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 analagous 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-

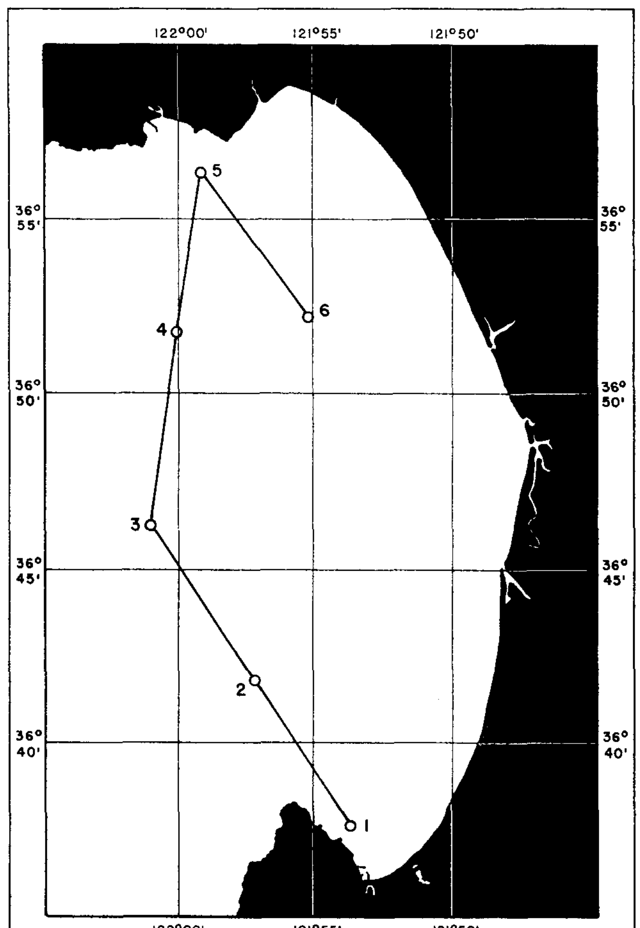

FIGURE 1. Monterey Bay, California, showing cruise pattern and station locations.

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manent buoys; each of the four remaining stations is considered to fall within a circular area of approximately ¼ 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 ¼ 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 ½ 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 °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

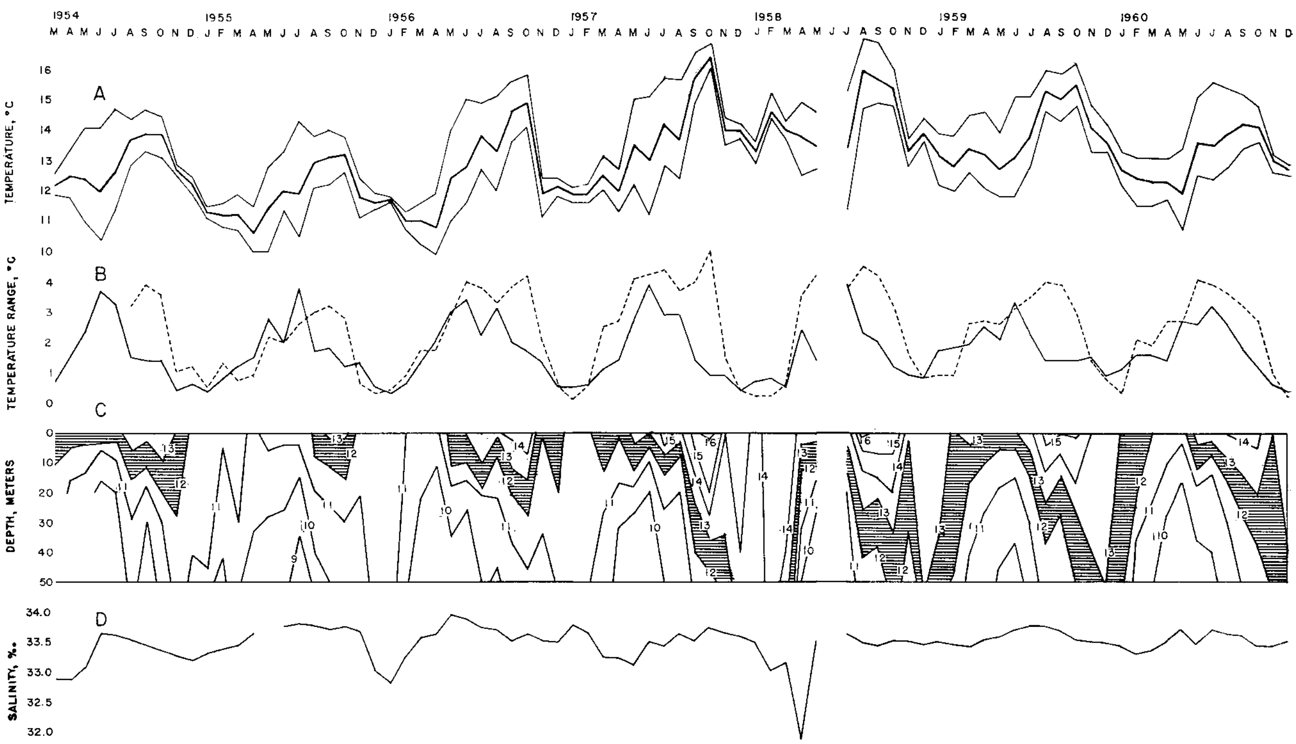

FIGURE 2. Monthly averages of temperature and salinity conditions in Monterey Bay for individual years 1954 through 1960. A. Surface temperatures (°C.) showing means, average monthly maxima and average monthly minima. B. Temperature spread (°C.) between average monthly maximum and minimum surface temperatures (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.

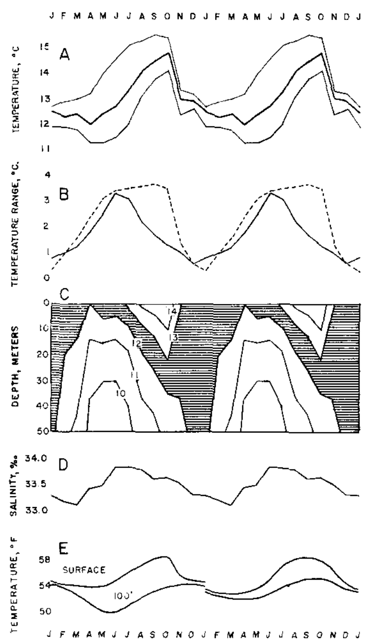

FIGURE 3. Average annual cycles of temperature and salinity, Monterey Bay, based on all the years 1954 through 1960. Figures A-D each show two identical complete cycles. A. Average surface temperatures (°C.); the central line traces the general average, the upper and lower lines trace the average monthly maxima and minima. B. Temperature spread (°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 (°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 Corioli'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 temperatures 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° C./50m. in October to 1.4° C./50m. 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 Corioli'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°C./50 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 characteristics. 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° 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 euphausid *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 declivifroms, Nematistius pectoralis* and *Kathetostoma averruncus* 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 chiliensis)*, 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 nannoplankton. 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 general 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

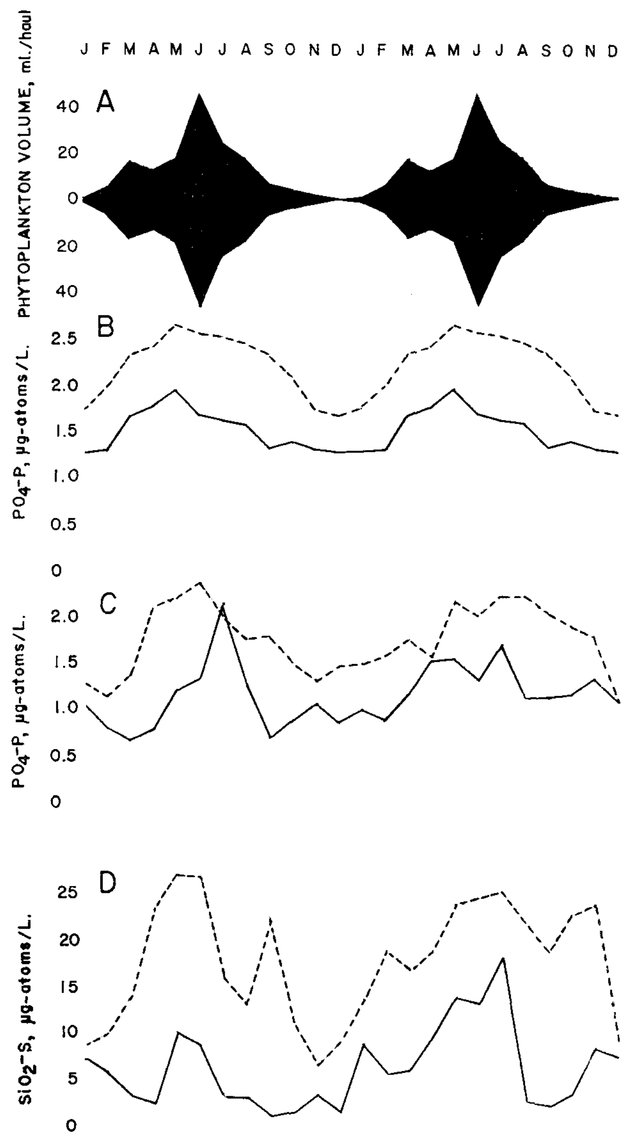

FIGURE 4. A. Average annual cyclic variation in phytoplankton standing crop (ml. per haul), based on all tows made during the years 1954-1960; two identical complete cycles are shown. B. Average annual cycle of phosphate-phosphorus, based on the period 1951-1955; two identical complete cycles are shown. 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 µg-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 simply 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 phophorus in µg-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).

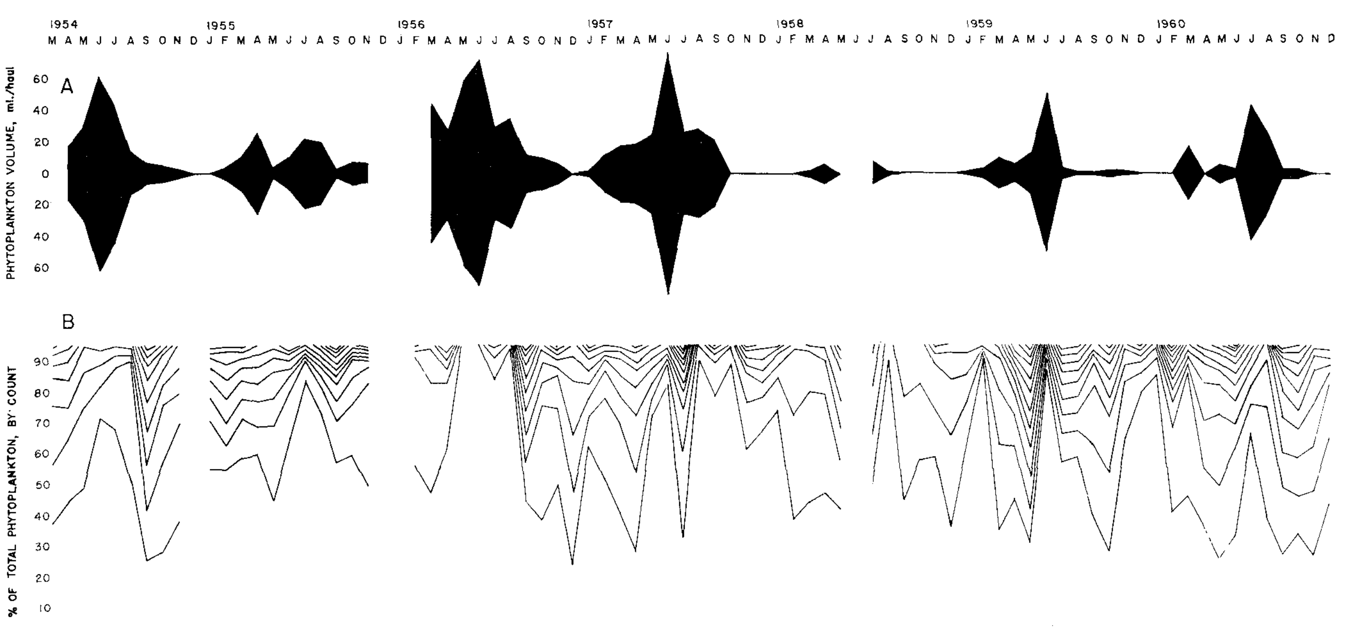

FIGURE 5. A. Monthly averages of the volume of the phytoplankton standing crop (ml. per haul), 1954 through 1960. B. Taxonomic composition of the phytoplankton, based on monthly averages of counts made on all hauls. The lowermost curve traces the percentage of the total phytoplankton contributed by the 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 µg-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 phosphate 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 innoculated 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 prectically 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-

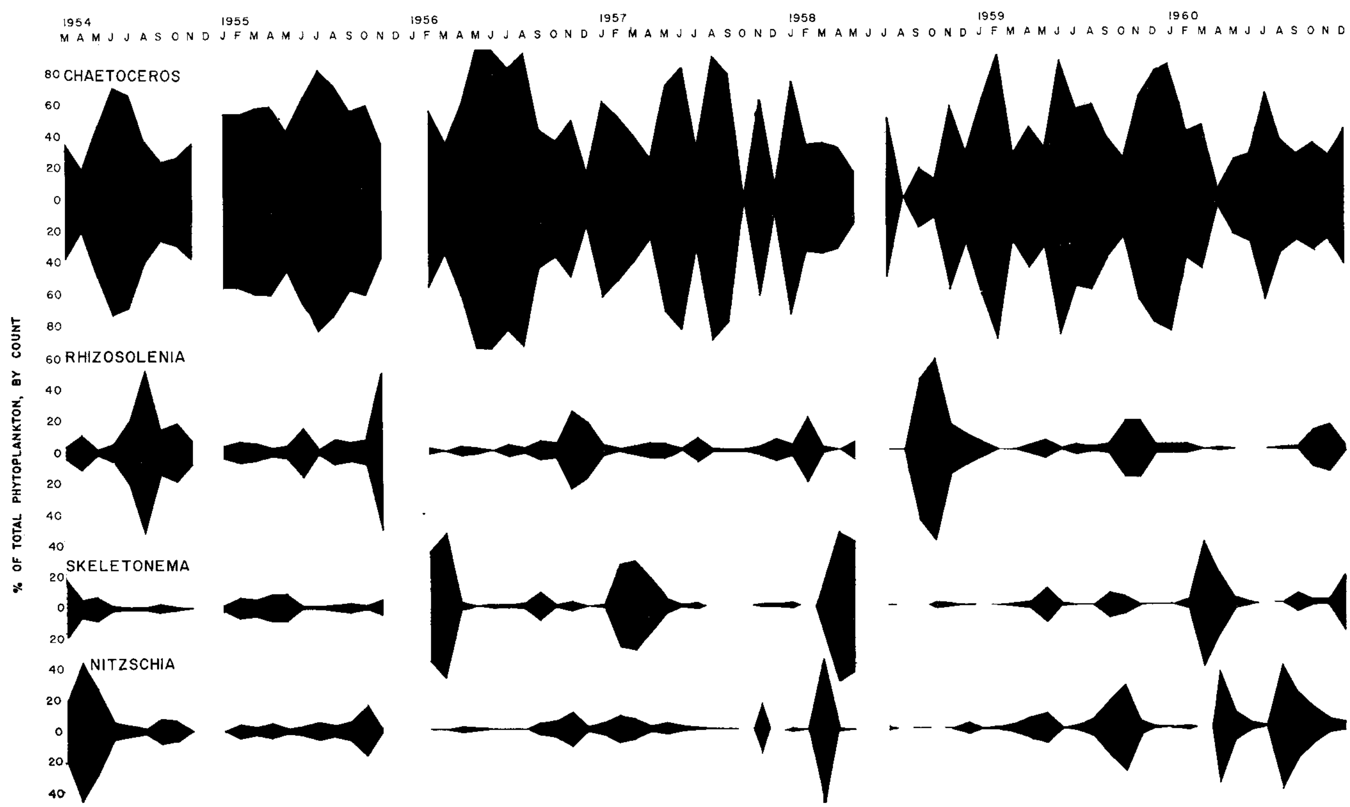

FIGURE 6. Relative abundance of the four commonest genera of diatoms, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

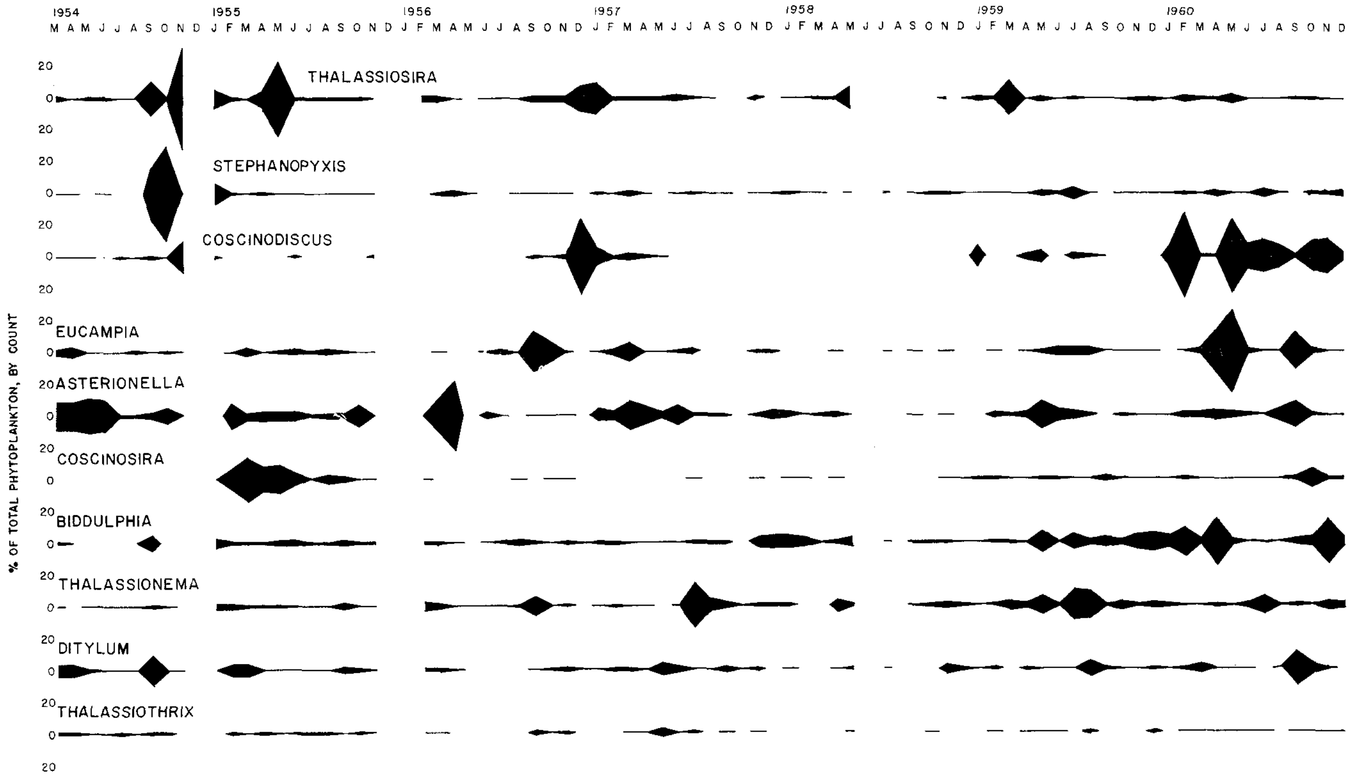

FIGURE 7. Relative abundance of ten genera of diatoms, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

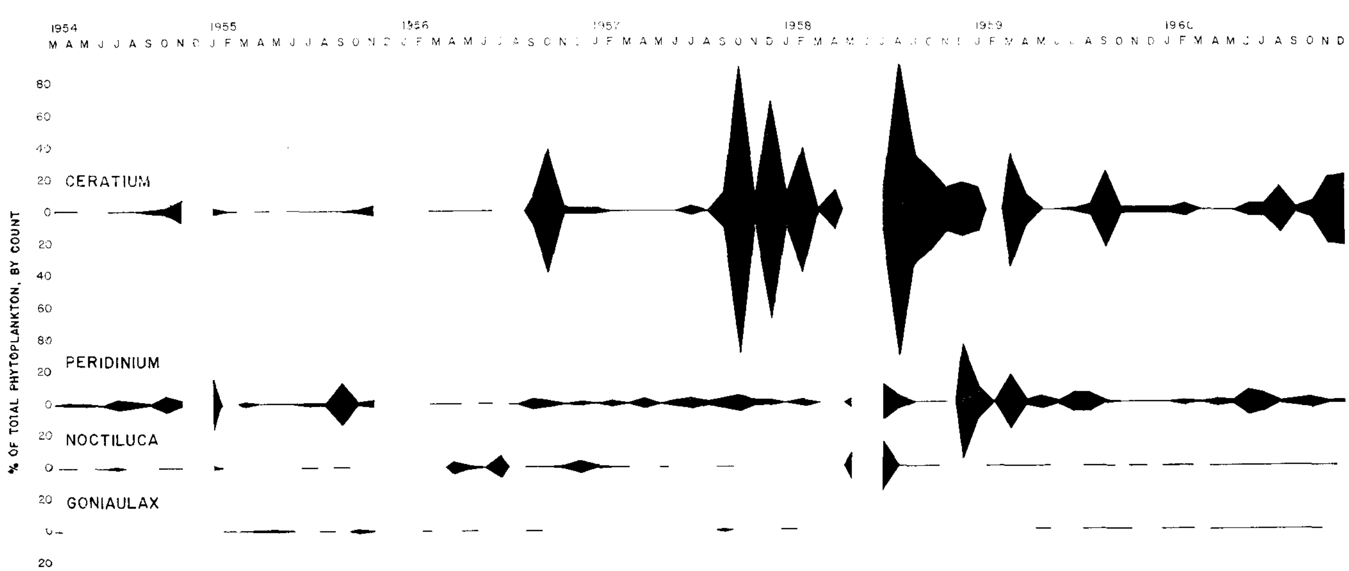

FIGURE 8. Relative abundance of the four commonest genera of dinoflagellates, expressed as percentage of the total phytoplankton; based on monthly averages of counts made on all hauls.

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
C. debilis	*C. didymus*	*C. lorenzianus*
C. decipiens	*C. affinis*	*C. costatus*
C. constrictus	*C. eibeni*	*C. messanensis*
C. radicans		*C. peruvianus*
C. convolutus		*C. daydi*
C. concavicornis		
C. socialis		

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 prominant 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. nitzschioides,* 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
R. styliformis	*R. stolterfothii*	*R. robusta (tolerant species)*
		R. calcar-avis
		R. acuminata
		R. bergonii
		R. temperei

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 scarely 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
C. lineatum	*C. dens*	*C. candelabrum*
C. azoricum (northern form)	*C. azoricum*	*C. horridum molle*
C. horridum var. genuinum	*C. extensum*	*C. macroceros gallicum*
———	———	*C. platycorne*
C. arcticum var. longipes	*C. furca*	**C. vultur pavillardi*
C. macroceros macroceros	*C. hexacanthum*	**C. trichoceros*
C. fusus	*C. massiliense*	**C. belone*
C. tripos	*C. arietinium*	**C. limulus*
		———
		C. gibberum

	Warm-water species
	*C. *axiale*
	C. *coarctacum*
	C. *contrarium*
	*C. *falcatiforme*
	*C. *inflatum*
	*C. *paradoxides*
	C. *pentagonum subrobustum*
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.	C. *semipulchellum*
	C. *strictum*
	C. *tenue*
	*C. *longirostrum*
	C. *kofoidii*
	C. *karsteni*

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 referrable 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 longicruris* 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 syliformis* 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 intermittant 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 *Thallassionema, 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 intermittant, 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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