baja California.

Routine plankton hauls made by the California Cooperative Oceanic Fisheries Investigations have revealed large numbers of hake larvae over the entire area surveyed from San Francisco, California to Cape San Lucas, Baja California, and offshore for at least 350 miles (Ahlstrom & Counts, 1955, p. 312).

¹ Submitted for publication, January, 1962.

Their greatest abundance, however, was between Point Conception, California, and San Quintin, Baja California. This location may also have been biased since their collections were made in regions of known sardine (*Sardinops caerulea*) spawning and may not have covered the true spawning range of hake.

SIZE OF FISH

In Commercial Landings

Surveillance of animal food landings and a survey of the ecological relationship of various species entering the otter trawl catch have provided 4,644 total length measurements. These measurements have been collected annually since 1950 at all ports from Eureka to Santa Barbara. The hake length frequencies were plotted separately by port and in each instance, the distribution was almost identical. The fish began entering the catch regularly at a length of about 45 cm; the mode of each distribution was at 57 cm, and the largest individuals at each port were 78 to 80 cm. Some fish smaller than 45 cm appeared in the catch at sporadic intervals. Only at Santa Barbara were fish shorter than 45 cm present to any degree; about 20 percent of the 217 fish sampled there were of that size. The maximum length recorded was 80 cm.

Since there was no size differential between ports, measurements for all ports were combined, grouped by 2 cm intervals, and plotted (Fig. 1).

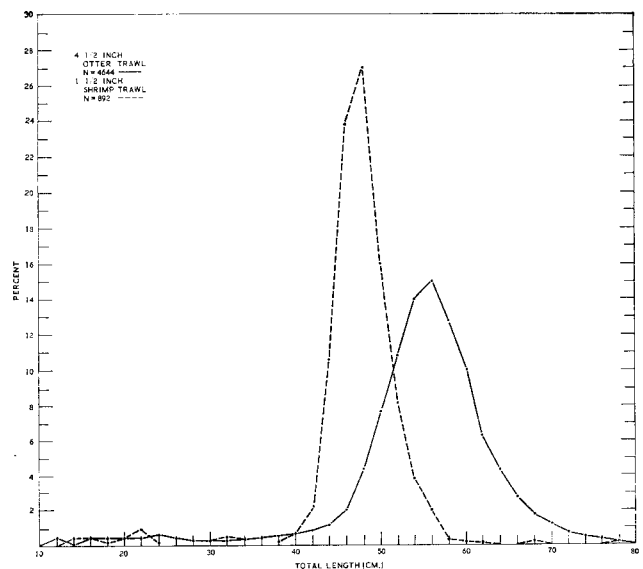


FIGURE 1. Length-frequency distributions of Pacific hake taken by 4½-inch otter trawl nets and 1½-inch shrimp trawls. Shrimp trawl data from Morgan and Gates (1961).

Otter trawl vessels are required to use nets with 4½-inch (inside the knots) mesh. This relatively large mesh selects only the larger hake that are accessible on the fishing grounds. It is obvious that hake do not become completely vulnerable to commercial otter trawls until they are 57 cm long.

Morgan and Gates (1961, p. 106) recorded the total lengths of hake caught off southern Oregon and northern California in shrimp trawls using 1½- and 1⅝-inch mesh cod-ends. Length frequencies of 892 of their hake have been handled in an identical fashion as our otter trawl measurements and plotted (Fig. 1). Their data substantiate our conclusion that hake enter the catch when they are about 45 cm long. However, the small mesh they used caught more small fish, so their mode was at 49 cm, and large fish (longer than 60 cm) were relatively scarce. One hake they reported was 78 cm long corresponding with the maximum size taken in our otter trawl fishery. This indicated that the larger fish were able to avoid the shrimp nets, which were also unsuccessful at taking smaller hake although the 1½-inch mesh used in them should have retained fish much smaller than 45 cm, if they were accessible. In fact, these same nets retained rex sole (*Glyptocephalus zachirus*) as small as 8 and 9 cm. Hickling (1933, p. 71) reported European hake (*M. merluccius*), about 30 cm long, were completely retained by trawl nets with 80-mm mesh (about 3¼-inches).

Investigations have revealed that European hake are not available on the bottom in large numbers until the end of their second year of life, at a length of about 20 cm (Hickling, *ibid.*, p. 50). A similar situation may prevail on our coast so that hake are not available in numbers to bottom-fishing trawls until they are 40 cm long. Hake killed by explosives fired near the surface in geophysical explorations off our coast during 1961 were uniform in length, ranging from 38 to 48 cm. Some small fish were found in our samples from the otter trawl fishery; the smallest was 12 cm long but only 129, or 2.8 percent, of the 4,644 measured were shorter than 40 cm.

SIZE BY SEX

Some of the hake sampled from San Francisco (1,194), Fort Bragg (173), and Eureka (547) were sexed. The ratio of males to females was 1: 1.9 at San Francisco, 1: 2.4 at Eureka, and at Fort Bragg all hake in the sample were females. The familiar picture of females reaching a larger size than males is exhibited by hake. The maximum size for males was 66 cm and for females it was 76 cm. Fish as long as 80 cm were measured but not sexed. There were no differences in the length frequencies of males or females between ports so the measurements were combined by sex, grouped by 2 cm intervals and plotted. The modal length for males was 55 cm and for females 59 cm (Fig. 2).

SIZE AT MATURITY

From the limited number of small fish observed it has been difficult to determine with any accuracy the

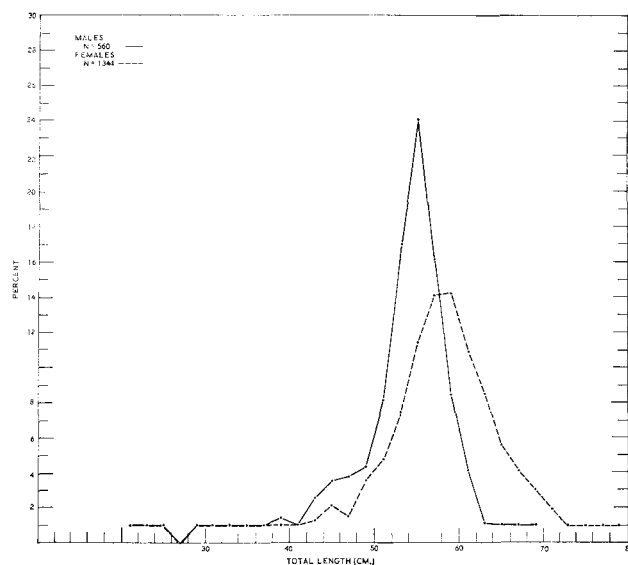


FIGURE 2. Length-frequency distributions of male and female Pacific hake in California landings.

size at which hake mature. Both male and female fish which were over 40 cm were mature. Only one fish shorter than 40 cm, a female 38 cm long, was mature. This fish was observed during October and, although the ovary was filled with maturing eggs, it was small. Obviously it was the first maturity for this specimen. Based on our limited observations, maturity appears to take place at a length of about 40 cm for both males and females.

LENGTH-WEIGHT RELATIONSHIP

A sample of 58 female Pacific hake, collected at Santa Barbara and Morro Bay, October 17-18, 1961, was used to compute a length-weight relationship. Measurements were made to the closest two mm on a flat measuring board and weights were determined within 1/64-pound on a five pound capacity Chatillon spring scale. Two individuals which exceeded the capacity of the scale were weighed on scales available at the processing plant. Weights were converted to hundredths of a pound.

The formula for female Pacific hake was calculated to be $\text{Weight (lbs.)} = 0.0000115 \text{ Length (cm)}^{3.06682}$ or $\log W = 3.06682 \log L - 4.95216$.

The average lengths and weights of hake, sexes combined, processed for animal food are available for the past five years. These data correspond with the calculated line for female hake (Fig. 3).

AGE DETERMINATIONS

No age determinations have been made in the past. However, studies currently under way indicate that otoliths are satisfactory for determining age. Otoliths have been used with fair success for determining the ages of *M. merluccius* (Hickling 1933, Bagenal 1954, and Figueras (1955) and *M. hubbsi* (Angelescu *et al.* 1958). Scales of the Pacific hake are highly deciduous

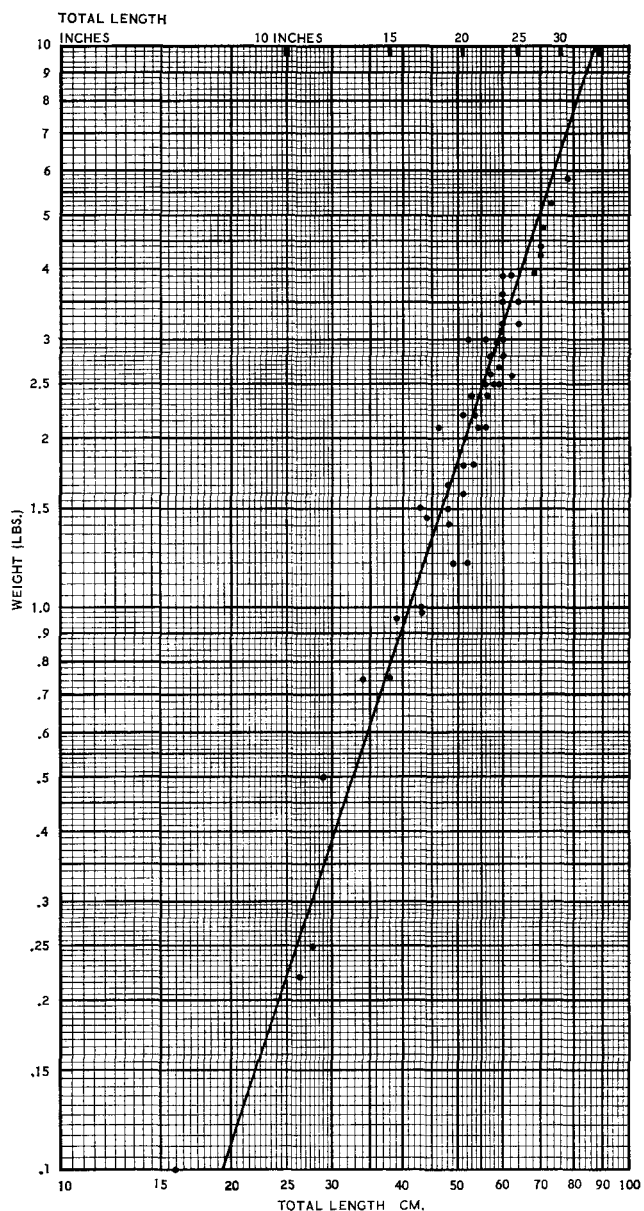


FIGURE 3. Length-weight relationship of Pacific hake. Solid line calculated from a sample of 58 female hake collected at Santa Barbara and Morro Bay, October 17-18, 1961. Dots represent average lengths and weights obtained while sampling the animal food landings.

and nearly impossible to find in trawl caught fish. Consequently, no attempt was made to use scales in age work.

Otoliths were collected during October and November, 1961, to supplement otoliths already on hand. All collections were made during winter months (October-February). Thus in many cases the annulus had not yet been formed. However, for the purposes of this paper, ages were calculated as if the annulus had been formed. That is, most of the fish listed here as one-year-olds had as yet not completed one full year of life. This method necessarily biases the average size at any age in a negative manner, particularly the younger ages.

Age determinations were made on otoliths from 464 hake. Sexes were combined for age groups I, II, and III; for the older age groups males were very scarce in the fishery at the time the otoliths were collected and were not used in age determinations. Therefore, groups IV and older represent female growth characteristics only (Fig. 4 and Table I).

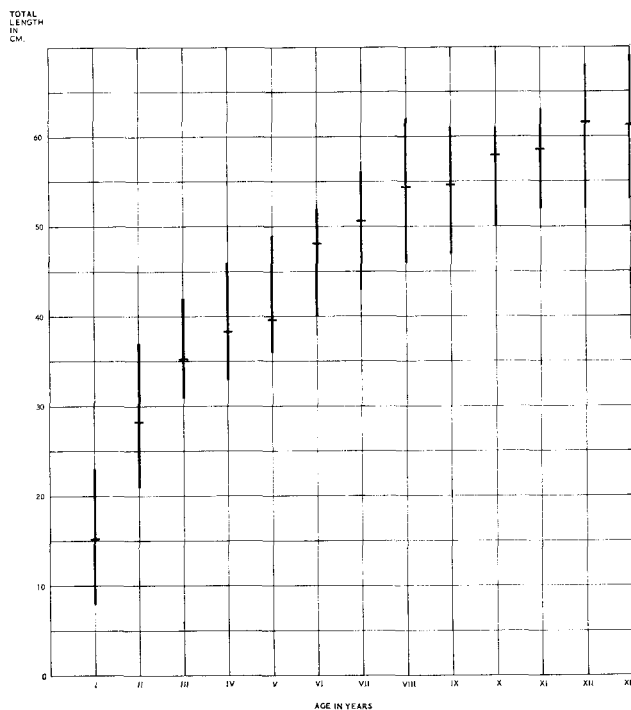


FIGURE 4. Growth curve of Pacific hake. Age groups I, II, and III represent combined sexes; age groups IV and older represent females only. Average size and range is shown for each age group.

As reported in the section on maturity, all hake over 40 cm were mature and only one fish shorter than 40 cm was observed to be mature. This means that the larger three-year-old fish and most of the four-year-olds would spawn. The mature 38 cm specimen was three years old.

TABLE I

Average total lengths of Pacific Hake by Age

Age	Number	Average Length (Cm)	Size Range (Cm)
I	186	15.5	8-23
II	93	27.4	21-37
III	91	35.4	31-42
IV	9	38.7	33-46
V	10	39.8	36-49
VI	9	48.1	40-52
VII	9	50.8	43-56
VIII	14	54.4	46-62
IX	10	54.5	47-61
X	10	57.9	50-61
XI	10	58.6	52-63
XII	7	61.6	52-68
XIII	6	61.3	53-69

DISTRIBUTION IN SPACE AND TIME

Space

Information on depth of capture is available for some of the samples collected at San Francisco and Eureka. At San Francisco, 96 percent of the sampled hake came from 124 fathoms or shallower, with 41 percent from water 50-74 fathoms deep. At Eureka, 88 percent were caught at depths shallower than 99 fathoms, with 43 percent in 25-49 fathoms. The remaining fish in both areas had been scattered throughout the deeper water with a small concentration at 175-199 fathoms. The deepest catch for both areas was from 275-299 fathoms (Table II). In all cases, the hake from the deeper areas were taken during the winter, coinciding with the spawning season as indicated by the occurrence of larvae (Ahlstrom & Counts, *op. cit.*, p. 312).

TABLE II

Depth distribution of 1,986 Pacific Hake at four localities

Depth Fathoms	Eureka		San Francisco		Monterey		Morro Bay	
	No.	Percent	No.	Percent	No.	Percent	No.	Percent
0-24	2	1	178	14	0	0	0	0
25-49	122	43	340	27	105	54	0	0
50-74	84	29	524	41	20	6	18	26
75-99	44	15	131	10	10	3	33	48
100-124	1	tr	51	4	31	9	18	26
125-149	1	tr	3	tr	5	1	0	0
150-174	5	2	3	tr	102	28	0	0
175-199	14	5	31	2	0	0	0	0
200-224	4	2	1	tr	0	0	0	0
225-249	8	3	1	tr	0	0	0	0
250-274	0	0	2	tr	0	0	0	0
275-299	2	1	2	tr	0	0	0	0
Total	287	101	1,267	98	363	98	69	100

Alverson (1951; 1953) reported taking a few hake as deep as 300-304 fathoms off Washington. Hake have been reported as deep as 491 fathoms off California (Clemens & Wilby, 1961, p. 163).

Much of our information indicates hake inhabit the relatively deep water of the continental shelf and beyond. However, this does not prevent them from chasing their prey on the surface and even into the surf where they become stranded (De Witt, 1952, p. 438). Van Hyning and Ayers (1960, p. 5) reported observing hake in brackish water within the Columbia River estuary.

Although hake have been recorded from these extreme depths, by far the greatest bulk has been taken from the bottom or near-bottom areas of the continental shelf. Experimental mid-water trawling has resulted in large catches of nearly pure hake but these have been rather sporadic. Schaefer and Powell (1958, p. 9) reported catching 5,500 pounds, mostly hake, in a 20-minute mid-water trawl. They also show Sea Scanar recorder traces of hake and rockfish (*Scorpaenidae*) that were located off Washington and British Columbia. During daylight hours there is a definite layer of fish from near the bottom to about 15 fathoms above the bottom. At night this

layer was much higher in the water and more scattered. A similar diurnal movement has been noted in the hake fisheries of the Atlantic Ocean and has been associated with feeding.

Time

At Eureka hake were relatively scarce during January-March, making up less than one percent of the sample, and reached their peak abundance during July-September (55 percent). The sequence at San Francisco was similar: one percent of the fish were taken during January-March and 52 percent during July-September. Small samples from Fort Bragg and Morro Bay indicated peak abundance at these local-

TABLE III

Occurrence, by quarter-year periods, of Pacific Hake in Otter Trawl samples at five California ports

Port	Jan.-Mar.		Apr.-June		July-Sept.		Oct.-Dec.		Total	
	No.	Per- cent	No.	Per- cent	No.	Per- cent	No.	Per- cent	No.	Per- cent
Eureka	6	tr	730	29	1,401	56	367	15	2,504	100
Fort Bragg	0	0	63	72	21	23	4	5	88	100
San Francisco	13	1	635	40	833	52	111	7	1,592	100
Monterey	0	0	200	55	63	17	100	28	363	100
Morro Bay	2	3	38	55	16	23	13	19	69	100

ities during April-June (Table III). There has not been enough sampling at Santa Barbara to determine seasonal abundance. Fish kills made during geophysical explorations off northern California tended to corroborate these data. Hake first appeared near Eureka during April and were last observed off Crescent City during August. On these surveys hake were observed only between Drakes Bay (near San Francisco) and Crescent City.

INTERSPECIFIC RELATIONS

Hake as a Predator

The food habits of hake have not been the object of any intensive study. However, some random observations on several hundred fish have been recorded. Hake apparently are opportunists, feeding on whatever is present.

Juvenile hake have been found gorged with pelagic red crabs (*Pleuroncodes planipes*), euphausiids, and small squid (*Loligo opalescens*). Stomachs of adult hake have contained anchovies (*Engraulis mordax*), small hake, queenfish (*Seriphus politus*), sanddabs (*Citharichthys* spp.), slender sole (*Lyopsetta exilis*), curlfin turbot (*Pleuronichthys decurrens*), euphausiids, the clam (*Solemya panamensis*), pink seaperch (*Zalembius rosaceus*), and large squid (Fitch, personal communication). Van Hyning and Ayers (*op. cit.*) and De Witt (*op. cit.*) reported that hake feed heavily on anchovies at times. In some cases they chase their prey into the surf with such abandon that they have been stranded by a falling tide.

The above cases represent only a few random observations and do not represent any qualitative or quantitative food habits study.

Hake as Prey

The large number of hake larvae that have been caught in the CCOFI nets indicate that this species is a handy food item for larger predatory fishes. Our observations have revealed that young hake often are food for several species of rockfish, and albacore tuna (*Thunnus germon*) feed regularly on zero age group hake. Large hake, arrowtooth flounders (*Atheresthes stomias*), and a bigmouth sole (*Hippoglossina stomata*) have been observed with young hake in their stomachs.

Adult hake have been found in the stomachs of Pacific lancetfish (*Alepisaurus richardsoni*), California bluefin tuna (*Thunnus saliens*), sablefish (*Anoplopoma fimbria*), lingcod (*Ophiodon elongatus*), soupfin shark (*Galeorhinus zyopterus*), great white shark (*Carcharodon carcharias*), and an electric ray (*Torpedo californicus*). Hake otoliths have been identified among the stomach contents of several marine mammals, including California sea lions (*Zolophus californianus*), an elephant seal (*Mirounga augustirostris*), Pacific white-sided porpoises (*Lagenorhynchus obliquidens*), and a Dall porpoise (*Phocoenoides dalli*) (Fitch, personal communication; Ripley, 1946).

Use

The animal food fishery in California started in 1953 and has been expanding each year. This industry has been the principal hake user in California (Best, 1959; 1961). In Oregon, hake have not been used to as great an extent for animal food because there is a tendency for hake-fed mink to become anemic and to lack pigment in the underfur, making their pelts valueless. A new process has been developed in which hake are subjected to a heat and acid treatment, making them much better mink food (Adair *et al.*, 1960; 1961).

Hake have also been used to some extent for pet food and in experimental diets at fish hatcheries operated by California, Oregon, and U.S. Fish and Wildlife Service. In most instances, the results at hatcheries were favorable; however, anemia did occur in some cases. These tests have been reported by Wales (1944), Burrows *et al.* (1951), Robinson *et al.* (1951), Hublou *et al.* (1955), and Jeffries *et al.* (1954). Jones (1959, p. 8) estimated that 50-60 million pounds of hake could be harvested annually from Pacific Northwest waters.

During World War II some experiments were carried out by the Oregon Agricultural Experiment Station to determine the Vitamin A content of hake liver and viscera. Large numbers of hake had been noted off the Oregon coast and some 1,500 pounds of hake livers were landed for experimentation. These tests indicated 1.65 million units of Vitamin A per pound of liver and 0.34 million units of Vitamin A per pound of viscera (Sinnhuber & Law, 1948). The Fisheries Research Board of Canada ran tests on an eight

pound sample of hake liver and found the liver to contain 31.5 percent oil and 6,000 U.S.P. units of Vitamin A per gram (Bailey, 1943).

No references could be found on the reduction of hake. Jones (*op. cit.* p. 5) indicated hake have a moisture content of 80 percent and a fat content of one to two percent. Fish meal made from Alaska pollock, *Theragra chalcogramma*, a species similar to hake, had a yield of only 10 to 12 percent (Wigutoff & Carlson, 1950, p. 72). This meal had a protein content of about 62 percent. Moisture content of pollock was 79 percent according to Landgraf, (1953).

SUMMARY

1. Although Pacific hake are relatively abundant on the Pacific Coast of North America, little use is currently made of them. About one million pounds are landed annually in California.
2. Commercial otter trawl fishing now accounts for the bulk of the catch. The fish begin entering the catch regularly at a size of 45 cm; the largest encountered was 80 cm.
3. Pacific hake females reach larger sizes than males.
4. The length-weight relationship for female Pacific hake was determined to be $W=0.0000115(L)^{3.06682}$, where W=weight in pounds and L=total length in cm.
5. Otoliths of Pacific hake are satisfactory for age determinations.
6. Hake were found all the way from the surf and estuarine waters to as deep as 491 fathoms.
7. The greatest concentrations vulnerable to the otter trawl fishery occur during the summer months. Few specimens are captured during the winter.
8. The large number of larval and juvenile hake makes them definite contributors to the food chain. Adult hake are also very efficient predators.
9. The animal food industry is the greatest user of hake at this time. Experimental work has been done on the use of hake as fish hatchery foods and as a source of Vitamin A.

ACKNOWLEDGMENT

John E. Fitch, California Department of Fish and Game, supplied most of the observations on hake food habits and age and identified the otoliths in the stomachs of the marine mammals. In addition, he contributed valuable editorial assistance for which I am grateful.

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PLANKTON VOLUME LOSS WITH TIME OF PRESERVATION

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The investigation of plankton volume decrease with time of preservation is an outgrowth of an investigation into the constituent composition of plankton samples collected in 1957, a year of marked change in the seasonal pattern of plankton volumes surveyed on cruises of the California Cooperative Oceanic Fisheries Investigations (Thraillkill 1959, pp. 4-8). The constituent study on the 1957 samples was begun about a year after the samples had been collected and the initial volume determinations made. It was soon noted

The difficulty in duplicating plankton volume measurements had been noted as early as 1949, but the magnitude of the volume loss was not appreciated until the systematic remeasuring of volume was begun on the 1957 collections.

The non-replicability of volume measurements stimulated us to make a quantitative study of plankton volume change with time of preservation. The investigation was carried out on a group of 12 test samples, (Table 1) selected to provide a variety of con-

TABLE 1. COLLECTION DATA FOR PLANKTON HAULS USED IN VOLUME LOSS STUDY¹

Cruise	Station	Position		Date (1959)	Hour P.S.T.		Vol. water strained (m. ³)	Depth of haul (m.)	Depth of water at station (fms.)	Temp. at 10 m. Depth °C
		Lat. N.	Long. W.		Start	End				
5902	110.33	29°50.5'	115°52.2'	II-14	1248	1257	279	0-84	50	16.3
	110.65	28°46.5'	117°59'	II-13	1911	1926	492	0-141	1800	17.3
	113.30	29°22.5'	115°17.5'	II-14	1732	1737	194	0-50	30	—
	113.40	29°02'	115°58.5'	II-14	2231	2246	475	0-142	960	16.8
	113.50	28°42'	116°37.5'	II-15	0526	0541	487	0-142	1750	17.1
	120.35	28°03'	114°54'	II-17	1253	1301	282	0-58	45	16.9
	123.42	27°17.2'	115°00.3'	II-19	1846	1901	465	0-140	650	18.3
	130.35	26°19'	113°48.5'	II-21	2216	2230	478	0-138	140	18.8
	133.30	25°55'	113°07.6'	III-22	0920	0934	472	0-141	104	19.0
5903	107.50	29°50.5'	117°23.5'	VII-27	0831	0846	513	0-137	1450	19.3
	107.55	29°40.3'	117°43'	VII-27	0546	0601	508	0-133	1600	20.2
5907	110.90	28°01'	119°36'	VII-26	0216	0231	544	0-130	2050	21.2

¹ Hauls taken obliquely with a standard CalCOFI plankton net, 1.0-meter in diameter at mouth, approximately 5 meters in length, and constructed of No. 30xxx grit gauze.

that the earlier plankton measurements could not be duplicated. Most samples not only contained a lesser volume than that which had been obtained earlier, but percentage decreases were much greater in samples in which non-crustacean plankters predominated.

stituent compositions. Volumetric measurements were made on the live collections, on the samples immediately after preservation, and at intervals thereafter until the samples showed little or no further decrease in volume with time; i.e. had reached their stable preserved volumes. The time spacing of observation was empirically determined by the rates of change observed (Table 2).

¹ This paper is a revised version of a manuscript presented at the ICES Symposium on Zooplankton Production, 1961 as contribution no. 12. Abstract in Rapp. et Proc.-Verb. 153:78.

TABLE 2. MEASUREMENTS OF VOLUMES OF 12 PLANKTON SAMPLES TO DETERMINE CHANGE IN VOLUME WITH TIME (in milliliters)

Cruise	Station	Before pres.	After pres.	Days after preservation						Months					
				1	2	3	7	10	16	20	1	2	4	12	24
5902	110.33	—	38	38	37	37	37	37	35	35	35	35	35	35	35
	110.65	57	47	30	30	30	—	24	24	24	24	24	24	20	20
	113.30	12	10	10	10	10	10	10	10	10	10	10	10	10	10
	113.40	50	42	40	39	—	—	35	35	35	34	34	34	32	32
	113.50	84	63	38	—	—	—	35	34	33	33	33	33	32	32
	120.35	13	12	12	12	—	11	11	11	11	11	11	11	11	11
	123.42	129	61	41	39	—	29	26	26	26	26	24	24	23	23
	130.35	25	19	15	15	—	13	13	13	13	13	13	13	12	12
	133.30	48	34	25	25	25	25	25	25	25	25	25	25	24	24
5903	107.50	93	60	37	—	30	23	21	20	18	17	15	14	13	*12
	107.55	42	26	16	16	16	15	14	13	13	13	13	12	10	*10
5907	110.90	77	48	38	35	33	31	31	31	31	30	30	29	28	*27

* 22 months after collection.

After the samples had attained comparative stability with respect to volume loss, they were intensively analyzed in order to relate volume loss to the constituent compositions of the test samples. The percentage composition by volume of the major groups of plankton organisms in each test sample was determined;

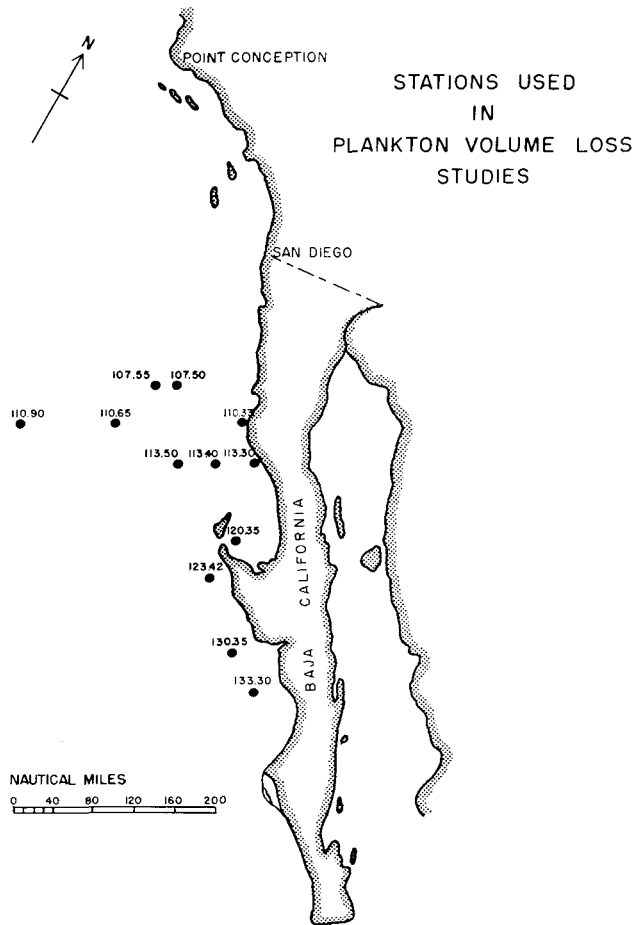


FIGURE 1. Stations at which samples were taken for plankton volume loss studies.

the kinds (species) of organisms were identified and enumerated; the proportion of the displacement volume of each sample that was due to included interstitial liquid was determined; the amount of dry substances, organic substances, ash and nitrogen was determined per gram of plankton without interstitial liquid.

The test samples were collected off central Baja California (Fig. 1), eight by the junior author in February, 1959, one in March, 1959, and the remaining three in July, 1959. Water temperatures in 1959 were warmer than usual; plankton volumes were the smallest in a decade. Some groups of organisms that had been conspicuous constituents of the plankton in previous years were absent from the 1959 samples. Among these, the most interesting group was the pyrosomes. These tunicates had become the dominant organism in many hauls made off central Baja California during the mid-1950's particularly from August, 1955 through April, 1957. Previous to their emergence as a dominant plankton constituent, pyrosomes had been so rare as to be curiosities; by 1958 they again had become uncommon and none was taken in the samples reported upon in this paper. Ctenophores also were absent from the test samples. The three test samples taken in July, 1959, were selected in order to have an adequate representation of samples containing salps and doliolids in the volume-loss studies; these groups also were markedly less abundant in 1958 and 1959 than during previous years.

The method of measuring displacement volume of "wet" plankton was kept uniform throughout the experiment. The total volume, plankton with its preserving liquid was measured, the plankton was then separated from its preserving liquid, and the volume of the latter determined. The plankton volume, hence, was the difference between the two measurements. The consistency of the measurements is one gauge of their reliability. Problems associated with "wet" volume determinations are discussed in a later section.

The percentage composition by volume of the major constituents of the twelve test samples is given in

TABLE 3. PERCENTAGE COMPOSITION BY VOLUME OF MAJOR PLANKTON CONSTITUENTS

Constituents	Cruise 5902								Cruise 5903	Cruise 5907		
	110.33	110.65	113.30	113.40	113.50	120.35	123.42	130.35	133.30	107.50	107.55	110.90
Crustaceans												
Copepods	81	19	68	25	8	77	8	38	20	6	11	19
Euphausiids	*	19	*	11	11	1	18	12	1	2	3	30
Decapod larvae	9	*	4	2	*	11	9	30	25	1	1	17
Ostracods	—	*	*	*	*	—	*	*	*	*	1	*
Amphipods	—	*	—	*	*	—	*	—	—	1	*	*
Other Invertebrates												
Chaetognaths	10	9	25	42	5	10	8	8	45	10	10	16
Siphonophores	*	47	*	8	70	1	*	5	*	21	26	12
Medusae	—	*	—	—	—	—	1	—	—	4	5	—
Salps and Doliolids	*	*	*	*	*	—	48	—	—	52	40	3
Larvaceae	*	*	*	*	*	*	*	1	1	1	1	*
Molluscs	*	6	*	9	6	*	8	1	8	1	*	1
Fish Eggs	*	—	3	*	*	*	*	5	*	*	*	*
Fish Larvae	*	*	*	3	*	*	*	*	*	1	2	2

* Present, volume less than 0.5%; —no individuals of category observed.

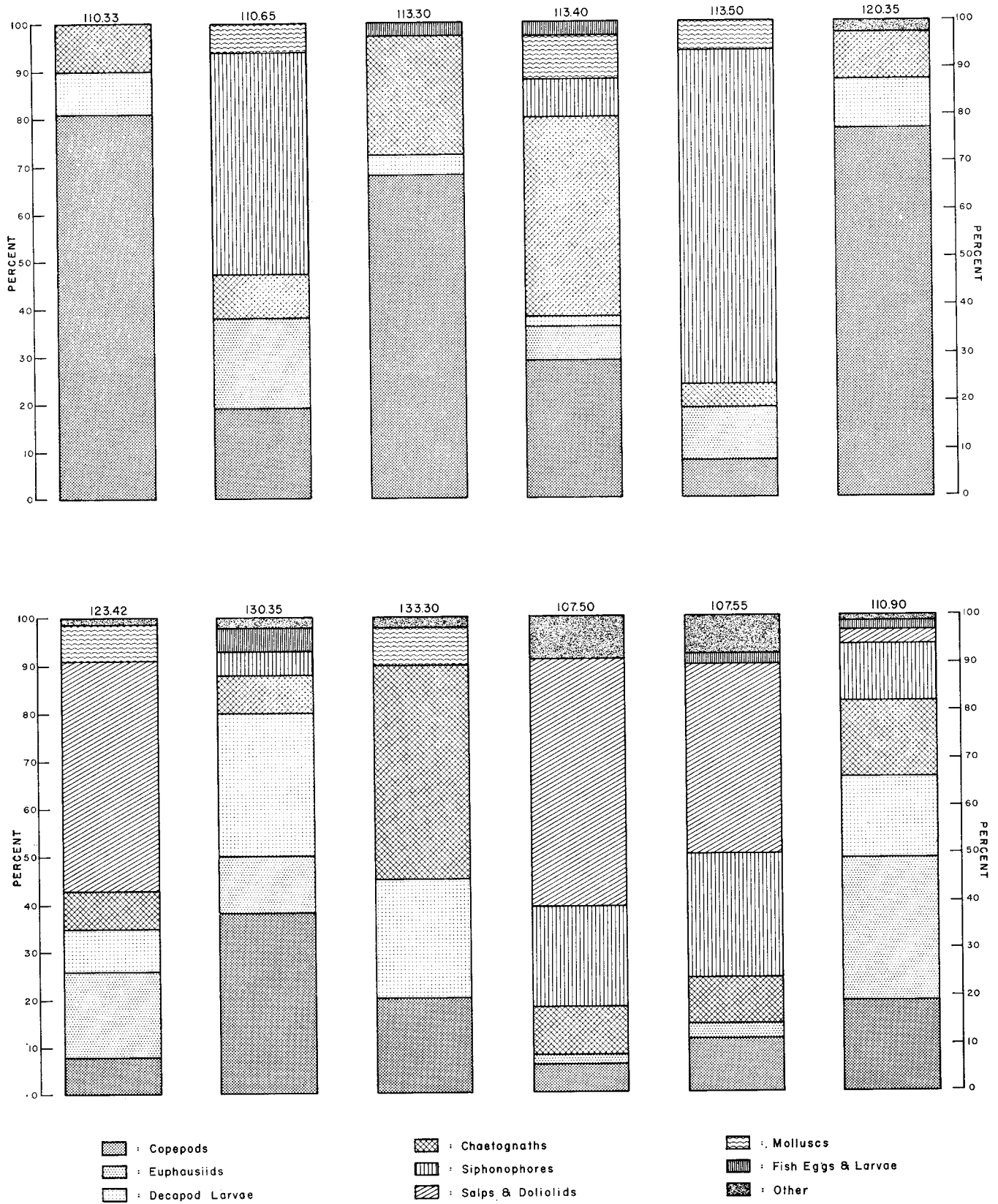


FIGURE 2. Diagrammatic representation of constituent compositions of test samples expressed as percentage of volume one year after collection.

table 3 and Figure 2. Crustacean constituents are grouped under five categories: copepods, euphausiids, ostracods, amphipods and decapod larvae. The important non-crustacean invertebrate constituents are placed in six categories: chaetognaths, siphonophores, medusae, salps and doliolids, larvaceae, and pelagic molluscs. The only vertebrate categories included are the planktonic stages of fish development—fish eggs and larvae. The volumetric determination of the major constituents was made a year or more after collection, at a time when the preserved volumes had attained comparative stability. This is an important point to keep in mind. Had the determination been made within the first few days of collection, the percentage composition would have been quite different—higher for salps and siphonophores, lower for crustacea, molluscs, and chaetognaths. Had the determination been made before preservation, it would have been more markedly different yet.

Volume shrinkage at preservation.

A striking change in the volume of plankton samples occurs at preservation (Fig. 3). The initial determination of wet volume was made on freshly collected material. Immediately following this measurement, the sample was preserved with three percent buffered formaldehyde solution. A measurement of the preserved volume was made within 10 to 15 minutes of preservation.

Information on volume loss at preservation is available for 11 of the 12 samples. Immediate shrinkage in volume at preservation ranged from seven percent to 53 percent of the live volumes. In only one sample was the percentage loss at preservation as little as ten percent, in only one was it as much as 50 percent; of the other nine samples, three had losses of 11 to 20 percent of the live volume, three had decreases of 21 to 30 percent, and three of 31 to 40 percent.

Volume loss during the first day after preservation.

The rapid shrinkage of the volume of many samples continued during the first 24 hours after preservation. Five samples showed a loss of between 32 percent to 40 percent of the initial preserved volume at the end of one day of preservation; in these, siphonophores and/or salps-doliolids predominated. Three samples showed no volume loss during this period: All three samples were composed almost entirely of crustaceans and chaetognaths. The remaining four samples showed intermediate losses of from five percent to 26 percent; in these samples crustaceans and chaetognaths predominated, but siphonophores and salps made up a part of the volume, except in the sample from station 5903—133.30. The rapid shrinkage of plankton organisms during the first day following preservation probably results from a water loss, especially marked in jelly-like constituents.

Several measurements were made on most samples during the first 24 hours of preservation, but the pattern of observation was not uniform enough from sample to sample to permit their incorporation into table 2. The sample from station 5907-107.50 had the

most marked volume decrease of any in the series. After 78 hours of preservation, the volume of the sample was less than a third of the live volume. The decrease noted at intervals during this period was as follows:

Sample from 5907-107.50		Vol. (ml.)
<i>Time of observation</i>		
Before preservation		93
After preservation	10 min.	60
" "	1 hour	56
" "	4 hours	50
" "	11 hours	41
" "	24 hours	37
" "	78 hours	30

This sample has shown a volume loss on each subsequent measurement. The final measurement (12 ml.), made 22 months after collection, was only 13 percent of the original live volume. Even after one year of preservation, salps and doliolids made up over 50 percent of the volume of this sample. Originally they may have constituted as much as 95 percent of the total volume (discussed in concluding section of paper).

The volume loss in the sample from station 5903-133.30 is different than that for any other sample in that there was a considerable shrinkage at and immediately following preservation but the sample soon reached an equilibrium volume:

Sample from 5903-133.30		Vol. (ml)
<i>Time of observation</i>		
Before preservation		48
After preservation	12 min.	34
" "	3 hours	25
" "	7 hours	25
" "	24 hours	25
" "	2 years	24

The equilibrium volume was reached within three hours of preservation. The change in volume of this sample during the succeeding two years amounted to only 1 ml. or four percent. With regard to the constituent composition of the sample—46 percent by volume consisted of crustacean plankton, 45 percent of chaetognaths and 8 percent pelagic molluscs. Since the exoskeleton of crustacea and the shells of pteropod molluscs prevent marked shrinkage (except for withdrawal of molluscs within their shells), the major adjustment in volume at this station must have occurred in the chaetognaths.

Volume loss subsequent to the first day of preservation.

The volume at one day after preservation is taken as the standard by which to gauge the subsequent shrinkage in plankton volumes of preserved samples. The rapid rate of shrinkage, observed for most samples at preservation and during the first 24 hours thereafter, was markedly slowed down after a day of preservation. Some samples showed little or no volume loss after the first day, others showed a continuing but decelerating decrease with time.

The percentage loss in plankton volumes from the reference volume at one day after preservation is shown for four time intervals in table 4: 10 days, 30

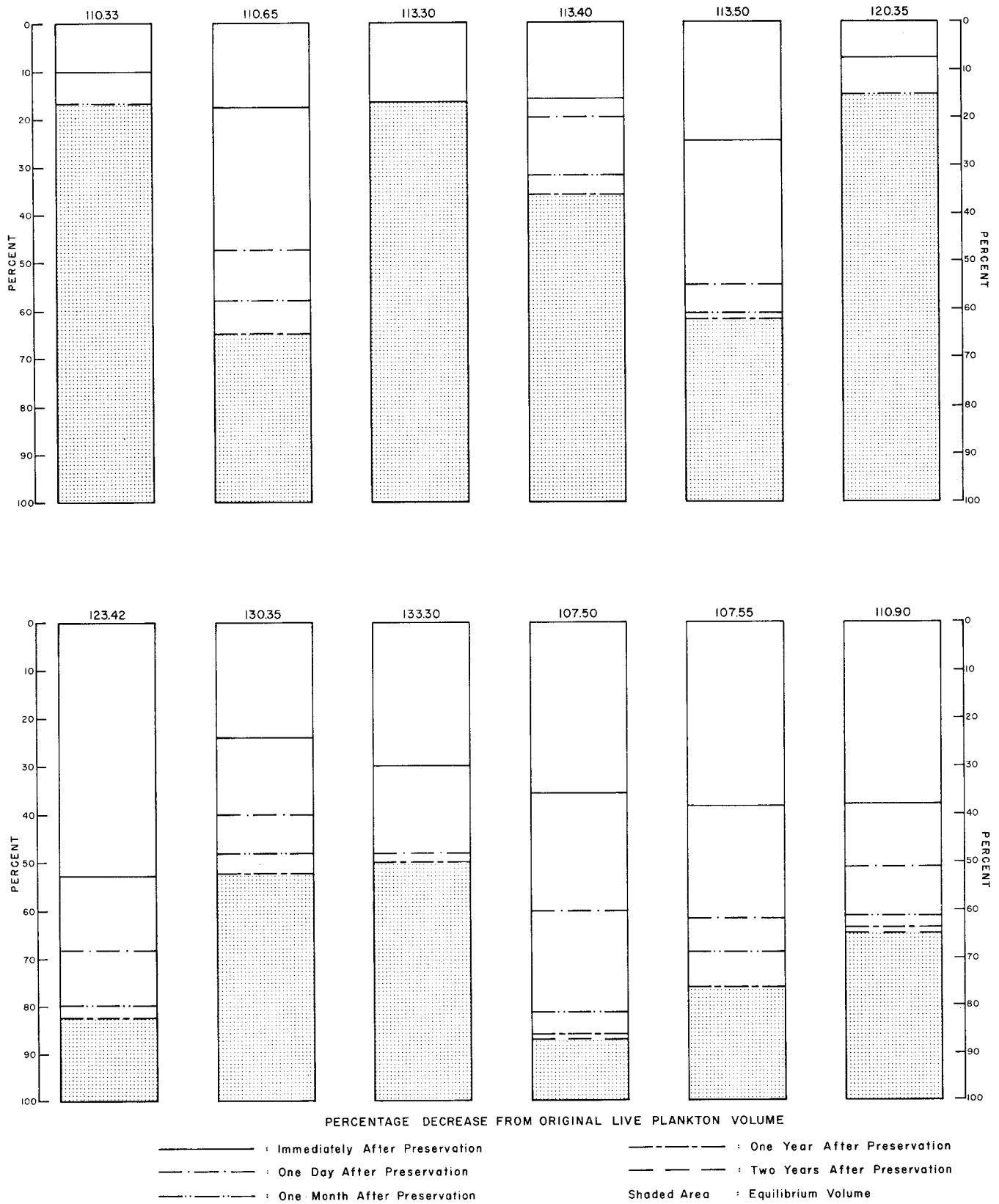


FIGURE 3. Temporal decrease in volumes of test samples, expressed as percentage of their live volumes.

days, one year, two years. The samples are arranged in this table according to increasing volume loss. In order to relate loss in volume to constituents, the gross composition of each sample is indicated under four categories: crustaceans, chaetognaths, coelenterate-thaliaceans and other constituents.

Four samples showed little or no volume decrease (zero to eight percent) over a two-year period. These samples contained less than one percent by volume of coelenterate-thaliacean constituents and 90 percent to nearly 100 percent of crustacean and chaetognath plankters.

At the other extreme, four samples showed losses of between one-third and two-thirds of their reference volumes. In these samples coelenterate-thaliacean constituents made up 47 percent to 78 percent of the volumes (after one year of preservation).

The samples that were intermediate in volume loss, had a preponderance of crustacean-chaetognath constituents, except for the sample from station 5902-113.50. This latter sample, in which siphonophores made up 70 percent of the volume, had only a moderate volume loss. It is commented upon more fully in a later section.

Constituents

The discussion thus far has dealt with the pattern of temporal decrease in plankton volumes as related grossly to dominant constituents. The specific composition of the samples is treated in table 5. It has been necessary to deal with numbers of individuals rather than their volumes in this table. The table has been assembled with the help of a number of scientists (see Acknowledgements). Specific identifications are not available for several minor constituent groups including ostracods, larvaceae, and some decapod larvae. Ctenophores were absent from the samples, annelids nearly so.

Copepods

Copepods were the dominant constituent in three of the four samples that showed the least volume loss with time (Table 3). The three "copepod" samples were collected near the coast, at stations having depths of 50 fathoms or less (Table 1).

Calanus helgolandicus was the most abundant species in two of the three samples (Table 5). In the sample from station 5902-110.33 it outnumbered the combined total of all other copepods by nearly five to one, while at station 5902-120.35 it was nearly as numerous as all other copepods. At station 5902-113.30, *Calanus helgolandicus* was outnumbered by *Paracalanus parvus*, but was still the dominant species in volume. It is interesting to note that although these three samples contained a larger number of copepods than the other test samples, they contained fewer species per sample. Copepods made up 6 percent to 38 percent of the volumes in the other test samples.

Euphausiids

This group contributed significantly to the volumes of six samples taken at night (11 to 30 percent) but was a minor element in day hauls (one to three percent). Undoubtedly this resulted from the vertical movement of larger individuals into the stratum sampled at night. Although there is no reason to assume that euphausiids would decrease appreciably in volume, if at all, during preservation, they were associated with samples that showed moderate to heavy volume losses. *Euphausia eximia* and *Nyctiphanes simplex* were the most consistently abundant species; *Nematoscelis difficilis*, *Euphausia gibboides*, *Stylocheiron affine*, and *Euphausia recurva* were important constituents in one or more of the samples.

TABLE 4. COMPARISON OF PLANKTON VOLUME LOSS WITH CONSTITUENT COMPOSITION OF SAMPLES

Cruise and Station	Percentage Loss in Plankton Volume from Volume at 1 Day After Preservation				Constituent Composition Expressed as Percentage of Volume at 1 Year After Collection			
	Time Interval				Crust.	Chaet.	Coel.-Thal.	Other Const.
	10 Days	30 Days	1 Year	2 Years				
5902-113.30	0	0	0	0	74	26	*	*
5903-133.30	0	0	4	4	46	45	1	8
5902-110.33	3	8	8	8	90	10	*	*
5902-120.35	8	8	8	8	89	10	1	*
5902-113.50	8	13	16	16	19	5	70	6
5902-130.35	13	13	20	20	80	8	6	6
5902-113.40	12	15	20	20	38	42	8	12
5907-110.90	18	21	26	**29	66	16	15	3
5902-110.65	20	20	33	33	38	9	47	6
5907-107.55	12	19	38	**38	16	10	72	2
5902-123.42	37	37	44	44	35	8	49	8
5907-107.50	43	51	65	**68	10	10	78	2

* Present, volume less than 0.5%.

** 22 months.

Abbreviations in Table 4: Crust., Crustaceans; Chaet., Chaetognaths; Coel., Coelenterates; Thal., Thaliaceans; Other Const., Other Constituents.

TABLE 5. SPECIES COMPOSITIONS OF PLANKTON SAMPLES USED IN VOLUME-LOSS STUDY—Continued

Crustacean Constituents	Cruise 5902							Cruise 5903	Cruise 5907			
	110.33	110.65	113.30	113.40	113.50	120.35	123.42	130.35	133.30	107.50	107.55	110.90
Euphausiids—Continued												
N. tenella												
“ “ A.....					1							
“ “ J.....		1										8
“ “ L.....												
Nyctiphanes simplex										4	12	
“ “ A.....				16	2	4	32	73				
“ “ J.....		24		24	8	32		288	58	88		
“ “ L.....		56		216	32	8	64	216	49	40		
Stylocheiron affine		40		56	8		40	2				8
“ “ A.....		96		88	88		8	12	8	12	4	24
“ “ J.....		40		48	48		0	4				0
“ “ L.....				8								
S. maximum				8								
Thysanoessa gregaria		1		8	1							
“ “ A.....												
“ “ J.....								4				
“ “ L.....												
Thysanopoda aequalis											8	16
Ostracods												
Conchoecia sp.....	0	296	12	504	108	0	40	68	96	84	36	104
Other.....				24						28	164	40
Amphipods												
Eupronoe minuta.....					4							
Eusiropsis riisei.....		4		3								8
Hyperia schizogeneios.....										8		
“ sp.....										4		
Hyperoche mediterranea.....		4										
Paraphronima crassipes.....											4	
Phrosina semilunata.....				10								
Platyscelus serratulus.....		2										
Primno macropa.....				3	4							
Pronoe capito.....								8				
Streetsia challengerii.....										4		
Viblia armata.....		3						32				
Viblia stebbingi.....		3										
Decapod larvae												
Panilurus interruptus.....											1	
Pleuroncodes planipes.....	10400	24	3720	2320	24	3200	2728	640	4300	4		72*
Brachyuran.....							8	2	16			
Caridean.....					8					20	36	
Pasiphaeid.....								12*				
Sergestid.....										84	28	64
Stomatopod.....						4	8	15				
Other.....								1				
Other Invertebrates												
Chaetognaths												
Sagitta bieri.....	50	175	1	440	204		168	112	656	36	19	900
S. bipunctata.....							16			18	4	
S. enflata.....	500	251	232	780	131	241	456	111	872	21	154	400
S. euneritica.....	2100		633	50	1	210		2		2		
S. hexaptera.....				1	1					10	4	
S. minima.....	450	50	1	350	14	154	32	5	192	23	15	200
S. pacifica.....		5			8			3	4	6	40	50
S. pseudoserratodentata.....		18		250	31		160	9	6	197	189	900
Krohnitta subtilis.....		6		78	6			5	192	1	3	
Pterosagitta draco.....		4			2			3		2		
Siphonophores												
Abylopsis eschscholtzii.....											4	
Agalma okeni.....		97										
“ “ Br.....		182										
Bassia bassensis.....										4	4	
Chelophyes appendiculata.....		17		10	1					118	108	51
“ “ Inf. N.....				8						52	29	17
Diphyes bojani.....										4		
Eudoxoides spiralis.....		78		96	4					79	407	992
“ “ Eud.....		280		200						114	709	1513
E. mitra.....							16	3				
Lensia campanella.....												
L. challengerii.....											8	8
“ “ Sup. N.....				17	1		16	11	2	2		
“ “ Inf. N.....							8	1				
“ “ Eud.....								9				
L. subtiloides.....		9		8							10	6
“ “ Sup. N.....												10
“ “ Inf. N.....		1									1	
Muggiaea atlantica.....	8			9		80		2	8	8		
“ “ Eud.....			8			8			16			
Nectodroma reticulata.....					73							
“ “ Br.....					50							
“ “ Gon.....					2							
“ “ Polyg.....												
Halitemma rubra.....							1					
Sulculeolaria sp.....				1							1	6
Medusae												
Aglantha digitalis.....												
Liriope tetraphylla.....							72			24	120	
Rhopalonema velatum.....		8								504	84	8

* Juveniles.

TABLE 5. SPECIES COMPOSITIONS OF PLANKTON SAMPLES USED IN VOLUME-LOSS STUDY—Continued

Crustacean Constituents	Cruise 5902								Cruise 5903	Cruise 5907		
	110.33	110.65	113.30	113.40	113.50	120.35	123.42	130.35	133.30	107.50	107.55	110.90
Salps and Doliolids (Thaliacea)												
Doliolid oozoid	3	20		33	26					216	97	274
Doliolum denticulatum										14		10
" " Gonzo.										6		16
" " Phozo.											16	
" " S.N.G.	3	4	2							10	1	
Doliolum gegenbouri												
Pegea confoederata							272					
Ritteriella picteti							24					
Thalia democratica										424	574	70
" " Agg.										72	72	8
" " Sol.												
Molluscs												
Cavolinia inflexa		2		6	5					2	4	
Creseis virgula		1		28		4			15	5		4
Cuvierina columella									1			1
Limacina inflata	8	5010	52	11860	4420	48	4000	352	2410	232	12	630
L. trochiformis		4		2		8	45	23	640			1
Peraclis sp.										1		
Desmopterus sp.										1		
Atlanta leusueri												6
A. peroni		11							55	35		12
A. sp.	8			42		8	3					
Pterygiotenthis sp.										1		
Pyrogopsis sp.										2		
Vertebrates												
Fish Eggs												
Sardinops caerulea	7		12			10				3		
Engraulis mordax	40	1	469	2		1						
Etrumeus acuminatus				3				40				
Leuroglossus stilbicus	1									20	8	23
Bathylagus wesethi								2				
Argentina sialus				3				2				
Nansenia sp.					2					1		
Vinciguerria lucetia	39				2			5		122	16	162
Stomias atriventer				2	1			12		4	2	
Synodus lucioceps						1			1			
Cololabis saira												
Citharichthys spp.	79		8			74		8	1			
Paralichthys californicus			13					23				
Pleuronichthys verticalis	1		2			1		1				
Merluccius productus	117		9	15			11	115	4			
Trachurus symmetricus												1
Chiasmodon sp.								6	152	4		
Lepidopus xantusi								6	7	13	5	21
Other	3		11	3	5	1	6					3
Fish Larvae												
Sardinops caerulea	1		3	1				1				
Engraulis mordax	45		48	414		14	25	4	4		3	
Bathylagus wesethi										1		6
Nansenia sp.												
Vinciguerria lucetia		14		9	10			1	10	2	43	101
Cyclothone sp.				2	1			1				2
Argyrolepeus sp.				2								
Stomias atriventer				1						1		
Macroparalepis macurus												2
Ceratocopelus townsendi				1								7
Diogenichthys atlanticus				7	2				3		1	5
D. laternatus				4								2
Electrona crockeri								1				4
Gonichthys tenuiculum												1
Hygophum atratum				1				2			8	9
Lampanyctus mexicanus			3	3							1	155
L. ritteri			1	9	1						2	
Myctophum californiense												
M. margaritatum												
Melamphaes spp.		2										2
Citharichthys spp.	2		1	5		2	1					
Paralichthys californicus	1											
Pleuronichthys verticalis				1								
Merluccius productus	9			1	4			7	37			
Trachurus symmetricus											1	
Cynoscion sp.				1								
Chiasmodon sp.		1		1								
Lepidopus xantusi				1								
Sebastodes spp.	10		9	26					1			
Other						1						1

Abbreviations in Table 5:

A—Adults
 J—Juveniles
 L—Larvae
 Nect.—Nectophore
 Sup. N.—Superior Nectophore

Inf. N.—Inferior Nectophore
 Br.—Bract
 Eud.—Eudoxid
 Gon.—Gonophore
 Polyg.—Polygastric stage

Gonzo.—Gonozooid
 Phozo.—Phorozooid
 S.N.G.—Stage not given
 Agg.—Aggregate
 Sol.—Solitary

Decapod larvae

Decapod larvae were important constituents in the samples studied; they made up 9 percent to 30 percent of the volumes in half of the samples and were present in all. The four samples that showed the least change in volume with time contained 4 percent, 25 percent, 9 percent and 11 percent by volume of decapod larvae, with *Pleuroncodes planipes* contributing all or most of the volume in each instance. The sample in which decapod larvae made the largest percentage contribution to the volume (5902-130.35) contained young of pasiphaeid shrimp. In only this instance did a decapod other than *Pleuroncodes* contribute significantly to test sample volumes.

Chaetognaths

Chaetognaths were consistently important constituents in the test samples; in a third of the samples their volumetric contribution ranged between 16 percent and 45 percent, in another third it was ten percent, and in the remaining third the contribution was between five percent and nine percent.

Chaetognaths were important constituents in the four samples that showed the least volume loss subsequent to the first day of preservation. The sample from station 5902-113.30, containing 26 percent by volume of chaetognaths, showed no loss during this time period and the sample from station 5903-133.30, containing 45 percent by volume of chaetognaths, suffered only a four percent reduction in volume. Thus chaetognaths appear to conserve their "preserved" volume.

We have, however, previously commented upon the fact that there must be a rather marked volume loss in chaetognaths at preservation. At least this is our interpretation of the volume loss in the sample from station 5903-133.30 at preservation. The "preserved" volume is just slightly more than half the "live" volume of the sample.

Chaetognaths made up 45 percent of the preserved volume. The only important constituent groups in this sample other than chaetognaths were crustacea and molluscs, both of which have an external skeleton that precludes shrinkage. The most abundant species of chaetognath in this sample, *Sagitta inflata*, is also the largest and the flabbiest. Most of the initial volume loss in this sample may be attributed to this species.

Siphonophores

The physonectid siphonophores fragment on collection, and the counts of nectophores and bracts, consequently, represent only parts of colonies. The less complex calycophorid siphonophores invariably had the inferior nectophores (if developed) separated from the superior nectophore in the polygastric stage and usually had bracts separated from gonophores in the eudoxid stage. The two types of nectophores are separately tabulated but counts (with one or two exceptions) of the eudoxid stage are based on counts of gonophores.

Siphonophores were an important constituent in over half of the test samples and the dominant constituent in two. These latter samples offer an interesting contrast. The dominant species in the sample from station 5902-110.65 was *Agalma okeni*. The nectophores of this species have now collapsed, the bracts have become limp. The sample had lost a third of its reference volume after 2 years of preservation. The sample from station 5902-113.50, containing a higher percentage of siphonophores, had lost only a sixth of its reference volume. The important species in this sample was *Nectodroma reticulata*, present in both the polygastric and eudoxid stages. Two polygastric specimens made up half the volume of this sample. These two specimens were removed and separately measured after the tenth day. They showed no subsequent volume loss. The bracts and gonophores of the eudoxid stage of this species occurred in much larger numbers, but occupied considerably less volume.

Of the remaining species of siphonophores in the test samples, some hold up less well in preservation than others. Nectophores of *Muggiaea atlantica* collapsed. On the other hand, *Eudoxoides spiralis* held its shape well. *Chelophyes appendiculata*, also stood up well, even with repeated handling. There can be little doubt that much of the volume loss in siphonophores results from collapse of nectophores, bracts, and gonophores, and that the amount of volume loss is variable from species to species.

Thaliacea

Salps and doliolids did not contribute significantly to the volumes of the test samples collected in February (5902), except at station 5902-123.42. For this reason, several additional samples containing salps and doliolids were selected and included in the test series during the July cruise.

The three samples which showed the largest volume loss during preservation contained from 40 percent to 52 percent by volume of salps and doliolids after one year of preservation. In two of these, 5907-107.50 and 5907-107.55, the dominant constituent was the salp, *Thalia democratica*, in the other sample, from 5902-123.42, the dominant constituent was the salp, *Pegea confoederata*.

Mollusca

The pelagic molluscs in the test samples were almost all shelled forms that retained their "live" volume, except for withdrawal into their shells. Only one species *Limacina inflata* was common to abundant in most samples, accounting for most of the volumes shown for mollusca. *Limacina trochiformis* was common in only one sample, although it occurred in half of the test samples. *Atlanta* spp. occurred in most samples but did not contribute significantly to the volumes.

Fish eggs and larvae

Fish larvae shrink on preservation, but soon come to an equilibrium volume. Fish eggs shrink but slightly, if at all. Neither would contribute significantly to volume loss after the first day of preserva-

tion. Fish larvae made up one percent to four percent of the volumes in four samples. Most of the contribution was made by *Engraulis mordax* larvae in sample 5902-113.40 while in the other three samples the important constituent was *Vinciguerria lucetia* larvae. Fish eggs made up three percent of the volume in station 5902-113.30 and five percent of the volume in station 5902-130.35. In the former, eggs of *Engraulis mordax* predominated, in the latter, those of *Lepidopus xantusi*.

“Wet” displacement volumes of plankton

Throughout the present study, “wet” plankton volumes were determined in a similar manner. The total volume of plankton plus preserving liquid was measured in a graduated cylinder. The sample was then poured into a funnel-shaped silk strainer, the plankton being retained, the preserving liquid being caught in another graduated cylinder. Each sample was allowed to drain for five minutes before a measurement was taken of the preserving liquid. The determination of the “wet” plankton volume was an indirect measurement, based on the difference in the volume of the sample plus its preserving liquid and that of the liquid alone. This type of measurement was utilized in order to keep the handling of the plankton itself to a minimum. In order to minimize loss of liquid by absorption into the screening material the strainer was dampened before use.

The plankton strainer is a cone of No. 56xxx grit gauze attached to a plastic rim. Early experiments had shown that for consistency in volumetric determination, it is essential that the silk strainer be free from contact with other objects. Such contact points often result in “water pockets” which prevent adequate draining.

There is a possibility that the periodic remeasurement of the volumes of the test samples hastens the volume loss in some samples. Volume loss currently is being followed in two collections of salps obtained off southern California in May, 1962. The salps from each collection were separated from the other constituents of the samples before preservation, and divided into two subsamples, one of which has been remeasured five times in four months, the other 24 times. The samples that have been repeatedly measured, show only one to two percent greater volume loss than the samples that have been measured only a few times.

Organism	Percentage decrease in volume during first four months after preservation of sample when remeasured	
	24 times	5 times
<i>Salpa fusiformis</i> —solitary form	51.5	49.7
<i>Salpa fusiformis</i> —aggregate form	51.2	50.0

Interstitial liquid

A measurement of a drained wet plankton volume consists of two quantities: the plankton itself and the adhering or interstitial liquid. Unfortunately, the latter quantity is far from negligible and is somewhat variable in relative amount from sample to sample.

Investigators have tried to minimize the amount of interstitial liquid by various techniques including blotting, air drying, and vacuum filtration. This problem has engaged the attention of a number of scientists: Ealey 1954, Yentsch and Hebard 1957, Frolander 1957, and Tranter 1960 are recent contributors. Most methods are devised for small samples and are impractical for the large volumes usually obtained on CalCOFI cruises.

We employed a colorimetric technique for determining the amount of interstitial liquid remaining in drained test samples. This technique is based on changes in optical density of an India ink standard that results from dilution by interstitial liquid when a wet plankton sample is added to it (Sutcliffe 1957). The “standard” solution is made up of one part of India ink in 6,000 parts of three percent formaldehyde solution. This is accomplished in two steps: first a stock solution is made up, consisting of one part by volume of India ink and 99 parts of three percent formaldehyde solution; a standard solution is made by mixing one part of the stock solution with 59 parts of a three percent formaldehyde solution. The standard solution is calibrated, using a Klett photoelectric colorimeter. Changes in optical density values that result from progressive dilution of the standard with three percent formaldehyde solution are determined, and a curve prepared.

The drained plankton sample is added to a known volume of standard, the plankton and standard are thoroughly mixed, and a quantity of the liquid is pipetted off. To prevent taking up plankton organisms in the supernatant liquid, the pipette is fitted with a small silk filtering cone. The optical density of the pipetted liquid is then obtained, and the amount of dilution by interstitial liquid is determined from the dilution curve of the standard.

Estimates of the amount of interstitial liquid in the twelve test samples are given in table 6 and Figure 4.

TABLE 6. DETERMINATION BY COLORIMETRIC METHODS OF THE AMOUNT OF INTERSTITIAL LIQUID IN DRAINED “WET” PLANKTON SAMPLES

Cruise & Station	Total volume of drained “wet” plankton (ml.)	Volume of interstitial liquid (ml.)	Volume of organisms only (ml.)	Percentage interstitial liquid
5902				
110.33	35	12.0	23.0	34
110.65	20	5.5	14.5	28
113.30	10	4.0	6.0	40
113.40	32	11.0	21.0	34
113.50	32	5.5	26.5	17*
120.35	11	5.0	6.0	45
123.42	23	7.5	15.5	33
130.35	12	5.0	7.0	42
5903				
133.30	24	8.0	16.0	33
5907				
107.50	12	4.5	7.5	38
107.55	10	4.0	6.0	40
110.90	27	9.0	18.0	33

* Samples from 5902-113.50 not strictly comparable with others (see text).

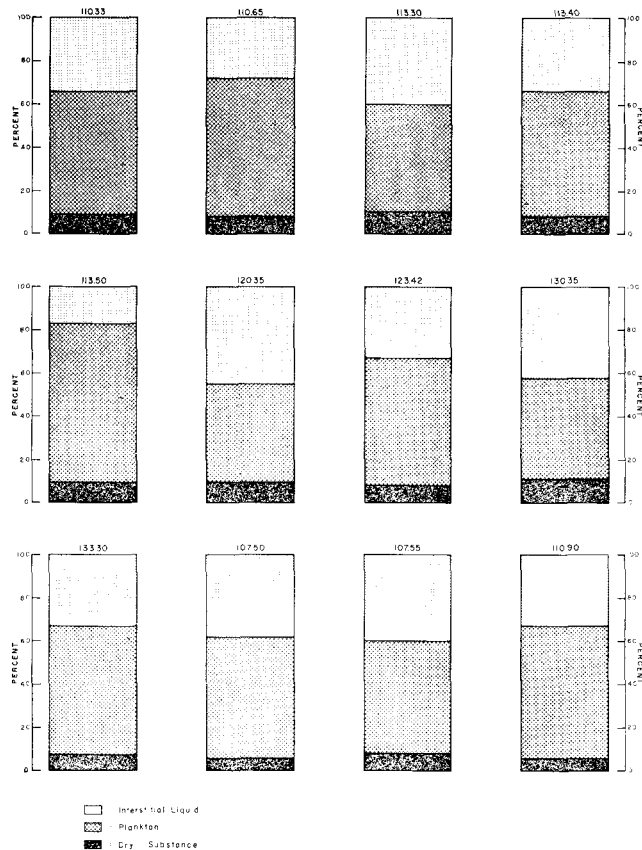


FIGURE 4. Diagrammatic representation of the percentage that interstitial liquid, plankton, and dry substances constituted of the stable preserved volume (weight) measurements of test samples.

The range in values is from 17 percent to 45 percent of the total wet volumes. Except for the sample from station 5902-113.50, no sample had less than one part of interstitial liquid to three parts of plankton and eight of the twelve samples contained between 31-40 percent of interstitial liquid. Several tests were made in order to eliminate adsorption as a possible source of error in our colorimetric determinations. Adsorption was found to be negligible.

The sample from station 5902-113.50 is not strictly comparable to the others, because of the circumstance that half its volume resulted from two specimens of the siphonophore, *Nectodroma reticulata*. Interstitial liquid was separately determined for these as follows:

	Wet vol. (ml.)	Amount of interstitial liquid in ml.	Vol. of plankton alone (ml.)	Percentage of interstitial liquid
Portion containing two specimens of <i>Nectodroma</i>	16.0	0.2	15.8	1
Remainder of sample.....	16.0	5.3	10.7	33

The portion of the samples containing the two specimens of *Nectodroma* caused practically no change in the optical density of the standard. This observation is interesting for two reasons: it shows how little interstitial liquid may adhere to larger specimens of "jellies", and it affords indirect evidence that adsorption of the colloidal carbon particles of the standard on the surface of the specimens was negligible. The remainder of the sample contained about 33 percent interstitial liquid, hence approximates the median value for interstitial liquid in the other test samples.

Our values of 28 to 45 percent interstitial liquid in the 12 test samples are only slightly higher than those reported by Riley, Stommel and Bumpus (1949) and Frolander (1957). The former investigators removed interstitial liquid by rolling plankton animals on filter paper. They obtained weight losses of between 20 and 30 percent in most samples tested in a group of about 20, but had losses as high as 45 percent. Frolander reported average volume losses of 19.4 percent for one group of 10 samples, 27.5 percent for a second group of 10 samples when interstitial liquid was removed by vacuum filtration.

Removal of interstitial liquid by blotting

The commonest techniques for removing interstitial liquid is by blotting. Determinations of interstitial liquid were made by both blotting and colorimetric measurement on a sample of 2,000 individuals of *Calanus helgolandicus*, separated from 5902-110.33. Dry weight and ash weight determinations also were made on this sample.

Determinations made on 2,000 *Calanus helgolandicus*

Wet volume.....	2.8 ml.
Interstitial liquid.....	1.5 ml.
Copepods only.....	1.3 ml.
Wet weight.....	2.68 g.
Blotted weight.....	1.15 g.
Dry weight.....	0.1694 g.
Ash weight.....	0.0077 g.
Percent ash/dry weight.....	4.55%

Interstitial liquid was determined by the colorimetric technique and found to be approximately 54 percent of the wet volume. The sample was washed with formaldehyde solution, allowed to drain for five minutes, and its wet weight determined. Interstitial liquid was then removed by blotting and air drying. The sample was again weighed and the weight loss attributable to interstitial liquid was determined to be approximately 60 percent of the wet weight. Considering the limits of precision of the two techniques, the resulting values for interstitial liquid are closely comparable. However, the values for interstitial liquid are greater than those obtained in mixed plankton samples.

In our experience the blotting technique is most reliable when used on organisms with an exoskeleton. Blotting of samples containing salps or siphonophores can give an overestimate of the interstitial liquid by

TABLE 7. DRY WEIGHT DETERMINATIONS OF PORTIONS OF TEST SAMPLES

Station	Wet ¹ weight	Percentage of wet weight due to plankton	Estimated weight of plankton alone	Dry weight (grams)	Ash weight (grams)	Dry substance per gram of plankton (grams)
110.33	3.420	66	2.257	0.215	0.0130	0.095
110.65	4.250	72	3.060	0.260	0.0223	0.085
113.30	1.285	60	0.771	0.085	0.0061	0.110
113.40	6.240	66	4.118	0.340	0.0350	0.083
113.50	2.565	67	1.719	0.170 ²	0.0133	0.099
120.35	1.985	55	1.092	0.110	0.0097	0.101
123.42	2.475	68	1.683	0.140	0.0090	0.083
130.35	2.520	58	1.467	0.170	0.0164	0.116
133.30	1.810	67	1.211	0.095	0.0114	0.078
107.50	1.825	63	1.150	0.065	0.0116	0.056
107.55	1.115	60	0.669	0.055	0.0048	0.082
110.90	2.820	67	1.876	0.180	0.0188	0.096

¹ Wet weight of plankton plus interstitial water.

² Two polygastric specimens of *Nectodroma reticulata* excluded from determinations.

removing part of the body liquids from the organisms (overdrying). The volume of the two polygastric specimens of *Nectogroma reticulata* from station 5902-113.50 was reduced to from 17 to 14 ml. by overdrying with a blotter. When put back in preservative these specimens regained their former volume after several days. Overdrying of salps such as *Iasis zonaria* on the other hand, has resulted in a permanent decrease in preserved volume. Overblotting of some kinds of salps and ctenophores has resulted in the physical breakup of specimens. Physical rupture of specimens was more often observed when the technique of vacuum filtration was employed to remove interstitial liquid, however. Vacuum filtration also may induce overdrying of specimens. This technique has to be used with caution.

For most plankton samples, weight and volume are readily convertible: 1 ml. of plankton weighs approximately one gram. This comparison has been made on a number of plankton samples and constituents; of the common constituents only pteropods do not conform. Hence in some parts of the discussion that follows, we have used grams or milliliters of plankton interchangeably. In many of our experiments, determinations of both weight and volume were made.

Dry weight

A dry weight determination of plankton has certain definite advantages. Water is eliminated, both interstitial and that within the organisms, only organic and inorganic substances contained in the bodies of the plankters remain. This determination, therefore, is a more basic one for evaluating the potential food value of the standing crop of plankton than a determination based on wet volume or wet weight.

Dry weight determinations made on fractions of the 12 test samples are given in table 7. These determinations were made 23 to 26 months after collection of the test samples (in June, 1961). The plankton used for dry weight determinations had two categories of organisms removed, pteropods and fish eggs and larvae. The former category was excluded because it was felt that their calcareous shells would make the dry weight determinations hard to interpret. Riley and Gorgy (1948) have shown that the dry weight of pteropods was approximately 83 percent ash and only 17 percent organic matter.

The 12 test samples are arranged in table 8 in descending order with respect to amount of dry substances (D.S.) per gram of plankton. Also contained in this table are organic substances (O.S.) and nitrogen content (ΣN) expressed in mg. per gram of

TABLE 8. COMPARISONS OF DRY SUBSTANCES, ORGANIC SUBSTANCES, ASH, AND NITROGEN CONTENT OF TEST SAMPLES, WITH THEIR CONSTITUENT COMPOSITIONS

Cruise & Station	Per gram of plankton			Per 100 mg. D.S.			Constituent composition (% by vol.)			
	D.S. mg.	O.S. mg.	ΣN mg.	O.S. mg.	Ash mg.	ΣN mg.	Crustacea	Chaetognaths	Coelenterates	Thaliacea
5902-130.35	116	105	13.3	90.4	9.6	11.4	85	9	5	1
5902-113.30	110	102	11.7	92.8	7.2	10.6	74	26	*	*
5902-120.35	101	92	9.7	91.2	8.8	9.6	89	10	1	*
5902-113.50	99	91	13.6	92.2	7.8	13.7	44	11	45	*
5907-110.90	96	86	10.6	89.6	10.4	11.0	68	17	12	3
5902-110.33	95	89	10.8	94.0	6.0	11.4	90	10	*	*
5902-110.65	85	78	9.3	91.4	8.6	10.9	40	10	50	*
5902-113.40	83	74	8.8	89.7	10.3	10.7	43	48	9	*
5902-123.42	83	78	9.5	93.6	6.4	11.4	38	9	1	52
5907-107.55	82	75	10.2	91.3	8.7	12.3	16	10	32	42
5903-133.30	78	69	8.3	88.0	12.0	10.7	50	49	*	1
5907-107.50	56	46	5.3	82.2	17.8	9.5	10	10	25	55

* Present, but less than 0.5% by volume.

D.S., Dry Substances; O.S., Organic Substances; ΣN , Nitrogen Content.

plankton, and in mg. per 100 mg. of dry substances (symbols adopted from Krey, (1958)). For ready comparison of the relation between D.S., O.S., and ΣN values, and constituent composition, the approximate percentage by volume of the four major groups of plankton organisms are listed for each sample.

A further summary of the material contained in table 8 follows:

Dominant organism	No. samples	Per 1 g. plankton		Per 100 mg. D.S.			Per 100 mg. O.S.
		D.S. ave. mg.	D.S. range mg.	O.S. ave. mg.	Ash ave. mg.	ΣN ave. mg.	
Crustacea.....	5	103.6	(95-116)	91.6	8.4	10.8	11.8
Crustacea-chaetognath.....	2	80.5	(78-83)	88.8	11.2	10.7	12.0
Crustacea-coelenterate.....	2	92.0	(85-99)	91.8	8.2	12.3	13.4
Thaliacean.....	3	73.7	(56-83)	89.0	11.0	11.1	12.5

The range in dry solids (D.S.) values is from 56 mg. to 116 mg. per gram of preserved plankton. The five samples in which crustaceans predominate (66 to 89 percent of sample volumes) averaged 103.6 mg. D.S. per gram plankton as compared to 73.7 mg. D.S. per gram plankton for samples in which salps and doliolids (thaliaceans) were dominant (i.e., made up 42 to 55 percent of sample volumes). The two samples containing crustacea and chaetognaths in about equal volumes averaged only 80.5 mg. D.S. per gram plankton, while the two samples in which crustacea and coelenterates each made up 40 to 50 percent of the volumes, averaged 92.0 mg. D.S. per gram plankton. The values for D.S. are strikingly more alike than had been anticipated. More of this later.

A number of authors give D.S. and O.S. determinations of plankton samples or of constituents. We have chosen for comment the following: Lovegrove (1961), Riley and Gorgy (1948), Tranter (1960), and Krey (1958).

Tranter (1960, table 6) reports D.S. values for plankton ranging from 24 mg. (salp swarm) to 160 mg. (sample predominantly euphausiids), with most values falling within the range given by us. His determinations on salp samples were made soon after collection, before the salps had "concentrated" to the extent that they had in our test samples.

Riley and Gorgy (1948) reported on D.S., O.S., and ash for representative plankton groups. The values they obtained for four constituent groups were as follows:

Constituent	Quantity in mg. per gram of constituent			Percent ash weight of dry weight
	D.S.	O.S.	Ash	
Copepods.....	173	147	26	15
Chaetognaths.....	134	98	36	27
Euphausiids.....	107	93	14	13
Thaliaceans.....	17	6	11	65

Their values are instructive in several respects. For one thing they point up the marked differences that obtain in both dry substances and organic substances between constituent groups at time of capture. The thaliaceans contain only four percent as much O.S. per gram of organism as do copepods, and six percent as much O.S. per gram of organism as do chaetognaths. Their values also show a higher inorganic (ash) content than was present in our test samples at equilibrium volume.

As noted previously, dry weight determinations were made on 2000 specimens of *Calanus helgolandicus*. The D.S. value of this sample is 147 mg. per gram of *Calanus*; ash content was only 6.7 mg., hence organic matter constituted 140 mg. per gram of *Calanus*. The latter value is quite similar to that given by Riley and Gorgy for copepods; the ash content is markedly less. The amount of biomass of *Calanus helgolandicus* required to yield one gram of organic matter is 7.15 grams. Lovegrove (1961) quotes a value of 6.8 grams of biomass per gram of organic matter for the closely related species, *Calanus finmarchicus*.

There appears to be both a water loss and an inorganic salt loss from the bodies of plankton organisms during preservation. The ash content of our samples ranged from 6.0 to 17.8 percent of the D.S. with only four values exceeding 10 percent. This is markedly less than the ash weights reported for the principal constituent groups by Riley and Gorgy. The three samples of our material in which salps dominated had ash contents that amounted to 6.4, 8.7, and 17.8 percent of the D.S. determinations. Based on Riley and Gorgy's determinations, the ash weight of these samples should have approximated 50 percent of the dry weight, had the inorganic salts been fully retained by the organisms during the period of volume concentration.

Krey (1958, table III) gives information on ΣN as well as O.S. and D.S. for various kinds of plankton samples. The ΣN values for four samples in which copepods predominated (80 to 100 percent copepods) ranged between 7.5 and 11.1 mg. per 100 mg. O.S. Our nitrogen values for "plankton" samples in which copepods dominated are somewhat higher, averaging 11.8 mg. N per 100 mg. O.S. Our higher values could result from a loss of some of the oils from the bodies of copepods, which would be shown as an increase in the protein content of O.S. Even so, our test samples with mixed constituents had a somewhat higher protein content (ΣN) than the samples in which crustacea were the dominant component.

Discussion

This study has drawn attention to the fact that the volume of organisms in a preserved sample is always less than their live volume. All of the test samples showed volume decreases subsequent to preservation.

The percentage decreases in volumes that were observed at selected time intervals are summarized in table 9. The time period required by the samples to reach their equilibrium volumes follows.

Equilibrium volume attained	No. samples
Immediately following preservation	1
1 day	0
10 days	1
1 month	1
1 year	7
2 years	2

Ten of the 12 test samples attained equilibrium volume within a year of collection. The remaining two samples showed only trivial losses during the second year. For all practical purposes, preserved plankton volumes can be considered to become stabilized within a year after collection.

The decreases in volume of plankton that occurred in test samples are from 15 to 87 percent of the live volumes. The amount of decrease is related to constituent composition, being least for samples in which crustacea made up most of the volume, greatest for samples in which salps were dominant.

The constituent compositions of samples when determined subsequent to preservation are not a measure of the amounts (by volume or weight) of the living constituents. Constituent determination of living material, however, is usually impractical. This cannot be done at sea on programs such as CalCOFI in which we are engaged. Hence this determination must be made at some subsequent time. The time to be preferred is when the samples have reached a relatively stable volume. Crustacean samples reach an equilibrium volume quite soon after preservation—salp samples slowly. Even salp samples show little change after one year of preservation, hence constituent volume determinations made one year after collection should be reproducible.

The constituent compositions (expressed as percentage by volume) of samples that have reached stable preserved volumes are useful, as long as their limitations are kept in mind. They would differ markedly from the original constituent compositions (percentage by volume) in some samples and would approximate them in others. In order to derive even moder-

ately reliable estimates of the original constituent compositions of preserved samples, more information is needed concerning volume losses suffered by the various constituent groups and by the more abundant species within these groups. Several volume loss studies on individual constituents are underway at our laboratory.

Rough estimates of the original constituent compositions were derived for several of the test samples containing a mixture of crustacean-chaetognath and jelly-like constituents. In these computations a shrinkage of 50 percent was allowed for crustacea, chaetognaths and molluscs. This is an "outside" estimate, for the crustacean-chaetognath samples showed a 15 to 50 percent decrease from their live volumes.

Sample from 5902-123.42

(Volume before preservation: 129 ml.; volume at time of constituent determination: 23 ml.)

	<i>Crustaceans- Chaetognaths</i>	<i>Thaliaceans- Coelenterates</i>
Percent by volume-one year after collection	51	49 (48% Salps)
Volume	11.7 ml.	11.3 ml.
Estimated original volume	23 ml.	106 ml.
Estimated percent by volume original collection	18	82

Sample from 5907-107.50

(Volume before preservation: 93 ml.; volume at time of constituent determination: 13 ml.)

	<i>Crustaceans- Chaetognaths</i>	<i>Thaliaceans- Coelenterates</i>
Percent by volume-one year after collection	23	77
Volume	3.0 ml.	10.0 ml.
Estimated original volume	6.0 ml.	87 ml.
Estimated percent by volume in original collection	6	94

The number of organisms in a sample does not change with time. Counts made several years after collection should not differ from counts made at the time of collection. Very few zooplankton constituents disappear from a preserved sample. Even ctenophores, such as *Pleurobrachia*, which break up in time and seemingly dissolve in the supernatant liquid, still leave

TABLE 9. PERCENTAGE DECREASE IN VOLUME OF PRESERVED PLANKTON SAMPLES FROM ORIGINAL LIVE VOLUME, GIVEN FOR SELECTED TIME INTERVALS

Cruise & Station	Orig. vol. ml.	Final vol. ml.	Percentage decrease from original live plankton volume					
			Imm. after pres.	1 day after pres.	10 days after pres.	1 mon. after pres.	1 year after pres.	2 years after pres.
5902-120.35	13	11	92.3	92.3	84.6	84.6	84.6	84.6
5902-113.30	12	10	83.3	83.3	83.3	83.3	83.3	83.3
5902-110.30	(44)	35	(87)	(87)	(85)	(80)	(80)	(80)
5902-113.40	50	32	84.0	80.0	70.0	68.0	64.0	64.0
5903-133.30	48	24	70.8	52.1	52.1	52.1	50.0	50.0
5902-130.35	25	12	76.0	60.0	52.0	52.0	48.0	48.0
5902-113.50	84	32	75.0	45.2	41.6	39.3	38.1	38.1
5902-110.65	57	20	82.4	52.6	42.1	42.1	35.1	35.1
5907-110.90	77	27**	62.4	49.4	40.3	39.0	36.4	35.1
5907-107.55	42	10	61.9	38.1	33.3	30.1	23.8	23.8
5902-123.42	119	23**	47.3	31.8	20.2	20.2	17.8	17.8
5907-107.50	93	12**	64.4	39.7	22.6	18.3	14.0	12.9

** 22 months after collection. Values in parentheses are estimates.

TABLE 10. ESTIMATES OF NUMBERS OF COPEPODS, EUPHAUSIIDS, AND CHAETOGNATHS PER MILLILITER OF SAMPLE IN 12 TEST SAMPLES

Station	Sample vol. ml.	Copepods			Euphausiids			Chaetognaths		
		Est. vol. ml.	Est. number	No. per ml.	Est. vol. ml.	Est. number	No. per ml.	Est. vol. ml.	Est. number	No. per ml.
110.33	35	28.35	41,300	1455	*	80	—	3.50	3100	885
110.65	20	3.80	7,765	2040	3.80	1443	380	1.80	509	285
113.30	10	6.80	20,004	2940	*	240	—	2.50	867	347
113.40	32	8.00	13,932	1655	3.50	840	240	13.45	1949	145
113.50	32	2.55	5,108	2005	3.50	470	135	1.60	398	250
120.35	11	8.45	31,000	3665	0.11	68	620	1.10	605	550
123.42	23	1.85	5,900	3190	4.15	728	175	1.85	832	450
130.35	12	4.55	10,600	2330	1.45	261	180	0.95	250	265
133.30	24	4.80	12,000	2500	0.25	152	610	10.80	1922	180
107.50	12	0.72	3,600	5000	0.25	244	975	1.20	316	265
107.55	10	1.10	2,676	2430	0.30	272	905	1.00	418	430
110.90	27	5.10	6,804	1335	8.10	1080	133	4.30	2450	570

* Present, volume less than 0.5%.

behind tentacle sheaths and comb rows as evidence of their presence. Hence, counts of organisms in a sample constitute a more conservative value than volume or weight.

Nevertheless, counts of individuals, to have value in quantitative assessments of biomass of standing crop, must be related in a meaningful way to volume or weight. Unless this is done, counts are of dubious utility. Obviously, 1,000 *Paracalanus parvus* are not equivalent in any meaningful way, except in number, to 1,000 *Calanus helgolandicus*. The volume occupied by the *Calanus* would be many times that occupied by the *Paracalanus*. Still other complications arise when dealing with numbers of organisms. Each species has a series of developmental stages that differ markedly in size. It might take a hundred or more larvae of *Euphasia eximia*, for example, to equal the mass of one adult.

Estimates of the number of individuals per ml. of wet volume have been derived for three groups: copepods, euphausiids, and chaetognaths (Table 10). Similar estimates can be derived for the other important constituent groups in the test samples. Copepods range in number from 1,335 to 5,000 individuals per ml., euphausiids from 133 to 975 individuals per ml., and chaetognaths from 145 to 885 individuals per ml. There are over seven times as many euphausiids per ml. in the sample from 5907-107.50 as in the sample from 5902-113.50, over six times as many chaetognaths in the sample from 5902-110.33 as in the sample from 5902-113.40. Obviously, data on numbers of individuals of a constituent group have limited value until they are related to volume or weight.

Although wet plankton volumes are over-estimates of the volume occupied by the organisms, due to included interstitial liquid, the amount of the latter can be determined with some precision. From determinations on test samples, interstitial liquid ordinarily makes up from 28 to 45 percent of the volumes of wet plankton samples, hence the amount is variable from sample to sample. Even so, a fairly adequate "average" value for interstitial liquid in our test samples would be 35 percent of the wet plankton volume.

The dry weight of a plankton sample is less subject to change with time than the "wet" weight (or volume). The major change in weight (volume) of "wet" plankton is due to water loss, which has the effect of concentrating the organic constituents. However, water loss is accompanied by an inorganic salt loss, which lowers the ash content of preserved samples. Organic substances appear to be more fully retained in the bodies of preserved plankton organisms. We have found only traces of nitrogen in the preserving liquids of undisturbed plankton samples that have been stored for considerable periods of time. Oils, however, are less fully retained. A verification of this loss is readily made on *Calanus*-rich samples in which the extracted oil can be seen as free-floating droplets.

Lovegrove (1961) has discussed some of the problems that arise in drying plankton for D.S. and O.S. determinations. Higher D.S. values are obtained when samples are dried by desiccation than when water is removed by oven drying, especially if the drying is done at temperatures above 60° C.

Most workers have related dry weights to wet weights of organisms. There has been little consistency in use of fresh or preserved material, perhaps because it was not appreciated that the volume measurements of live and preserved materials are not comparable. As is evident from our studies, volume determinations of preserved material will be less than "live" volumes by a variable amount depending on constituent composition and the time interval intervening since preservation. Obviously, dry weights should be related to the weight of freshly collected material, from which interstitial water has been removed. There is considerable merit in the oft-made suggestion that a plankton sample should be partitioned on collection, one part to be preserved, the other to be used for a dry weight determination. Technical difficulty in carrying out this suggestion has prevented its adoption as a standard technique.

A dry weight determination can be expressed as the amount of organic substances in a standard volume of water (1000 m³, for example). This determination bypasses most of the technical problems associated with relating dry weight to wet weight of plankton.

We have been intrigued by the strikingly similar dry weight determinations obtained on our test samples after two years of preservation, despite the marked differences in constituent compositions. The range in values of 56 mg. to 116 mg. per gram of preserved plankton (without interstitial liquid) constitutes a range of only 2X; furthermore, most values were grouped much more closely together. Apparently the nutrient compositions of samples have been made roughly comparable per unit volume (or weight) of plankton through the process of concentration of the volumes of jelly-like constituents relative to that of crustaceans and other constituents with an exoskeleton. An implication of this finding is that plankton volume determinations, *per se*, made on plankton samples that have reached their equilibrium volumes after a year of preservation, constitute meaningful measures of the standing crop of zooplankton.

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