BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
Volume 15

Oceanography of Long Island Sound, 1952-1954

Issued February 1956

published by
Peabody Museum of Natural History
Yale University
New Haven, Connecticut, USA
www.peabody.yale.edu

Contents

Yale University

BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY

VOLUME XV

OCEANOGRAPHY OF LONG ISLAND SOUND, 1952–1954

BY

GORDON A. RILEY
SHIRLEY A. M. CONOVER
GEORGIANA B. DEEVEY
ROBERT J. CONOVER
SARAH B. WHEATLAND
EUGENE HARRIS
HOWARD L. SANDERS

Issued February, 1956
New Haven, Conn., U. S. A.

OCEANOGRAPHY OF LONG ISLAND SOUND, 1952–1954[1]

By

Gordon A. Riley
Shirley A. M. Conover
Georgiana B. Deevey
Robert J. Conover
Sarah B. Wheatland
Eugene Harris
Howard L. Sanders

Volume XV

BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
Peabody Museum of Natural History
Yale University

Issued February, 1956
New Haven, Conn., U. S. A.

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and Yale University; reproduction in whole or in part is permitted for any purpose of the United States government.

OCEANOGRAPHY OF LONG ISLAND SOUND, 1952–1954

IV. PHYTOPLANKTON

By

Shirley A. MacMillan Conover

Bingham Oceanographic Laboratory

TABLE OF CONTENTS

ABSTRACT

The annual phytoplankton cycle in Long Island Sound has been considered from the standpoint of changes in the total population as estimated by cell counts and chlorophyll values, from the behavior of major taxonomic groups, and from seasonal variations in the abundance of individual species. Phytoplankton data have been correlated with environmental factors, and experimental work was undertaken to provide additional information about the physiology of the organisms and to test conclusions drawn from field data.

The annual cycle was characterized by a large late-winter flowering, lower numbers throughout spring and summer, small sporadic flowerings in summer and early fall, and minimal populations in late fall and early winter. Light and turbulence were the critical factors that determined population size in fall and winter. From the termination of the spring flowering until the breakdown of stability in late summer, nutrient supplies were the controlling factors; nitrogen appeared to be the most important limiting nutrient. Grazing may also have had some influence on the size of the summer populations. Turbulence was sufficient to maintain a nearly homogeneous vertical distribution. Although there was a difference in population numbers per unit volume of water between inshore and offshore waters, events in the phytoplankton cycle occurred at about the same time in both areas.

The population was dominated by diatoms except in summer, when dinoflagellates and probably other smaller flagellates largely replaced the diatoms. There was a clear-cut species succession, but environmental differences influenced the relative importance of certain species from year to year. Several examples of the way in which the environment controlled species abundance were afforded by this study. The importance of the physiological state of the natural population has been demonstrated experimentally.

THE ANNUAL CYCLE

Methods. Two types of analyses were employed to describe the quantity of phytoplankton, namely, estimation of chlorophyll *a*[1] and

[1] Rabinowitch (1952) described chlorophyll *a* as the ultimate photosynthetic pigment. That is, the accessory pigments of the plant cell may absorb light energy, but only chlorophyll *a* can convert this light energy to useable chemical energy. Consequently, the abundance of chlorophyll *a* ultimately determines the amount of photosynthesis.

cell counts. Samples were collected at weekly intervals at each of the stations visited from March 1952 through March 1954. Water for chlorophyll determination was taken from several depths and was analyzed using the method described by Riley and Conover in this volume. Samples for direct counts were taken at only the one-meter level except at St. 2, where proportional aliquots from each of the four or five depths were combined to give one composite sample. 225 ml of water were preserved with 25 ml of neutral formalin. The samples were allowed to settle for at least 48 hours and were then concentrated by siphoning off the supernatant liquid. The sample was transferred to a vial and the settling and concentration process was repeated. The concentrated sample was counted in a haemocytometer.

Certain objections have been raised to this counting method. Formalin preservation is inadequate for certain types of phytoplankton, particularly the small naked flagellates. Consequently this was probably a serious source of error in the summer samples. Also, there is the possibility that some of the sample was lost when the supernatant liquid was drawn off. However, when the supernatants from different samples obtained during periods of active growth were passed through a millipore filter and the latter was cleared for microscopic examination, the error was found to be less than 0.2%.

Description. From mid-December or early January, a steady increase in the phytoplankton population took place (Fig. 1). The climax of the flowering, the annual maximum, came after three weeks of rapid increase in early March 1953 and in mid-February 1954. After the climax was passed, the population decreased rapidly. Within a month it had passed through the period of decay that follows the flowering and had entered the spring and summer phase. The warmer months were characterized by small oscillations in abundance. A fall flowering was observed in the second year of the survey but not in the first. The annual minimum occurred sometime in the fall, and small populations were recorded throughout late fall and early winter.

The phytoplankton cycle as found in Long Island Sound is not unique. Late winter flowerings in temperate waters have been recorded in similar semiprotected areas. In New England waters, Bigelow, *et al.* (1940) found that the spring flowering commenced earlier in the partially protected bays than in the open waters of the Gulf of Maine. Fish (1925) and Bigelow (1926) reported that it

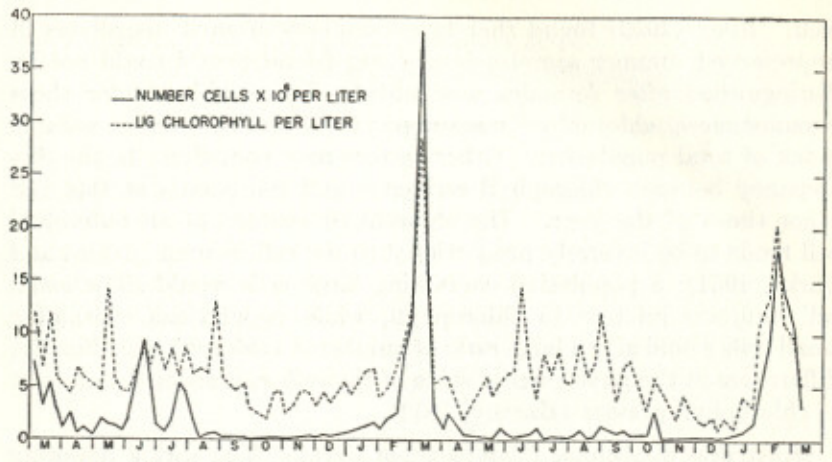

FIGURE 1. Phytoplankton cell numbers and chlorophyll, average surface values for all stations.

occurred even earlier in the shallow semienclosed bays of Cape Cod than in Long Island Sound. Records of similar observations along the Norwegian coast have been briefly summarized by Braarud, *et al.* (1953), and Steemann-Nielsen (1937) found the same pattern in waters around Denmark. The vernal flowering occurs later in British waters near Plymouth than in the more northern but more protected Scandinavian waters (Harvey, *et al.*, 1935). As in Long Island Sound, spring and summer populations in these areas were significantly smaller than in the vernal flowering. Atkins and Jenkins (1953) found an annual chlorophyll minimum in June at the Eddystone station off Plymouth, England. In Long Island Sound, the fall flowering was observed in late September and October. A small September phytoplankton peak was found at the Eddystone by Atkins and Jenkins (1953), but in an earlier study by Harvey, *et al.* (1935) in the same region, the late summer-early fall peaks were larger and one occurred later. A small September peak was found in the North Sea by Grøntved (1952). In winter all of these waters were characterized by small populations.

Chlorophyll-Cell Count Discrepancies. The data on the amount of chlorophyll and cell numbers paralleled each other reasonably well except in summer, when the chlorophyll values were significantly higher than the cell counts (Fig. 1). As was mentioned above, formalin does not preserve all segments of the plant population equally

well. Riley (1952) found that large numbers of small flagellates in unpreserved summer samples from Long Island Sound could not be distinguished after formalin was added. Presumably, under these circumstances, chlorophyll measurements would be a more reliable index of total population. Other factors may contribute to the discrepancy between chlorophyll estimates and cell counts at this and other times of the year. The chlorophyll content of an individual cell tends to be inversely proportional to the cell volume (Atkins and Parke, 1951); a population containing large cells would show small cell numbers relative to chlorophyll, while populations containing small cells would give a large ratio of numbers to chlorophyll. Finally, differences in the physiological state of the cells can affect the amount of chlorophyll present (Harvey, 1953).

Differences in Annual Phytoplankton Cycles. The spring flowering in 1954 was three weeks earlier than that in 1953. Fig. 1 and Table I show that cell numbers from the climax of the spring flowering through August were considerably greater in 1952 than in 1953; the same trend of differences, though less pronounced, was shown by the chlorophyll data. In 1953 a small flowering occurred in September and October, while in 1952 the lowest phytoplankton concentrations for the year were found in this period. Possible explanations for these differences will be considered when the population structure and the environment are discussed later.

Coefficients of Increase and Decrease of the Standing Crop. Weekly phytoplankton estimates can be used to calculate a coefficient K, which measures the relative rate of increase or decrease of the standing crop. An increase in the population may result from increased growth rates, decreased grazing rates, a decrease in the rate of loss by turbulence, introduction of a more concentrated population from another area, or any combination of these circumstances. A decrease in the standing crop may result from the converse of these conditions. K was calculated for both chlorophyll and cell numbers by using the following equation:

$$\ln P_t - \ln P_0 = Kt, \qquad (1)$$

where P_0 is the initial population, P_t the population at time t. K values are plotted in Fig. 2.

The values of the coefficients during the spring flowering did not exceed those found at other times of the year, but there was a sustained

TABLE I. MONTHLY MEANS.

	Estimated radiation, g cal/cm²/day								
	Surface			1 meter			5 meters		
Month	1952	1953	1954	1952	1953	1954	1952	1953	1954
Jan.	—	121	125	—	58	67	—	4	4
Feb.	—	251	186	—	122	83	—	7	2
March	321	253	(259)	194	113	(199)	26	6	(23)
April	401	345	—	262	242	—	48	40	—
May	480	440	—	299	288	—	50	58	—
June	530	651	—	284	389	—	24	48	—
July	623	608	—	319	314	—	27	30	—
Aug.	480	519	—	231	271	—	15	19	—
Sept.	422	446	—	254	267	—	34	43	—
Oct.	336	327	—	161	155	—	13	19	—
Nov.	171	177	—	88	77	—	9	3	—
Dec.	126	140	—	60	60	—	3	3	—

	Surface Temperature, °C			Phosphate P, μg-at/l			Nitrate N, μg-at/l		
Month	1952	1953	1954	1952	1953	1954	1952	1953	1954
Jan.	—	3.97	3.08	—	1.92	2.21	—	14.6	15.1
Feb.	—	3.11	1.68	—	1.69	1.41	—	13.5	4.0
March	3.11	3.93	(3.59)	0.99	0.82	(0.94)	2.1	2.74	(0.08)
April	6.68	6.80	—	1.09	0.61	—	3.0	0.44	—
May	10.87	13.01	—	0.64	0.47	—	1.8	0.20	—
June	17.30	16.02	—	0.39	0.41	—	0.3	0.08	—
July	21.22	21.33	—	0.85	0.62	—	0.31	0.17	—
Aug.	22.80	21.73	—	1.15	1.14	—	0.50	0.21	—
Sept.	21.41	21.48	—	1.58	1.29	—	2.32	1.68	—
Oct.	15.52	17.31	—	2.50	1.82	—	10.4	3.62	—
Nov.	11.77	12.33	—	2.28	2.07	—	13.7	8.9	—
Dec.	7.39	8.57	—	2.35	1.93	—	16.3	12.0	—

	Chlorophyll, μg/l			Cell numbers × 10³/l		
Month	1952	1953	1954	1952	1953	1954
Jan.	—	5.8	2.9	—	1296	969
Feb.	—	8.2	14.2	—	3422	11347
March	9.0	15.4	(7.5)	4754	17216	(6936)
April	5.6	4.6	—	1333	1405	—
May	6.9	5.1	—	1244	511	—
June	7.0	7.6	—	5836	641	—
July	7.7	7.0	—	2822	309	—
Aug.	8.1	7.0	—	826	495	—
Sept.	4.7	7.8	—	233	900	—
Oct.	3.6	4.5	—	197	1127	—
Nov.	3.7	3.0	—	269	239	—
Dec.	4.2	1.8	—	442	269	—

period of positive values at that time. The vernal flowering apparently resulted from conditions that were favorable to steady growth with population accumulation rather than from a sudden change in the physiological state of the phytoplankton with a resultant increase in growth rate. Note that the highest spring flowering values of K occurred at irregular intervals during the flowering period.

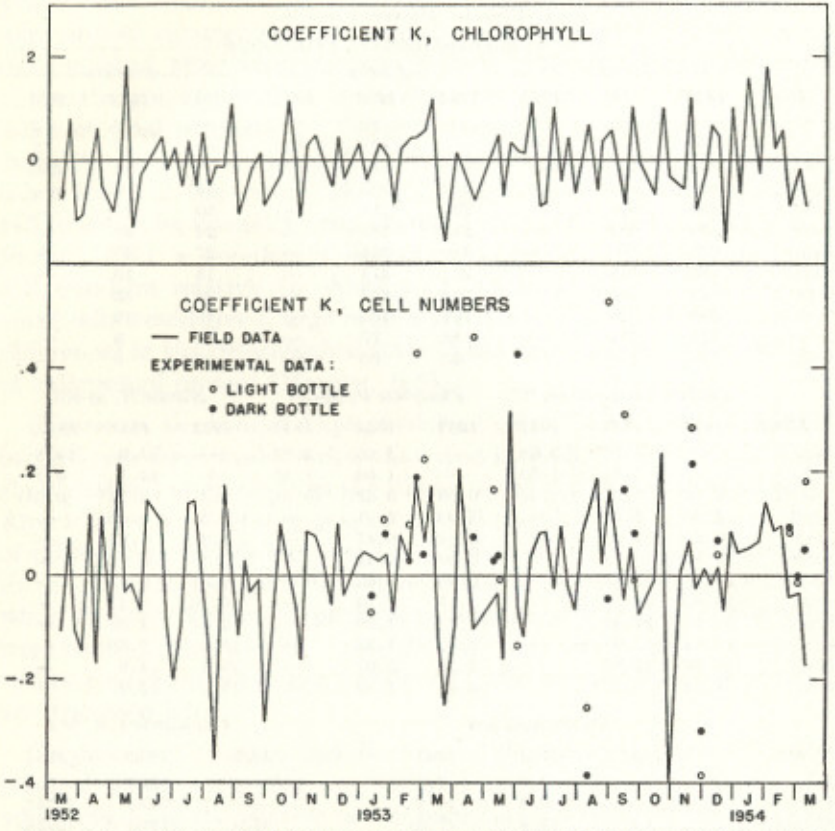

FIGURE 2. Coefficients K, based on cell numbers and chlorophyll; average surface values for all stations.

The natural population did not necessarily follow the classical logistic growth curve demonstrated for laboratory cultures. In the post-flowering period, the negative coefficients were larger than the positive values found during the flowering development. Fluctuation between positive and negative values was characteristic of the spring and summer months, but a greater number of positive values were recorded in 1952 than in 1953. The values of the coefficients for the two years reflected differences in the early fall cycles; in 1952 K values were largely negative, while in 1953 a distinct positive trend was observed from August through October. Late fall and early winter coefficients showed small fluctuations about zero (Fig. 2), indicating

that the population was merely maintained. The first stages of the spring flowering were indicated by the predominantly positive values of K in January.

Vertical Distribution. Unlike the deeper and more exposed southern New England waters such as Block Island Sound (Riley, 1952), concentrations of phytoplankton in the shallow and turbulent waters of Long Island Sound were fairly uniform from surface to bottom (Fig. 3). At times, particularly during active growth, there were

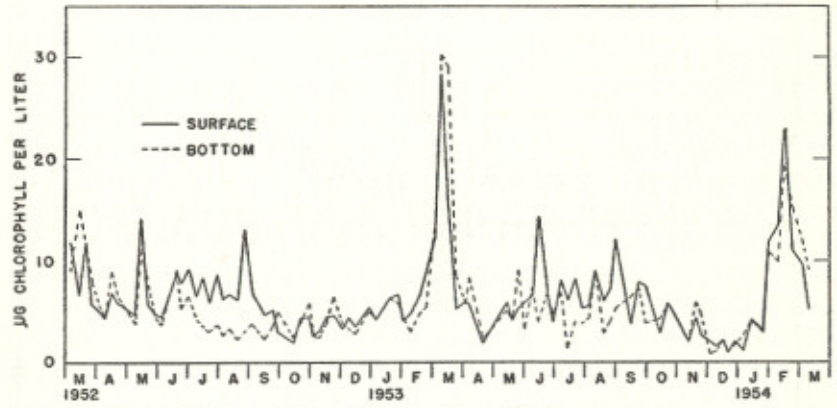

FIGURE 3. Distribution of chlorophyll in surface and bottom waters; average values for all stations.

greater concentrations in surface than in bottom waters. More chlorophyll was found in bottom waters just after the termination of periods of active growth and throughout the fall months. The horizontal movement of water masses could also account for some of the vertical variations in quantity. However, all such variations were small compared with the differences commonly observed in deeper and more stable waters.

Horizontal Distribution. At times there was a pronounced difference in concentration of surface phytoplankton between inshore and offshore stations (Fig. 4). In general, both cell numbers and chlorophyll concentrations per unit volume tended to be larger in the inshore waters. However, the total amount of phytoplankton underlying a unit area of sea surface was frequently greater offshore, as indicated in Table II. Chlorophyll estimates in Table II represent the average

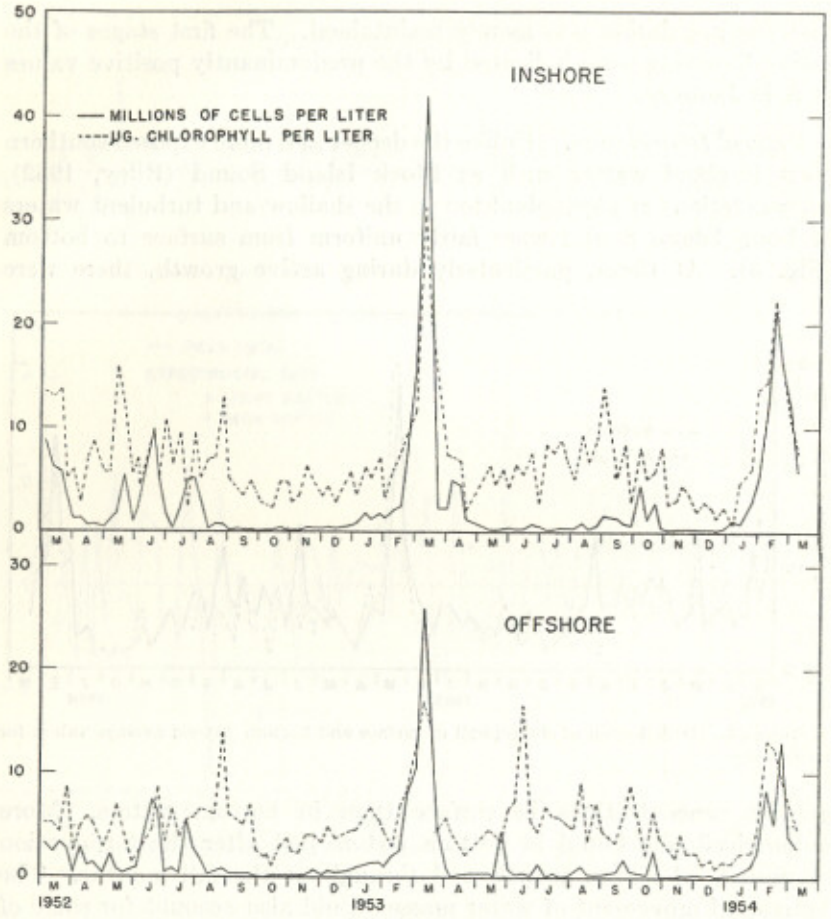

FIGURE 4. Cell number and chlorophyll distribution at inshore and offshore stations.

concentration at the several depths sampled multiplied by the depth of the water column. The estimate of cell numbers is a relatively crude one, since all of the counts were of surface samples, excepting St. 2. The latter is used in Table II to represent offshore conditions; the inshore estimate is based on the average surface concentration for all inshore stations multiplied by the average inshore station depth.

The concentration of phytoplankton in the Sound was considerably greater than that in other New England waters, and the quantity

TABLE II. COMPARISON OF CHLOROPHYLL AND CELL NUMBERS UNDER 0.1 M² OF SEA SURFACE FROM INSHORE AND OFFSHORE POSITIONS IN LONG ISLAND SOUND

	μg chlorophyll		Cell numbers × 10^6	
Date	*Inshore*	*Offshore*	*Inshore*	*Offshore*
May 14, 1952	1367	1381	181.6	149.6
July 22	713	591	497.5	641.0
Oct. 21	424	1036	36.4	24.8
Dec. 29	563	772	54.5	136.2
March 9, 1953	3342	3511	4166.3	5184.0
June 8	742	1154	31.5	68.4
Aug. 18	397	666	26.0	59.6
Oct. 21	661	979	273.6	502.6
Feb. 17, 1954	1925	2870	2133.8	1023.8

per unit area probably averaged slightly more. However, the highest spring flowering figures in the Gulf of Maine (Bigelow, *et al.*, 1940) were larger than those for Long Island Sound. In the waters around the Eddystone, Atkins and Jenkins (1953) obtained figures considerably larger than those for Long Island Sound; chlorophyll concentrations per cubic meter were comparable to those of Long Island Sound, but the column of water was four times deeper than that at the average offshore station in the Sound.

Although the size of the phytoplankton population per unit volume of water at inshore and offshore stations was often different, the sequence and occurrence of specific events corresponded closely in the two areas (Fig. 4). There are two possible explanations for this uniformity. Either the environmental character of the inshore and offshore waters was not significantly different, or else there was sufficient horizontal mixing to prevent differences in time of occurrence of specific events such as were found between coastal and offshore waters in the Gulf of Maine and in the North Sea. The spring flowering peak of 1954 was a minor exception; it occurred offshore one week later than inshore. However, this difference might simply have resulted from a sampling error.

Phytoplankton Composition. A breakdown of the population into groups, *i.e.*, centrate diatoms, pennate diatoms, dinoflagellates, and silicoflagellates, gives information which is masked in the consideration of the population as a whole and is lost in the detail of species analysis (Fig. 5). The spring flowering was made up chiefly of centrate diatoms. Although pennate diatoms and silicoflagellates showed distinct increases at this time, their numbers were insignificant in comparison with the centrate diatoms. Centrate diatoms con-

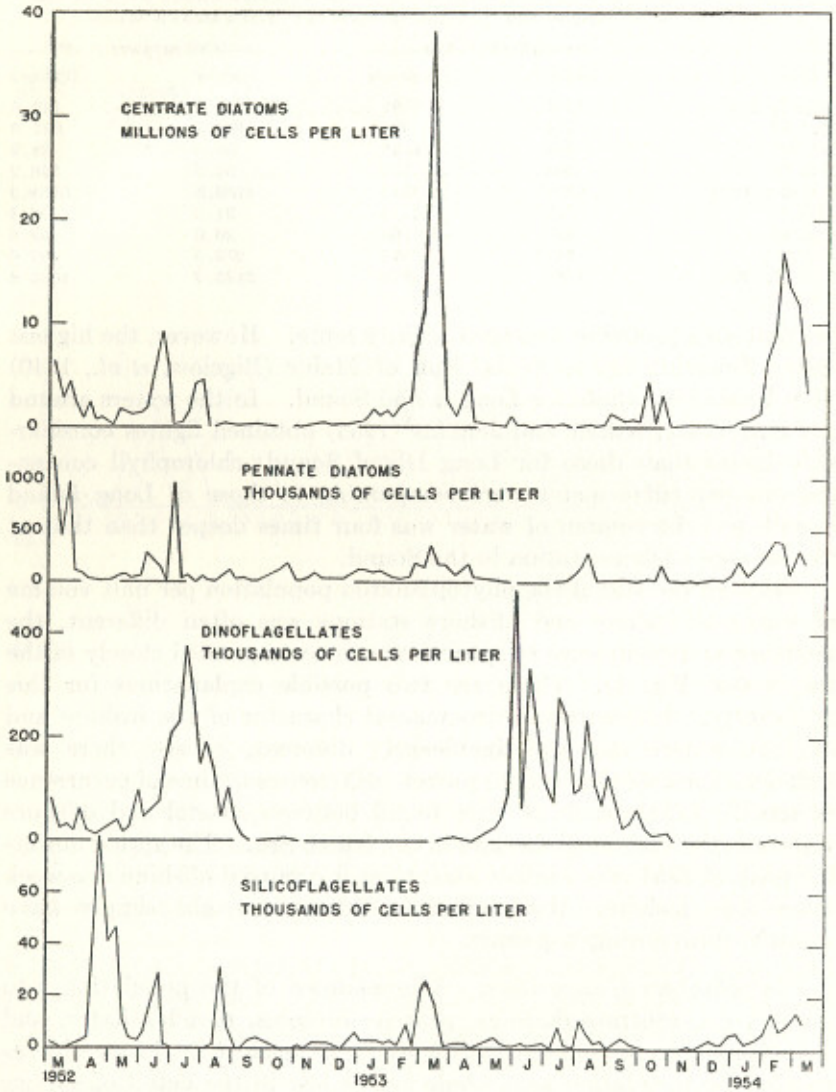

FIGURE 5. Distribution of the major taxonomic groups, averaged for all stations.

tinued to be dominant through the spring months. In the summer, dinoflagellates comprised the most abundant segment of the population; the possible importance of small flagellates at this time has been mentioned previously. The difference between the spring and summer periods of 1952 and 1953 is re-emphasized by these data. In the spring and early summer, centrate diatoms were much more abundant in 1952 than in 1953, and the peaks of phytoplankton numbers typical of this period in 1952 were due to diatoms (Fig. 1). Conversely, in 1953 the population of dinoflagellates in late spring and summer was much greater than that of the same period in the previous year. In late summer, centrate diatoms became dominant again, and the fall flowering of 1953 was made up largely of this group. The small late fall and early winter populations were composed of centrate diatoms, pennate diatoms, and silicoflagellates, the centrate diatoms being the most abundant. The latter continued to dominate the population as it entered the spring flowering phase. As the flowering progressed, the large proportion of centrate forms relative to the other groups became even more exaggerated. When the annual crop of phytoplankton is considered, the greatest proportion, either numerically or with respect to weight of organic matter produced, was contributed by the centrate diatoms. Only in summer did another group, the dinoflagellates, assume a dominant position in the phytoplankton community.

The seasonal distribution of the major constituents of phytoplankton in the Sound is similar to that reported for Norwegian coastal waters by Braarud, *et al.* (1953). During winter, when the light intensity was low, they found that the surface waters became enriched through turbulence. As the light increased in spring, a diatom succession characteristic of the locality took place. After the diatom bloom had lowered nutrient supplies, the dinoflagellates became dominant. According to Grøntved (1952), the same group succession was found in the southern North Sea if nutrient renewal was sufficient and if grazing was not too severe. He believed that the late spring change from diatom to dinoflagellate dominance resulted from the establishment of thermal stability which prevented nutrient renewal through turbulent mixing; the nutrients were not completely depleted in the euphotic zone before the change took place. It was suggested that reduced competition between major phytoplankton groups, selective grazing by zooplankton, and "ecological conditions" aided

the cause of the dinoflagellates. Interestingly enough, the replacement of diatoms by dinoflagellates was later in 1947, the cooler year, than in 1948.

EXPERIMENTAL STUDIES

Experiments were designed to measure the effect of variations in light, temperature, and nutrients on the natural phytoplankton populations at various times during the year. Measurements were made of the amount of oxygen produced in photosynthesis and consumed in respiration. Changes in size and composition of the population were determined in all experiments, and in some, changes in chlorophyll and nutrient concentrations were also measured. These experiments were done with raw sea water, so that bacteria and small zooplankton as well as phytoplankton were included in the experimental bottles.

Methods. Sea water for the experiments was usually taken at one of the regular stations. If the experiment was a small one, the bottles were filled directly from the Nansen bottle. For larger experiments a carboy was filled, thoroughly agitated, and experimental aliquots were drawn off into the appropriate bottles. In experimental work that involved oxygen determinations, a glass bottle of suitable volume which contained a few glass beads for mixing purposes was completely filled with water, tightly stoppered, and thoroughly mixed twice; the oxygen bottles were then filled from this in the usual manner.

The light and dark bottle technique was employed to measure oxygen production and consumption, using 125 ml reagent bottles. Some of the bottles were exposed to natural illumination while others were placed in black cloth bags. At the end of an experiment, Winkler reagents were added to the bottles, care being taken to retain any bubbles of gas. Aliquots for cell counts and other analyses were taken from other bottles which had been treated in the same manner as the oxygen bottles. Furthermore, in the 1954 experiments, some of the bottles were covered with different thicknesses of cheesecloth so as to alter the amount of illumination received by the enclosed phytoplankton. The amount of light transmitted by the different amounts of cheesecloth was estimated in the Klett-Summerson Colorimeter; a glass microscope slide was wrapped in the required number of thicknesses of cloth and immersed in water in the measuring cell. Several different colored filters were employed, but the wave length had

little effect on the percentage of light transmitted. The average values are summarized in Table III.

TABLE III. Radiation Transmitted and Depth Equivalents in Meters for Gauze-Enclosed Experimental Bottles

No. layers of gauze on bottle	*% light penetration*	*Depth equivalent when Secchi disc equals:* 1 m	2 m	3 m
2	24	0.8	1.6	2.5
4	8	1.5	2.9	4.4
6	3	2.1	4.1	6.1
8	1	2.7	5.4	8.1

Five experiments during the spring flowering of 1954 measured the effect of increased temperature on phytoplankton. Bottles were kept in tanks at the Milford Laboratory near a north window at a higher temperature than the rest of the experiment. Light conditions in these warmer bottles were probably not exactly the same as those in the bottles suspended in Milford Harbor, but they were close enough so that differences in results in the two sets of bottles must be attributed to temperature and not to light.

The effects of nutrients were also tested, singly and in various combinations. *P* and *N* were employed in all experiments, and in some experiments iron, manganese, citric acid, soil extract, and dextrose were used as well. Nitrogen was added as $NaNO_3$, phosphorous as KH_2PO_4, manganese as $MnCl_2$, and iron as ferric citrate with citric acid as a chelator (Rodhe, 1948). *P* and *N* were never added in quantities greater than the maximum quantities found in the Sound. The other inorganics were added in similar small amounts. Additions of soil extract were 1% or less of the volume of the experimental water.

Usually the experimental bottles, placed in wire cages, were suspended to a depth of 0.5 m in Milford Harbor, Connecticut. The cage was hung from a boat mooring line to eliminate changes in depth with tidal fluctuations. In this manner natural conditions of light and temperature were duplicated as closely as possible. A few oxygen experiments were done at anchor stations in the summer of 1953. Here water was taken from a series of depths, and the experimental bottles were resuspended at those depths for the duration of the experiment. Three experiments in February 1954 were kept in the dock house at the Milford Laboratory because the Harbor was iced over; light conditions in these experiments were unnatural, since

the bottles were immersed in tanks in a building with only small windows.

Oxygen Experiments. Fig. 6A summarizes the results of the oxygen experiments. Moderate to high production of oxygen and low

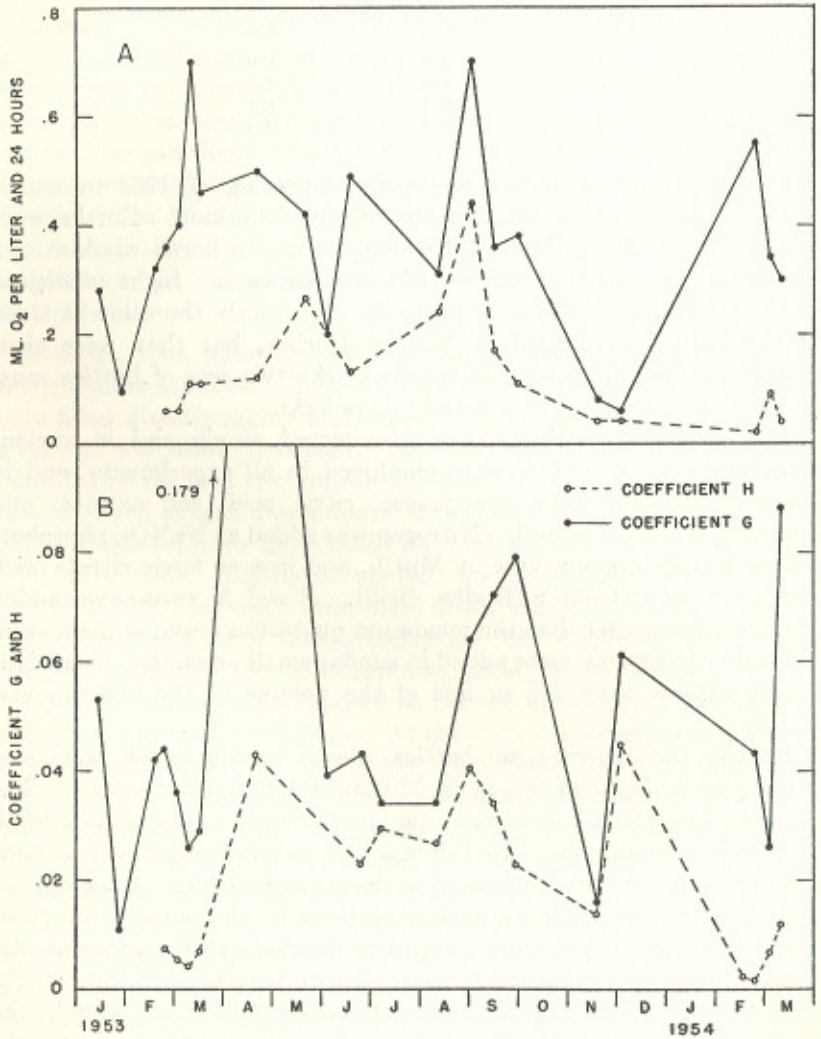

FIGURE 6. A. Oxygen production (solid circles) and consumption (open circles). B. Coefficients of oxygen production (Coeff. G) and consumption (Coeff. H).

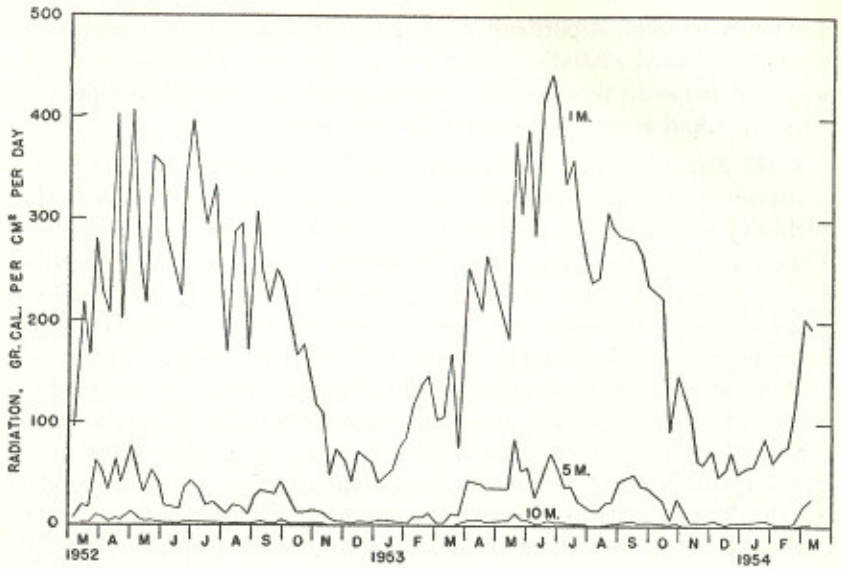

FIGURE 7. Estimated light reaching several depths in Long Island Sound over a two year period.

respiration were associated with the spring flowering and the spring period generally. In summer, oxygen production was less and oxygen consumption was markedly higher than in the earlier months. Moderate to high oxygen production was characteristic of the fall months, while consumption decreased progressively from the summer maximum. Winter was a time of minimum oxygen production and consumption.

To make results of the oxygen experiments comparable, coefficients of photosynthesis and respiration were calculated as the amount of oxygen produced or consumed in ml per 24 hours per μg of chlorophyll. These data are plotted in Fig. 6B. When Figs. 6A and 6B are compared, it is obvious that the amount of oxygen produced or consumed was not simply a function of the amount of chlorophyll present. For instance, during the spring flowering in 1953, production coefficients in late February for the early stages of the flowering were higher than those observed during the climax a few weeks later.

The photosynthetic and respiratory coefficients were compared with growth coefficients in natural and experimental populations, initial nutrient concentrations, light, and temperature. This com-

parison was only superficial, since the data were not adequate to warrant detailed statistical treatment. The only obvious correlation was that between temperature and respiration, although temperature may have had some influence on photosynthesis as well.

Light Experiments. The amount of light available to the phytoplankton in the natural environment varies with incident radiation, turbidity of the water, and the depth of the cell in the water column. Experimentally, light was varied by means of the gauze bags described above. Measurements of oxygen production showed that there was a relationship between the amount of radiation received by the experimental bottle and the photosynthetic coefficient. The results of four experiments are graphed in Fig. 8. While photosynthesis appears to depend on the amount of available light, all of the curves for the four experiments are different, suggesting that light is not the only factor that influences oxygen production. The population which showed greatest growth in enrichment and temperature experiments was also affected most strikingly by variations in light intensity (Fig. 8). The two higher curves were obtained with populations taken at the peak of the spring flowering and several weeks after the climax. The population that was present immediately after the climax of the flowering had a much lower level of response to light, suggesting a possible depression in the physiological state of the cells at that time.

Although maximum cell numbers and maximum chlorophyll values did not necessarily occur in the same bottle, the highest values for chlorophyll and cell production were found consistently in bottles receiving less than the maximum available light, and they were also found occasionally in bottles receiving the minimum amount (see Table IV). In an early summer experiment in 1954, the greatest increase in cell numbers occurred in an unenriched bottle covered with two layers of gauze. This increase was due to growth of several diatoms, namely *Leptocylindricus danicus*, *Skeletonema costatum*, and *Thalassionema nitzschioides*. In this experiment higher chlorophyll values were obtained in some of the enriched bottles, but this increase appeared to result primarily from the growth of small flagellates.

Some of the most important results of the light experiments were found in the response of different species to varying amounts of radiation. Experiments during the early spring flowering of 1954 showed that *Skeletonema costatum* had the highest growth rate coef-

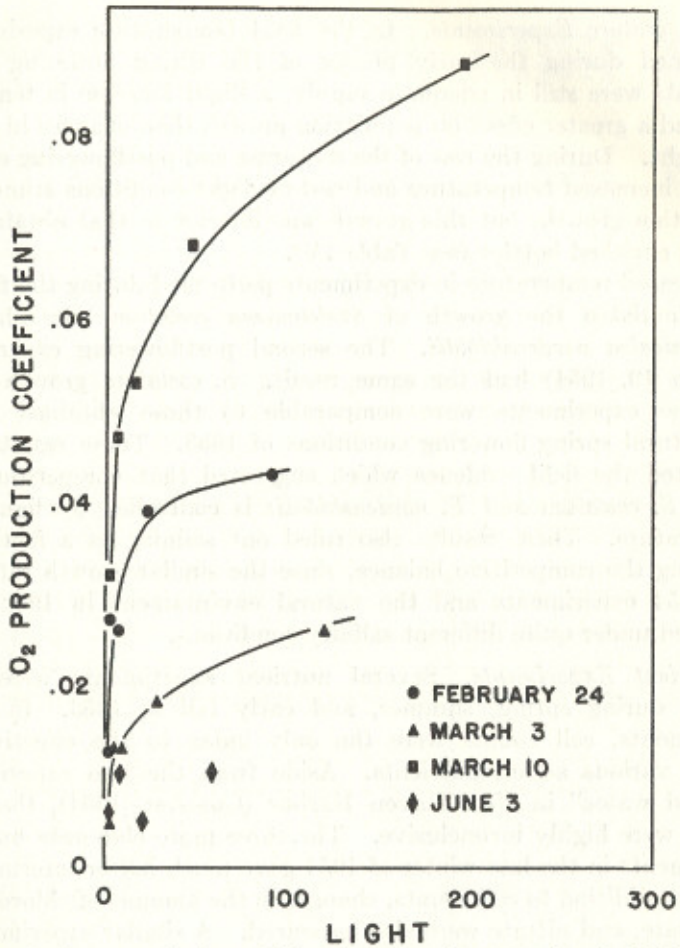

FIGURE 8. Oxygen production coefficients in four experiments as related to light intensity (g cal/cm³ in a day).

ficient K in bottles receiving greater amounts of light. In bottles receiving smaller amounts of radiation, *Thalassiosira nordenskiöldii* had the highest K values, and those were almost all greater than any of the *S. costatum* K values.

K values in dark bottles usually had the same sign (*i.e.*, positive or negative) as the K values in the corresponding light bottles, but they were smaller. The K values obtained in the bottles and in the Sound for the same population often were quite different (Fig. 2).

Temperature Experiments. In the 1954 temperature experiments, performed during the early phases of the spring flowering when nutrients were still in adequate supply, a slight increase in temperature had a greater effect on population growth than changes in available light. During the rest of the flowering and postflowering experiments, increased temperature and certain light conditions stimulated population growth, but this growth was inferior to that obtained in certain enriched bottles (see Table IV).

Increased temperature in experiments performed during the flowering stimulated the growth of *Skeletonema costatum* but inhibited *Thalassiosira nordenskiöldii*. The second postflowering experiment (March 10, 1954) had the same result. *S. costatum* growth rates in these experiments were comparable to those obtained under the natural spring flowering conditions of 1953. These results corroborated the field evidence which suggested that competition between *S. costatum* and *T. nordenskiöldii* is controlled by light and temperature. These results also ruled out salinity as a factor influencing the competitive balance, since the similar growth rates for the 1954 experiments and the natural environment in 1953 were obtained under quite different salinity conditions.

Nutrient Experiments. Several nutrient experiments were conducted during spring, summer, and early fall in 1953. In these experiments, cell counts were the only index to the effectiveness of the various added nutrients. Aside from the two experiments on "red water" in New Haven Harbor (Conover, 1954), the 1953 results were highly inconclusive. The three more elaborate nutrient experiments in the late winter of 1954 gave much better information, since, in addition to cell counts, changes in the amount of chlorophyll, phosphate, and nitrate were also measured. A similar experiment in the summer of 1954 showed conclusively that cell counts were not an adequate measure of change in the enriched experimental bottles. Great increases in chlorophyll and utilization of nutrient supplies were not reflected in a corresponding change in cell numbers, so it may be assumed that many of the actively growing organisms did not withstand formalin. These results suggest that the 1953 experiments were inadequate for the purpose, in that insufficient measurements were made of the various aspects of population growth. However, they provided a small amount of useful information that will be included under the discussion of individual species.

TABLE IV. SUMMARY OF DATA FOR SIX EXPERIMENTS IN THE WINTER AND SPRING OF 1954. WHEN NUTRIENTS WERE USED, THEY WERE ADDED IN THE FOLLOWING AMOUNTS PER LITER: 20 µg-at NO_3-N, 2 µg-at PO_4-P, 1 µg-at Mn, and 0.2 µg-at Fe. A WEIGHT OF CITRIC ACID (CA) EQUAL TO THE WEIGHT OF FERRIC CITRATE WAS USED PER LITER. IA = INITIAL ANALYSIS; LB = LIGHT BOTTLE; DB = DARK BOTTLE; 2 G = 2 LAYERS GAUZE, ETC. ALL EXPERIMENTS EXCEPT THE FIRST TWO HAD APPROXIMATELY NORMAL LIGHT EXPOSURE, LISTED AS g cal/cm²/day.

	Oxygen experiments				*Other experiments*						
	No. days	*Est. rad.*	*Av. temp.*	O_2 *ml/l*	*No. days*	*Est. rad.*	*Av. temp.*	*P µg-at/l*	*N µg-at/l*	*Chlor. µg/l*	*Thous. of cells/l*
February 10. Experiment kept in unnatural light conditions in dock house.											
IA	—	—	—	8.27	—	—	—	1.23	1.4	15.5	14,085
LB	2	—	1.7	9.06	2	—	1.7	1.53	1.1	26.8	17,160
LB & 2G	2	—	1.7	8.76	2	—	1.7	1.64	1.1	30.7	14,550
LB & 4G	2	—	1.7	8.71	2	—	1.7	1.67	1.1	22.6	16,200
LB & 6G	2	—	1.7	8.65	2	—	1.7	1.66	1.2	28.2	14,070
LB & 8G	2	—	1.7	8.61	2	—	1.7	1.58	1.2	21.9	19,040
DB	2	—	1.7	8.48	2	—	1.7	1.67	1.1	23.7	14,230
With increased temperature:											
LB		—	—	—	2	—	5.0	1.51	0.0	33.4	17,050
LB		—	—	—	2	—	8.0	1.51	0.0	33.4	19,150
LB		—	—	—	7	—	5.0	0.95	0.0	25.7	18,203
LB		—	—	—	7	—	8.0	0.78	0.0	39.4	29,020
February 17. Experiment kept in unnatural light conditions in dock house.											
IA	—	—	—	8.50	—	—	—	1.19	0.03	23.1	32,390
LB	2	—	2.4	8.75	2	—	2.4	1.12	0.03	24.2	16,390
LB & 2G	2	—	2.4	8.65	2	—	2.4	1.11	0.03	32.5	23,530
LB & 4G	2	—	2.4	8.54	2	—	2.4	1.18	0.05	23.7	26,031
LB & 6G	2	—	2.4	8.50	2	—	2.4	1.17	0.7	24.6	20,530
LB & 8G	2	—	2.4	8.42	2	—	2.4	1.21	0.05	16.4	19,920
DB	2	—	2.4	8.41	2	—	2.4	1.21	1.5	22.8	21,700
With increased temperature:											
LB		—	—	—	2	—	5.0	1.04	0.0	27.7	26,030
LB		—	—	—	2	—	8.0	1.01	0.0	21.1	19,320
LB		—	—	—	7	—	5.0	0.89	0.2	24.7	24,400
LB		—	—	—	7	—	8.0	1.24	0.0	30.6	28,750

TABLE IV.—*Continued*

	Oxygen experiments				Other experiments						
	No. days	*Est. rad.*	*Av. temp.*	*O_2 ml/l*	*No. days*	*Est. rad.*	*Av. temp.*	*P µg-at/l*	*N µg-at/l*	*Chlor. µg/l*	*Thous. of cells/l*
February 24.											
IA	—	—	—	8.48	—	—	—	1.06	0.1	12.8	12,340
LB	2	91	3.7	9.54	5	107	3.8	0.83	0.1	13.0	18,570
LB & 2G	2	22	3.7	9.44	5	26	3.8	0.89	0.1	16.6	25,200
LB & 4G	2	7	3.7	9.09	5	9	3.8	0.95	0.06	12.5	20,200
LB & 6G	2	3	3.7	9.14	5	3	3.8	0.89	0.00	17.0	23,560
LB & 8G	2	0.8	3.7	8.76	5	1	3.8	0.82	0.05	11.4	22,850
DB	2	—	3.7	8.44	5	—	3.8	1.06	0.1	13.3	19,260
LB with nutrients added:											
P	—	—	—	—	5	107	3.8	2.88	0.05	17.2	16,360
N	—	—	—	—	5	107	3.8	0.56	12.6	24.4	25,370
Mn	—	—	—	—	5	107	3.8	0.86	0.03	12.8	18,360
Fe	—	—	—	—	5	107	3.8	0.86	0.00	15.0	16,840
Ca	—	—	—	—	5	107	3.8	0.84	0.06	13.3	15,850
P,N	—	—	—	—	5	107	3.8	2.32	12.5	29.7	22,350
P,N,Mn	—	—	—	—	5	107	3.8	2.38	11.5	23.5	21,080
P,N,Fe	—	—	—	—	5	107	3.8	2.29	9.3	29.6	20,920
P,N,CA	—	—	—	—	5	107	3.8	2.30	10.6	28.2	21,690
P,N,Mn,Fe	—	—	—	—	5	107	3.8	2.34	9.9	31.7	16,340
P,N,Mn,CA	—	—	—	—	5	107	3.8	2.30	8.9	29.3	23,470
With increased temperature:											
LB	—	—	—	—	5	5	7.0	0.77	0.2	19.3	31,690
LB	—	—	—	—	7	5	7.0	0.62	0.06	17.2	22,960
March 3.											
IA	—	—	—	8.09	—	—	—	0.76	0.06	13.2	21,730
LB	2	119	3.7	8.59	5	163	2.7	0.68	0.05	16.6	19,870
LB & 2G	2	28	3.7	8.39	5	39	2.7	0.73	0.03	21.6	21,300
LB & 4G	2	9	3.7	8.26	5	13	2.7	0.79	0.04	16.6	25,270
LB & 6G	2	5	3.7	8.26	5	5	2.7	0.80	0.00	22.5	25,200
LB & 8G	2	2	3.7	8.06	5	2	2.7	0.75	0.05	16.6	19,440
DB	2	—	3.7	7.92	5	—	2.7	0.84	0.03	17.9	21,480

TABLE IV.—*Continued*

	Oxygen experiments				Other experiments						
	No. days	*Est. rad.*	*Av. temp.*	*O_2 ml/l*	*No. days*	*Est. rad.*	*Av. temp.*	*P µg-at/l*	*N µg-at/l*	*Chlor. µg/l*	*Thous. of cells/l*
LB with nutrients added:											
P	—	—	—	—	5	163	2.7	2.61	0.03	21.9	18,650
N	—	—	—	—	5	163	2.7	0.57	21.7	17.9	16,940
Mn	—	—	—	—	5	163	2.7	0.73	0.01	21.1	14,120
Fe	—	—	—	—	5	163	2.7	0.74	0.12	14.9	16,435
CA	—	—	—	—	5	163	2.7	0.71	0.06	17.5	14,570
P,N	—	—	—	—	5	163	2.7	2.33	21.5	23.8	20,320
P,N,Mn	—	—	—	—	5	163	2.7	2.44	15.4	17.6	16,450
P,N,Fe	—	—	—	—	5	163	2.7	2.39	16.6	23.7	17,430
P,N,CA	—	—	—	—	5	163	2.7	2.40	13.2	19.9	19,270
P,N,Mn,Fe	—	—	—	—	5	163	2.7	2.44	14.1	24.0	21,240
P,N,Mn,CA	—	—	—	—	5	163	2.7	2.53	14.1	24.8	20,430
With increased temperature:											
LB	—	—	—	—	5	8	7.0	0.61	0.12	19.3	16,560
March 10.											
IA	—	—	—	7.82	—	—	—	1.16	0.04	3.4	2,658
LB	2	196	3.7	8.33	7	134	3.4	0.73	0.09	8.5	9,600
LB & 2G	2	47	3.7	8.20	7	32	3.4	0.91	0.12	11.8	9,600
LB & 4G	2	16	3.7	8.10	7	11	3.4	0.84	0.05	8.7	7,998
LB & 6G	2	6	3.7	8.05	7	4	3.4	0.87	0.11	10.9	7,860
LB & 8G	2	2	3.7	7.95	7	1	3.4	0.96	0.03	5.9	8,430
DB	2	—	3.7	7.74	7	—	3.4	1.03	0.18	6.5	3,708
LB with nutrients added:											
P	—	—	—	—	7	134	3.4	2.50	0.11	9.7	12,340
N	—	—	—	—	7	134	3.4	0.56	13.8	19.9	16,170
Mn	—	—	—	—	7	134	3.4	0.84	0.05	11.6	8,145
Fe	—	—	—	—	7	134	3.4	0.83	0.05	8.6	10,710
CA	—	—	—	—	7	134	3.4	0.86	0.07	9.1	11,220
P,N	—	—	—	—	7	134	3.4	2.27	12.5	23.0	13,680
P,N,Mn	—	—	—	—	7	134	3.4	2.23	7.7	20.0	13,400
P,N,Fe	—	—	—	—	7	134	3.4	2.18	7.3	22.5	14,500
P,N,CA	—	—	—	—	7	134	3.4	2.28	7.3	17.8	12,720
P,N,Mn,Fe	—	—	—	—	7	134	3.4	2.37	8.4	25.4	14,940
P,N,Mn,CA	—	—	—	—	7	134	3.4	2.37	8.2	19.2	16,920

TABLE IV.—*Continued*

	Oxygen experiments				Other experiments						
	No. days	*Est. rad.*	*As. temp.*	O_2 *ml/l*	*No. days*	*Est. rad.*	*As. temp.*	*P µg-at/l*	*N µg-at/l*	*Chlor. µg/l*	*Thous. of cells/l*
With increased temperature:											
LB	—	—	—	—	7	6	7.0	0.91	0.07	10.4	11,690
June 3.											
IA	—	—	—	6.12	—	—	—	0.52	0.07	1.9	850
LB	2	246	17.6	—	8	202	16.7	0.41	0.07	1.6	365
LB & 2G	2	59	17.6	6.00	8	48	16.7	0.31	0.27	2.8	3,293
LB & 4G	2	20	17.6	5.84	8	16	16.7	0.50	0.81	1.2	868
LB & 6G	2	7	17.6	6.00	8	6	16.7	0.40	0.27	1.5	996
LB & 8G	2	2	17.6	5.87	8	2	16.7	0.40	—	1.4	1,227
DB	2	—	17.6	5.71	8	—	16.7	0.57	0.10	0.4	232
LB with nutrients added:											
P	—	—	—	—	8	202	16.7	1.63	0.14	2.2	1,521
N	—	—	—	—	8	202	16.7	0.00	10.9	10.5	1,385
Mn	—	—	—	—	8	202	16.7	0.17	0.10	3.7	918
Fe	—	—	—	—	8	202	16.7	0.28	0.24	2.8	1,243
CA	—	—	—	—	8	202	16.7	0.24	0.10	4.7	1,534
P,N	—	—	—	—	8	202	16.7	0.68	0.68	13.3	1,809
P,N,Mn	—	—	—	—	8	202	16.7	0.70	0.14	16.6	2,089
P,N,Fe	—	—	—	—	8	202	16.7	0.68	0.20	10.6	1,123
P,N,CA	—	—	—	—	8	202	16.7	0.76	0.03	13.7	1,016
P,N,Mn,Fe	—	—	—	—	8	202	16.7	0.67	0.10	18.3	1,718
P,N,Mn,CA	—	—	—	—	8	202	16.7	1.48	0.10	9.9	2,419

In the spring flowering experiments, addition of nitrate had the greatest effect of all nutrients on population growth. In two of three experiments it restored the population to the natural flowering level, suggesting that depletion of this nutrient was the chief cause of the termination of the flowering. Addition of phosphorous and iron brought about small population increases, and when either or both were added along with nitrogen, slightly greater population increases took place than when nitrogen was added alone. Citric acid showed a smaller stimulatory effect. Manganese alone had no stimulatory effect; in fact, the results might be interpreted as a slight inhibition. When added with other nutrients, however, manganese appeared to have some favorable effect (see Table IV).

The experiments also emphasized the importance of the physiological state of the organisms. Laboratory culture experiments have suggested that the postflowering population is in a physiological state of senescence. A lag period during which there is a shift from a maintenance metabolism to active growth is demonstrated by such populations when they are placed under conditions favorable to active growth. The postflowering experiments on March 3, 1954 showed that this was taking place in a natural population. This was the only experiment in which spring flowering levels were not restored, even though the length of time, light, and temperature were comparable to other experiments.

The summer experiments of 1954 gave results similar to the spring flowering experiments. Highest chlorophyll levels attained in the enriched bottles were almost as high as the spring flowering ones. Nitrogen was again the nutrient that brought about the greatest increases. The other four nutrients had some stimulatory effect, phosphorous and manganese being somewhat more effective than iron and citric acid. The nutrient effects were almost additive in this experiment (see Table IV).

SPECIES ACCOUNTS

In order to separate the more important species of phytoplankton in Long Island Sound from the less important ones, two rather arbitrary categories were set up. The major constituents were defined as species which occurred in numbers greater than 5% of the total phytoplankton at least once in the two years of study. The minor constituents were always found in numbers less than 5% of the total

population. Since the total population size varied from week to week, the 5% demarkation represents no real number.

Some 40 species may be classified as major constituents. Some species were present during most of the year while others were restricted to a particular season. Nearly 150 species were found as minor constituents. The minor constituents can be further subdivided into two groups: those which were found often or in sufficient numbers to indicate that they were growing in the Sound; and those which were found only occasionally in small numbers and which were probably immigrants unable to establish themselves in the Sound. Only the first group of minor constituents will be considered in this paper.

In addition to notes on the occurrence and abundance of the various species, other pertinent information obtained from the environmental and experimental data is included. Any significant difference in distribution between inshore and offshore waters is also recorded. If a species is found chiefly inshore it may have requirements for land-derived nutrients, lower salinity, or some favorable light or nutrient condition associated with the shallow water column. More frequent occurrence of a species offshore might suggest requirements for higher salinity or some other condition associated with the deeper water column. The highest concentration, unless otherwise noted, represents the highest count obtained in a single sample.

Certain species in the following list are marked with an asterisk (*) to call attention to the fact that, although the cell numbers are low, the cells are large and undoubtedly made a greater contribution to the economy of the Sound than their numbers would suggest.

Major Species

Centrate Diatoms

Cerataulina pelagica.[2] A bloom of this species in May 1952 when the water temperature was around 10° C lasted several weeks. Another shorter but larger bloom occurred in late summer 1953 when the water temperature was 23°. Cell concentrations in a single sample reached nearly 2 million. Traces were found throughout most of the rest of the two year period. Field and experimental

[2] Hendey's (1954) checklist of British marine diatoms was used throughout as the model for names and spellings.

data suggest that it grows well in moderate light conditions if the water contains some inorganic nutrients.

Chaetoceros affine was found in August and September of both years. A few cells were also recorded in winter. It was not found in salinities lower than 27‰, and it was observed offshore more often than inshore. Highest concentration 90,000 cells/l.

Chaetoceros compressum, found the year round, was most common in August 1952, from the spring flowering through May in 1953, and in the spring flowering of 1954. Experiments suggest that it prefers lower light intensities and is not found when nutrients are low. Highest concentration 259,000 cells/l.

Chaetoceros curvisetus was found from July through October, with a peak in September. It was a major constituent of the population at this time of the year. Traces in November 1952 and March 1954 were the only other occurrences. Maximum temperatures and moderately high radiation values characterized its period of abundance. Highest concentration 368,000 cells/l.

Chaetoceros debile, occurring occasionally and in small numbers from the end of the spring flowering through October, was more common inshore. Greatest concentration 87,000 cells/l.

Chaetoceros didymum, taken in small numbers sporadically from the end of the spring flowering through fall, was more common offshore. Seasonal distribution and results of one experiment suggest that this species has a high light requirement.

Chaetoceros radians-Chaetoceros tortissimum. These two species are combined since there was some confusion in identification. Large numbers were found from January until several weeks after the spring flowering, with smaller numbers in late spring and early summer. These species were completely absent only in fall and early winter. Highest concentration, during the spring flowering, 2,348,000 cells/l.

Corethron criophilum was found from August through December in both years, with a trace in March 1952. The populations were larger in 1953 than in 1952. Salinities were always above 27‰ at these times, and it was taken offshore more often. Marked increases were recorded in light bottle experiments. Radiation means for the period of occurrence were higher in 1953 than in 1952. Highest number 36,000 cells/l.

**Coscinodiscus perforatus cellulosa* was taken regularly from July through January, with maximum abundance around mid-September.

An occasional cell was found in the spring plankton. Found offshore slightly more often. Highest concentration 21,000 cells/l.

Coscinodiscus radiatus was taken the year round in small numbers, but the greatest concentrations were found in August of both years, with slightly smaller numbers in May and June 1952. Maximum concentration 24,000 cells/l.

**Eucampia zoodiacus* was found only in 1952. Common in the spring diatom population, it reached a peak concentration in May. It occurred again in August and then disappeared.

Guinardia flaccida, found from April through July, was most abundant in May 1952. Only a trace of it was found during the corresponding period in 1953. Greatest number 156,000 cells/l.

Lauderia borealis was a late winter and spring flowering form. The peak came in mid-March, following or coinciding with the spring flowering. In 1952, when phytoplankton was generally more abundant, the species was observed through April, while in 1953 it disappeared four weeks earlier. Temperatures under 10°, with an optimum from 3–7°, are suggested for this species by the field data.

Leptocylindricus danicus. Included here are two forms which, had intergrades not been found, could have been called *Leptocylindricus danicus* and *L. minimus*. The two year cycle is shown in Fig. 9. The highest concentration was found in June 1952, although it was common throughout the preceding spring months. Corresponding spring and early summer populations were insignificant in 1953. It was taken slightly more often inshore.

It increased under all conditions of light, temperature, and nutrient enrichment in experiments during the spring flowering period. In light experiments early in the season, the greatest increases occurred in bottles receiving the most light; with the seasonal progression in incident radiation, the greatest increases took place in the gauze-covered bottles. In the June 1954 experiment, this species did not increase significantly in any bottles that were exposed to the maximum available light, including enriched ones, but it did increase significantly in the bottle receiving about 25% of the maximum.

Paralia sulcata (Fig. 9). Throughout most of the annual cycle this species was found in small numbers, but in fall and winter it became a chief constituent and was an important species in any fall flowering that occurred. In experiments, it grew best in light of low intensity,

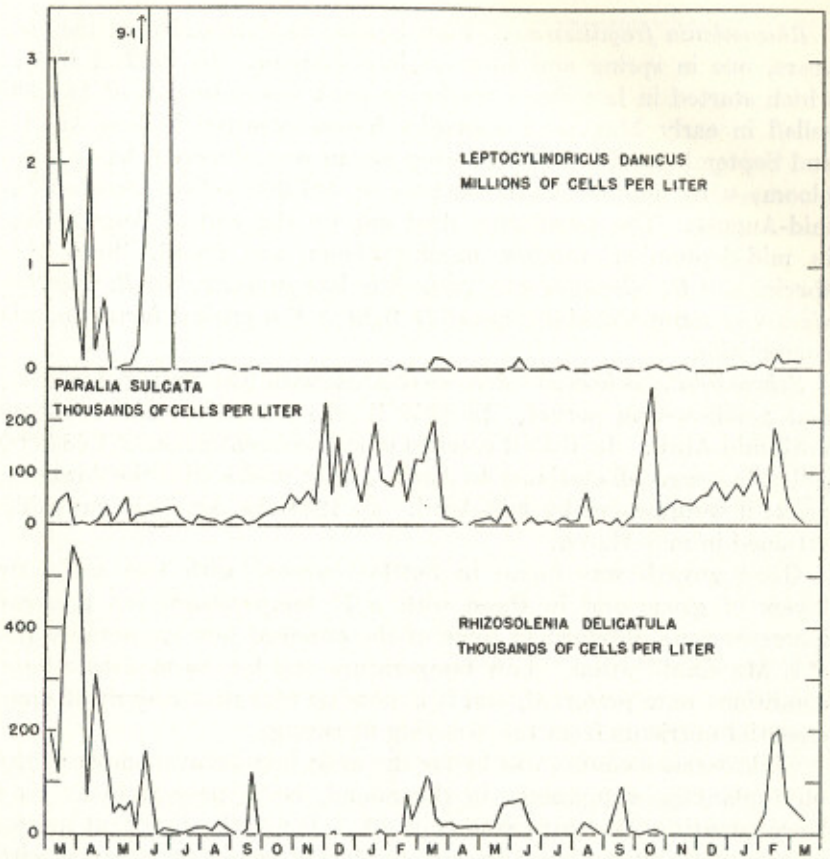

FIGURE 9. Distribution of *Leptocylindricus danicus*, *Paralia sulcata*, and *Rhizosolenia delicatula*.

with enrichment and with a temperature of at least 7°. The experimental evidence helps to explain its abundance in fall and winter.

Rhizosolenia delicatula (Fig. 9). Maximum numbers were found in spring 1952. Smaller numbers occurred in spring 1953 and in the fall of both years. As the incident radiation increased in the spring, this species was more successful in experimental bottles that received less than the maximum light available. It also did well in enriched bottles, *N* and *P* taking first and second place respectively as the most essential nutrients. In one experiment this species disappeared from light bottles, whether enriched or not.

Rhizosolenia fragillissima. Four blooms were recorded in the two years, one in spring and three in late summer. In 1952, a bloom which started in late April reached a peak concentration of 144,000 cells/l in early May, and a smaller bloom occurred in late August and September. In 1953 no spring bloom was observed, but a large bloom, with highest concentrations of 387,000 cells/l, occurred in mid-August. The population died out by the end of August, but in mid-September another smaller bloom was found. Both this species and *R. delicatula* were present in late summer, but *R. fragillissima* was more abundant; possibly light is the critical factor in this competition.

Schroederella delicatula was associated with the spring flowering and postflowering period. In 1952 it was found in small numbers until mid-April. In 1953 it reached a peak concentration of 1,558,000 cells/l (average, all stations) on April 1, three weeks after the flowering peak; it disappeared by mid-April. In 1954 the peak was probably attained in mid-March.

Good growth was found in bottles covered with two and four layers of gauze and in those with a 7° temperature, but greatest increases were obtained in some of the enriched bottles, notably the P,N,Mn combination. Low temperature and low to moderate light conditions were preferred, and it is possible also that it derived some essential nutrients from the decaying flowering.

Skeletonema costatum was by far the most important member of the phytoplankton community in the Sound, being present in at least trace quantities the year round (Fig. 10). It was the dominant species of the 1953 spring flowering, and in 1954 it shared dominance with *Thalassiosira nordenskiöldii.* During spring and summer, small blooms took place, these being much larger in 1952 than in 1953. A small bloom was also recorded in the fall flowering of 1953.

In most experiments during the spring flowering of 1954, this species had a greater growth rate in light bottles and in those covered with two layers of gauze than did *Thalassiosira nordenskiöldii.* It increased most rapidly at this time at temperatures slightly higher than the environmental temperature of 1954. In later experiments during the spring flowering, good growth occurred in uncovered bottles and in bottles kept at higher temperatures, but best growth took place in enriched bottles, *N* being the most critical nutrient. In other experiments during the warm months of 1953, *S. costatum*

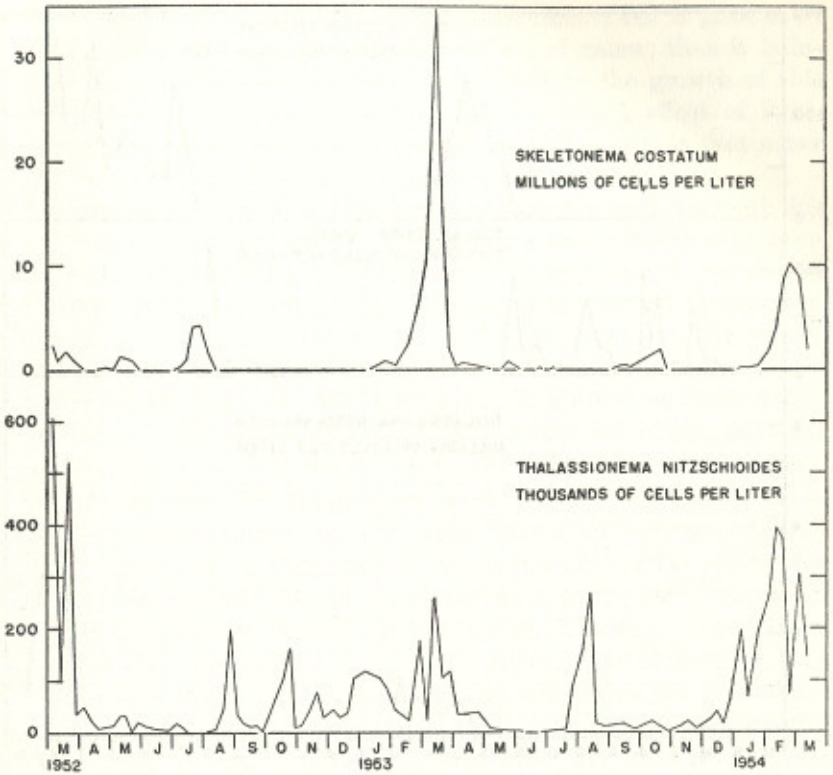

FIGURE 10. Distribution of *Skeletonema costatum* and *Thalassionema nitzschioides.*

exhibited some growth in enriched bottles, but better growth was often obtained in control bottles. In the 1954 summer experiment, best growth took place in the bottle covered with two layers of gauze. Experimental data indicate that there were limits of light and temperature below which *S. costatum* was less successful than other species, but there was a wide range of conditions above these minima in which it was dominant over most of the others. The summer of 1953 imposed some limits on *S. costatum* which were not present in 1952. Braarud (1945) found this species more successful at 10° C than any other species in his experiments.

Thalassiosira decipiens. The three most important species of *Thalassiosira* followed each other in regular succession throughout the year (Fig. 11). *T. decipiens* was the fall and winter species.

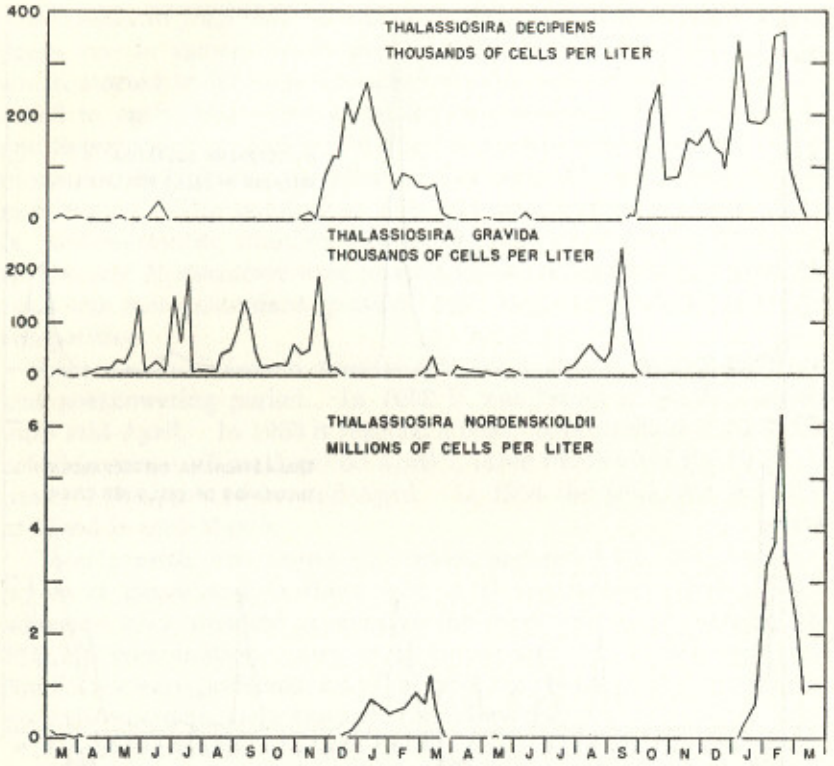

FIGURE 11. Distribution of *Thalassiosira nordenskiöldii*, *T. decipiens*, and *T. gravida*.

It appeared in late September or October and was taken continuously until the end of March. Small numbers were occasionally found in spring and early summer. It was a chief constituent of the 1953 fall flowering, and this species and *Paralia sulcata* were the two most abundant forms throughout late fall and winter. During the spring flowering in 1954, it was found to be most successful experimentally at temperatures higher than those of the Sound, in gauze covered bottles, and in enriched bottles. These results help in interpreting the fall and winter abundance of this species.

Thalassiosira gravida was the spring, summer, and early fall form of this genus. Fig. 11 shows that, like many other diatoms, it was more successful in 1952 than in 1953. In both years there was a bloom just before it was replaced by *T. decipiens*. In the 1954

summer experiment it did well with N enrichment, but it grew even better in the bottle covered with two layers of gauze; thus it is indicated that, while abundant nutrients stimulate the growth of this species, they only partially overcome the inhibiting effect of light. An alternative interpretation of the light bottle results is that other species successfully outcompete *T. gravida*.

Thalassiosira nordenskiöldii was the spring flowering form of this genus. It was merely present in 1952, had a small bloom that coincided with the 1953 spring flowering, and, with *S. costatum*, dominated the 1954 spring flowering (Fig. 11). As was pointed out above, spring flowering temperatures and light were lower in the earlier 1954 flowering than they were in 1953.

Experimental work showed that this species grew best and had a higher growth rate than *S. costatum* at low light intensities but that it was dominated by *S. costatum* when the temperature was increased. Good growth was also obtained in bottles enriched with N and P. Thus, low temperatures and low light intensities are suggested as optimal, assuming no deficiency in the nutrient supply. If proper light and temperature conditions prevail at a time when the rest of the conditions are favorable for the spring flowering, this species will either share dominance with or outcompete *S. costatum*.

Thalassiosira rotula occurred only sporadically throughout the year. Small blooms took place during and just following the spring flowering, in May–June, in mid-July, and in September and October. Small numbers occurred throughout the rest of the year. Maximum concentration 375,000 cells/l in autumn 1953. Found more often inshore.

Pennate Diatoms

Asterionella formosa, properly speaking, is a freshwater form. It is undoubtedly carried by rivers into the Sound, where it can perhaps exist marginally. It was found from January to May and was most abundant, as might be expected, after periods of high precipitation. Highest concentration 57,000 cells/l. Normally the numbers were much smaller.

Asterionella japonica was more successful in 1952 than in 1953. Highest numbers were found in March, and it was abundant from May through July 1952. It disappeared in August and was not found again until January 1953. One peak in 1953 coincided with

the spring flowering; smaller peaks were found in April and July. A moderate bloom was found in October 1953 at the beginning of the fall flowering. After this it disappeared and was not found again until March 1954. Found more often inshore. Largest numbers 1,454,000 cells/l.

In the March 1954 experiments this species grew best in some of the gauze-covered bottles. It was also successful in a bottle with a raised temperature as well as in bottles enriched with citric acid only and with a combination of N,P,Mn, and citric acid. All evidence indicates that this species can grow in a wide range of temperature conditions and that it prefers moderate light conditions provided nutrients are present in concentrations greater than the minimum in the Sound. The more frequent occurrence of this species inshore, coupled with its success in bottles enriched with citric acid, suggests a possible requirement for organic substances.

Nitzschia delicatissima. This species, found in the spring and late summer months of 1952, was taken only in May 1953. It was never really successful in Long Island Sound. Highest concentration only 12,000 cells/l. Its seasonal distribution suggests moderate light and nutrient requirements. It was found under a wide range of temperature conditions.

Nitzschia longissima was found from March through December. Principal periods of growth were late spring 1952, October 1952, mid-July 1953, and mid-September 1953. Highest concentration 31,000 cells/l. Found more often inshore.

In the 1953 and 1954 summer experiments it did well in light bottles, but it was even more successful in enriched bottles, concentrations being ten times higher than the greatest natural ones. While this response was clear-cut, one cannot discount the possibility that increased surface area provided by the bottles favored the growth of this pennate diatom. Higher temperatures, moderate to high light intensity, and enriched waters seemed favorable.

Nitzschia pungens atlantica, found from April to December 1952, appeared only in October of 1953. Highest concentration 27,000 cells/l in June 1952 and October 1953. Found more often inshore. Moderate light, moderate temperature, and at least moderate amounts of nutrient enrichment are suggested as requirements.

Thalassionema nitzschioides. Highest numbers were found in early March 1952 (Fig. 10). Other small blooms occurred from August

1952 through the spring flowering of 1953. Another peak was noted in August 1953, but there was no increase at the time of the fall flowering, and high concentrations were not found again until the spring flowering in 1954. Though continually present in Long Island Sound, it was seldom abundant enough to be classed as a dominant species. Taken slightly more often offshore.

In the 1954 spring flowering experiments, best growth was often obtained in bottles covered with four layers of gauze; good growth was also obtained in bottles enriched with P,N, and additional nutrients. In the 1954 summer experiment, good growth occurred in the bottle covered with two layers of gauze, but better growth occurred in some of the heavily enriched bottles. Growth was also obtained in enrichment experiments in summer 1953. Maximum light conditions were indicated as too high, but beyond this nothing specific can be said.

Dinoflagellates

Dinophysis acuminata was found in all months of the year except January and February. In 1952 there were small blooms in mid-April and late May. The largest numbers in both years occurred from mid-June through July, the maximum being 67,000 cells/l. In 1953 a small bloom occurred at the end of June, and a larger one took place in July, with 48,000 cells/l in one sample. Taken more often inshore.

Exuviella apora was found only from June to September. The largest concentration, at the end of June 1952, was 306,000 cells/l. A much smaller peak was found at the end of July. In 1953 small peaks occurred around the end of June and the first of September, the latter one being the larger. The distribution indicated a preference for maximum light and temperature conditions.

Peridinium elongatum was found from May through August, sometimes in numbers great enough to constitute more than 5% of the population.

Peridinium trochoideum. This species, found in trace quantities the year round, was fairly common in the warm months of the year. There was a small bloom in March 1952. The characteristic May-June flowering was much larger in 1953 than in 1952; the highest number for this period in 1952 was 141,000, in 1953 1,121,000 cells/l. Found more often inshore. It is probably significant that it was one of the

few species which did better the second year than the first during late spring and early summer.

Prorocentrum scutellum[3] occurred from June through February, with peak concentrations in July and August. The summer bloom in 1952 was slightly larger than that in 1953. A small bloom was also found in September and October of both years. The distribution suggested that greatest abundance coincided with the seasonal maxima in temperature and probably light. Maximum concentration 600,000 cells/l in 1952. Found slightly more often offshore.

Silicoflagellates

Distephanus speculum was recorded throughout the year except for a short period in October. The largest bloom was around the end of April 1952, with a peak concentration of 109,000 cells/l. In both 1953 and 1954, small blooms took place during the spring flowering. In the spring of 1954 it did well in bottles with reduced light as well as in bottles enriched with P,N, and other nutrients, and in one experiment with raised temperature. This evidence, plus field data, indicates a preference for moderate light and temperature and at least moderate nutrient conditions.

Ebria tripartita occurred the year round, except for a short period in midfall. It exhibited best growth in August of both years, with smaller blooms in May 1952 and during the 1954 spring flowering. The summer bloom in 1952 was larger than that in 1953. Highest concentration in 1952 during this period 49,000 cells/l.

Other Forms

In Long Island Sound, a phytoplankter was quite frequently observed which may have been an aberrant dinoflagellate, but it resembled more closely a freshwater Euglena. It was nearly always found inshore, where it was taken sporadically the year round, although it was most abundant in summer. Highest concentration 217,000 cells/l. It was always associated with "red tides" in New Haven Harbor, but it was never a major red tide organism. In the experiment performed with "red water" on July 7, 1953, this species

[3] This may not be the correct identification of this organism. In many ways it resembles *Prorocentrum micans*, but it lacked that species' pointed apex of the cell body. Clearly identifiable *P. micans* have been found in Long Island Sound (see p. 100).

did particularly well. The initial concentration of 741,000 cells/l at least tripled in all bottles except the high salinity replicate enriched with N. It increased to ten times the initial concentration in the replicate which was enriched with N but in which the salinity was not changed. Thus requirements for high temperature and abundant light are indicated, together with good enrichment, possibly derived from shore. The optimum salinity may be below the range usually found in Long Island Sound.

Minor Species

Centrate Diatoms

Actinoptychus senarius occurred throughout the year.

**Biddulphia aurita* was found in small numbers from October through February, reached peak numbers in March, disappeared in April, and reappeared occasionally in the summer. This species consistently increased in the raised temperature experiments in the spring of 1954. It also did well in some of the gauze-covered bottles.

**Biddulphia aurita obtusa*. Small numbers in May.

Chaetoceros breve. May 1952.

Chaetoceros constrictum commonly occurred from January through April in small numbers.

Chaetoceros costatus was found the year round during periods of high nutrient concentrations.

Chaetoceros danicum occurred in greatest abundance from February through April, with lesser peaks in May and July. It was found in small numbers throughout the rest of the year.

Chaetoceros decipiens appeared in January, reached a climax in March, experienced minor blooms from May through September, and disappeared in October. It did well in N-enriched experiments.

Chaetoceros gracile was taken only in 1952. Greatest concentrations were found in March, smaller ones in July. It disappeared in August.

Chaetoceros lauderi was found only in July 1952 when it was relatively abundant.

Chaetoceros simile. March, April, and July 1952 and late winter 1954.

Chaetoceros subsecundum occurred as a trace in February and was most abundant in March.

Chaetoceros teres. Present in July and August of 1952.

**Coscinodiscus centralus pacifica* was found from June through

December, with a peak in August. This suggests a high temperature preference. It showed a significant increase in one fall experiment enriched with P.

Coscinodiscus concinnus was found mainly in August, although a few were also present in December.

**Coscinodiscus excentricus*, present in small numbers throughout much of the year, reached peak concentrations during May and October. During the latter month it was sometimes difficult to make a clear distinction between this species and large single cells of *Thalassiosira decipiens*.

Coscinodiscus lineatus was found throughout 1952, being most common in May and October.

Coscinodiscus oculus-iridis. January to April 1953.

Coscinosira polychorda. Small numbers in May 1953.

**Ditylum brightwellii* was most common in 1952; in other years it was found only as an occasional trace. In 1952 it was most abundant in March, common from April to August, and present as a trace from October to December.

Hemiaulus hauckii and *H. sinensis*. August 1952 only.

Lithodesmium undulatum. Small numbers in September and October 1953.

Melosira italica (?), like *Asterionella formosa* (see p. 93), is properly a freshwater form, but it was occasionally found in Long Island Sound, apparently in a viable condition, chiefly in the spring months after heavy rains.

Rhizosolenia calcar-avis was found as a trace in August 1952.

Rhizosolenia hebatata occurred as a trace in May 1952.

**Rhizosolenia setigera* was common the year round. Smallest numbers occurred in November and December; highest numbers were found from February to May; a small peak was also found in September. This species showed some increase in a bottle covered with six layers of gauze and in several of the bottles enriched with only one inorganic element.

Rhizosolenia styliformis and *R. styliformis longispina* were found in a few samples in April and May 1952.

Pennate Diatoms

Bacillaria paxillifer. May and July 1952.

Diatoma elongatum. Small numbers in the spring of 1952.

Fragillaria crotonensis. October to December 1952.

Grammatophora marina. Small numbers from October to December and from March to May.

Licmophora abbreviata and *Licmophora* spp. were found in small numbers in March, April, and September.

Navicula distans occurred from September to May, with a peak in November.

Nitzschia bilobata was found from March through July in 1952, but only in March 1953.

Nitzschia closterium was obtained from December to August, with a peak in March. In two summer experiments this species increased in bottles enriched with only N.

Nitzschia pacifica. Small numbers from May through July.

Pleurosigma normani occurred the year round, with highest concentrations in May and November.

Rhaphoneis amphiceros was found in a few samples in March and September.

Rhabdonema minutem occurred as a trace in October.

Striatella interrupta was taken in June and in the fall months, with greatest numbers in October.

Surirella fastuosa recendens. Small numbers in August and December.

Thalassiothrix frauenfeldii. March through May in 1952 only.

Dinoflagellates

Ceratium fusus occurred from May through July, with highest numbers in June.

Ceratium lineatum was found from April through August, with a peak in June and July. In a mid-June experiment in 1953 this species increased significantly only in bottles enriched with soil extract.

Dinophysis acuta was found as a trace in March 1952 and in small numbers from June through August 1953.

Dinophysis arctica. Small numbers in July and August 1952.

Dinophysis caudata. April 1953 only.

Dinophysis recurva. March 1952 only.

Exuviella baltica was taken from March through July, with a peak in May. Greater numbers were taken in 1952 than in 1953.

Glenodinium dinobryonis was present from March through August, with a peak in May and a smaller one in July.

Glenodinium gymnodinium. April and May.

Glenodinium lenticula was found from March through October, with greatest numbers from March to May 1952.

Glenodinium pilula. Small numbers from May to October; it was more abundant in 1953 than in 1952.

Glenodinium rotundum was found as a trace in May and June 1952.

Goniaulax africana (?) and *G. cochlea* (?) were the chief red tide organisms (see Conover, 1954). They were found in small numbers in the Sound, almost always at the inshore stations. Their existence in open Sound waters was marginal at best.

Goniaulax minima was found from June through September, with greatest concentrations in June. It was often associated with red tides.

Gymnodinium canus. March through June, with a June peak; also September through November.

Gymnodinium caput. April through June, with a small peak in the latter month.

Gymnodinium heterostriatum. Trace quantities in March 1952 and May 1953.

Peridinium breve. March through July, with a peak in May.

Peridinium bulla. April and May, with greatest abundance in the latter month.

Peridinium fimbriatum was found from May through July, with the highest concentrations in May. The 1953 May peak was larger than that of the year previous.

Peridinium globulus was taken from February through July, being most abundant from March to May.

Peridinium hyalinum. April through July, with peak numbers in June and July.

Peridinium minusculum. March through August, with a peak in May.

Peridinium triquetum. Small numbers from May through August.

Peridinium spp. is a general category for many individuals not easily identified. Individuals in this group were taken from March through September, but by far the greatest numbers were taken in the summer months when the other members of this genus were generally most abundant.

Prorocentrum micans. March through September, with small peaks in March and in June and July.

Prorocentrum triestinum. August through October.

Silicoflagellates

Dictyocha fibula was taken occasionally in September and January.

Coccolithophores

Individuals of this group were occasionally found; most often they resembled descriptions of the genus *Acanthoica.* They were never taken in large numbers and were found only in March and April.

Other Forms

At least two species of green or blue-green algae, one resembling *Anaebena,* were occasionally taken in the samples. They were probably freshwater forms that were washed into the Sound. They were taken most often in summer.

PHYTOPLANKTON ASSOCIATIONS

Even the most cursory glance at the previous section reveals a regular succession of important species through the annual cycle; furthermore, this succession was repeated from year to year. Of course, the two annual cycles were not exactly the same. There were slight shifts in the time of various events, and many species did not occur in the same abundance each year. The most important variations between the two years, as pointed out previously, were the greater number of dinoflagellates and the markedly smaller numbers of diatoms in the late spring and summer of 1953 as compared with 1952, and the presence of a fall flowering in 1953 which was absent the previous year.

The spring flowering was dominated by either *Skeletonema costatum* alone or by *S. costatum* and *Thalassiosira nordenskiöldii* together. Other species were typically found in significant numbers at this time as well. *Chaetoceros compressum* and *C. radians-C. tortissimum, Leptocylindricus danicus, Rhizosolenia delicatula, Thalassionema nitzschioides, Peridinium trochoideum,* and *Distephanus speculum* were abundant. *Asterionella japonica, Lauderia borealis,* and *Schroederella delicatula* appeared during the flowering and reached climaxes a few weeks after the main flowering peak. This was particularly striking in the case of *S. delicatula;* perhaps this species is favored by the presence of products of the decaying flowering. The actual numbers and relative importance of these spring flowering species varied from year to year.

In the spring months, another group of phytoplankton species became abundant. From April through early June, *Skeletonema costatum* persisted, as did *Chaetoceros compressum, Rhizosolenia delicatula, Thalassiosira rotula,* and *Asterionella japonica. Asterionella formosa* commonly occurred in the spring plankton. *Thalassiosira gravida* replaced *T. nordenskiöldii* as the most abundant member of this genus. Highest concentrations of *Distephanus speculum* occurred in April. In May, blooms of *Cerataulina pelagica, Guinardia flaccida,* and *Rhizosolenia fragillissima* were observed. *Peridinium trochoideum* reached highest concentrations in May and June, *Leptocylindricus danicus* in June.

Peridinium trochoideum, Dinophysis acuminata, and *Exuviella apora* shared dominance during late June and early July, and several species of *Ceratium* were present. In late July *Prorocentrum scutellum* became plentiful, and in 1952 the ubiquitous *Skeletonema costatum* had another bloom at this time. Early in August *Ebria tripartita* and *Rhizosolenia fragillissima* were abundant. In late August and September, *Cerataulina pelagica, Chaetoceros affine, C. compressum,* and *C. curvisetus* were found. If conditions became suitable for a small general bloom, some or all of these species dominated it. As the season progressed into October, *Corethron criophilum, Coscinodiscus perforatus cellulosa, C. radiatus,* and *Skeletonema costatum* appeared in greater numbers. *Thalassiosira gravida, T. rotula, Asterionella japonica,* and *Thalassionema nitzschioides* were taken regularly in this period as well.

Corethron criophilum, Coscinodiscus perforatus cellulosa, C. radiatus, Thalassiosira gravida, T. rotula, and *Thalassionema nitzschioides* persisted through October but occurred in diminishing numbers as the season advanced. *Rhizosolenia delicatula, Skeletonema costatum,* and *Peridinium trochoideum* were also common at this time. *Paralia sulcata* and *Thalassiosira decipiens,* which rapidly became dominant in late October, continued abundant through December and early January. If an October flowering occurred it was dominated by these two species plus *Skeletonema costatum. Thalassionema nitzschioides* also was common.

In January, other species began to succeed *Paralia sulcata* and *Thalassiosira decipiens* as conditions gradually became favorable for a spring flowering, but they continued to be found in decreasing numbers until the time of the flowering climax.

The following species occurred in markedly greater numbers in 1952 than in 1953: *Cerataulina pelagica, Chaetoceros compressum, Ditylum brightwellii, Eucampia zoodiacus, Guinardia flaccida, Leptocylindricus danicus, Rhizosolenia delicatula, R. fragillissima, Skeletonema costatum, Thalassiosira gravida, Asterionella japonica, Nitzschia pungens atlantica,* and *Distephanus speculum. Peridinium elongatum, P. fimbriatum,* and *P. trochoideum* were more abundant in 1953 than in 1952.

ENVIRONMENTAL CONDITIONS AND THE ANNUAL CYCLE

In the marine environment there are several ecological factors which control the increase and decrease of the standing phytoplankton crop as measured by cell numbers and the amount of chlorophyll. Only one factor directly alters the number of cells in the water column, namely, grazing by herbivores; other factors operate indirectly by affecting the physiology of the cells. Of the five essentials in autotrophic plant growth and maintenance, namely carbon dioxide, water, oxygen, light energy, and nutrients, probably only the last two need be considered in Long Island Sound. However, the complexities of the oceanic environment are such that many factors influence the rate of supply of the essentials. These factors will be discussed briefly before proceeding with an analysis of the seasonal cycle.

The light available to the phytoplankton in the Sound is summarized in two ways. Fig. 7 shows the estimated incident radiation at the surface together with estimates for two other depths calculated from the formula $I_z = I_o e^{-kz}$; I_z is the radiation in g cal/cm²/day at depth z, I_o is incident radiation, and k is the extinction coefficient per meter as determined from Secchi disc readings, using the conversion method described by Poole and Atkins (1929). (See Riley's paper on PHYSICAL OCEANOGRAPHY in this volume.) Monthly means are given in Table II.

Light and dark bottle experiments have shown that a small amount of photosynthesis occurs at depths of 15 m or more in summer. Analyses of oxygen distribution (see Riley's paper on PRODUCTION and UTILIZATION in this volume) indicate that photosynthetic oxygen production exceeds oxygen consumption by the plankton community in the upper 10 or 15 m during summer but only in about the upper 2.5 m during winter. In the latter case particularly, the depth of water and the amount of turbulence will have an important effect

on the amount of light available for any individual cell. Optimum conditions for growth are to be found in shallow water or in deeper but vertically stable water that permits retention of cells near the surface where they can grow actively. Conversely, growth will be reduced by vertical turbulence, which has the net effect of reducing the amount of light available for each cell in the population, or by lateral mixing, which tends to reduce the shallow water population.

It is also apparent from the experimental work that inorganic nutrients, particularly nitrogen, influence the rate of increase of the population; these are probably the most important controlling factors during spring and summer.

There are two other factors which indirectly control the phytoplankton population, namely temperature and salinity. Perhaps their most obvious effect is the influence on species composition. Temperature also influences the rates of photosynthesis, nutrient uptake, and respiration (Barker, 1935a, 1935b; Hoagland, 1948; Margalef, 1954), and perhaps it affects the sinking rate by altering the viscosity of the water. Loss of cells by sinking may also be influenced by various other factors that alter the physiological state of the organisms.

Midwinter. The environment at this time was characterized by minimum radiation, decreasing temperature, slight stability and strong vertical turbulence, and large concentrations of phosphate and nitrate. Experimental measurements of daily photosynthesis of the surface phytoplankton population averaged 0.15 ml O_2/l in December and January, or about half the annual mean. In view of the small amount of phytoplankton in the water, this indicates a relatively high rate of production in the surface layer. However, the observed distribution of oxygen indicates that production exceeded consumption only in the upper few meters. Thus it seems likely that low light intensity and strong vertical turbulence were responsible for suppression of growth in the population as a whole.

The Flowering Period. A winter bloom appears to be common in Long Island Sound. The flowering here tends to be earlier than that in more exposed New England waters, such as Block Island Sound, Georges Bank, and the Gulf of Maine, but it is later than that which occurs in some very shallow protected bays (Fish, 1925; Bigelow, 1926).

In 1953 the flowering started between February 18 and 24 and culminated about March 16. The following year it was three weeks earlier. Both blooms fell within the period of gradually increasing vernal radiation. But there were no pronounced differences in the radiation pattern from one year to the next; hence the general level of radiation was significantly lower at the time of the 1954 flowering.

A slight amount of surface warming, with accompanying reduction in vertical turbulence, occurred during the 1953 flowering. In 1954, this did not occur until near the end of the bloom, and calculated values for vertical turbulence were larger than those in the flowering period of the preceding year. Thus the earliness of the 1954 flowering cannot be explained on the basis of radiation or vertical stability. There were indications of greater horizontal stability in 1954 in that the density difference between inshore and offshore waters was considerably greater than that in 1953. If the climax occurred a week earlier inshore, as is suggested by the data, then the case for the importance of horizontal stability is strengthened. Under such conditions, events in the inshore waters should be largely independent of those in the offshore environment. The effective radiation would presumably reach the critical level in the shallow water before conditions became favorable offshore, and retention of the population inshore would therefore promote an early flowering.

The magnitude of exchange between inshore and offshore waters is highly variable and has not been analyzed in quantitative terms, so that its importance in the present study cannot be evaluated precisely. It is reasonable to suppose that horizontal stability helped to promote an early flowering in 1954 but was not necessarily the major factor.

Another aspect that needs to be considered is the species composition during the flowering and the physical requirements of the dominant species. The bloom was dominated by centrate diatoms, although pennate diatoms and silicoflagellates also showed considerable growth. The two most important species were *Skeletonema costatum* and *Thalassiosira nordenskiöldii*. Both were present during the midwinter period. As the 1953 flowering progressed, *S. costatum* became excessively dominant; at the stations sampled on March 9 it achieved a maximum concentration of 36 million cells/l compared with one million *T. nordenskiöldii*. In 1954 *T. nordenskiöldii* was relatively more important. It increased to a maximum of six million on Febru-

ary 17 while *S. costatum* achieved a peak concentration of nine million the following week. Since the former is a much larger species, it clearly dominated the early part of the flowering with respect to volume of plant material if not total numbers.

The experiments during the 1954 flowering period showed that *T. nordenskiöldii* was successful in competition with *S. costatum* at temperatures of less than 2–3° C, while the latter species was more successful at higher temperatures. There are indications too that *T. nordenskiöldii* could grow actively at lower light intensity than that required by *S. costatum*.

The experiments readily explain the observed differences in species composition in the Sound. The winter of 1953 was one of the warmest on record, and the mean water temperature was 3.2° in February and 3.7° in March. More nearly normal conditions were found in 1954, with a mean temperature of 1.7° in February. This undoubtedly favored the growth of *T. nordenskiöldii;* it is further suggested that the tolerance of this species to low light intensity was important in promoting an early flowering.

The growth coefficients indicate that the large amounts of phytoplankton at the peak of the flowering resulted from a steady population growth under favorable environmental conditions rather than from a sudden change in growth rate. Growth rates were quite high throughout this period but were not significantly higher than those at other times of the year. A graph of K values against time did not resemble the theoretical logistic observed in laboratory cultures, since growth rates appeared to be relatively constant so long as the population numbers were increasing. However, coefficients of oxygen production and consumption suggest that the phytoplankton was physiologically more active two weeks before the climax than on the day when maximum numbers were observed. Possibly the point designated as the climax of the flowering in Fig. 1 was actually in the early post-flowering phase, in which case senescence might explain the lower coefficient of oxygen production; however, the data from the intervening week indicate that the coefficient of oxygen production actually started to decline while the population was still increasing.

Termination of the flowering was clearly brought about by nutrient depletion. Addition of inorganic nutrients, nitrogen being the most important, restored the phytoplankton population to flowering levels within the period of the experiments except in one case, previously discussed, where the physiological state of senescence probably introduced a lag.

The zooplankton increased slightly during and after the flowering, but experiments (see R. J. Conover in this volume) indicate that the grazing factor was not sufficiently important to control the flowering. Moreover, from the peak of the bloom through the postflowering stage, maximum chlorophyll concentrations occurred at the greatest depth sampled, suggesting that the senescent diatoms were sinking to the bottom.

Spring and Summer. Small oscillations in abundance occurred from the time of re-establishment of growth after the spring flowering through August. As was mentioned above, there were distinct differences in this period between the two years, both as to size of population and species and group composition.

These facts were supplied from the weekly analyses. Radiation values continued to increase from the time of the flowering until the annual maximum in June and July. There was somewhat higher radiation in 1953 than in 1952, but variations in the monthly distribution were probably more important. In 1952 more light was available in April and May and less in June and August than in the same months of 1953. Monthly temperature averages show some differences; April and July were about the same in each year, but May was colder and June warmer in 1952. Also, there was marked salinity stratification; the salinity pattern was somewhat different in the two years as the result of spring flooding in 1953. In 1952 there was some increase in nutrients after the spring flowering, but in 1953 there was little renewal. The yearly nutrient minimum occurred in June of both years, and by August some replenishment had taken place.

Probably the most critical factor at this time of year was the supply of nutrients, although zooplankton grazing may have been critical at times. In the June 1954 experiment, chlorophyll increased to spring flowering levels in enrichment experiments. Since only simple inorganic elements were added to obtain this growth, it was concluded that these were the limiting factors. Nitrogen was found to be the most important nutrient. Since light conditions were favorable for continuous growth, nutrients were utilized by the actively growing cells as soon as they became available. Thus the upper limit of population size would be determined by the rate of

nutrient renewal. Case 4 of Braarud, *et al.* (1953) was applicable to an increasingly larger area of Long Island Sound as the days grew longer. In shallow waters the euphotic zone extends to the bottom, and a well developed bottom community (including pennate diatoms) would develop and compete with the pelagic forms for critical nutrients as they are renewed from bottom sources. Although case 1 of Braarud, *et al.* (1953) superficially resembled conditions at the deeper stations in the Sound, there was no nutrient stratification as in the Norwegian waters. Calculations based on temperature data suggest that vertical turbulence was active in spite of significant stratification (see Riley's paper on PHYSICAL OCEANOGRAPHY in this volume). The explanation for low spring and summer nutrient concentrations in the Sound would seem to be immediate utilization by plants at all levels in the water column.

The amount of light was also significantly lower in June 1952, the time of the last large diatom bloom. Experimental results suggest that light intensity may be an important factor in the competition between diatoms and dinoflagellates. In the experiment of June 1954, raw sea water of low nutrient concentration was enriched and suspended in the Sound at a depth of 0.5 m for several days. At the same time, a series of bottles containing unenriched Sound water was exposed to several different light intensities. Chlorophyll increased in some of the enriched bottles, but apparently the species favored by this enrichment were destroyed by formalin. On the other hand, diatom growth was obtained without enrichment merely by cutting down the amount of light available. The largest increase was obtained at an estimated 25% of the light available at 0.5 m. Some growth was obtained in bottles receiving even less light. Although the intensity of light appears to be important in the control of competition between diatoms and dinoflagellates, no safe generalization about the light available in the natural environment can be made without consideration of turbulence.

Temperature may also play a part in the transition from diatoms to dinoflagellates. Grøntved (1952) found that dinoflagellate replacement was delayed in the cooler year of his study. In Long Island Sound, May was cooler in 1952 than in 1953; however, the June 1952 temperature averaged warmer than 1953.

Autumn and Early Winter. Light again became the most critical factor during autumn. Not only was incident radiation decreasing

toward the annual minimum, but also strong vertical mixing by turbulence and convective cooling followed destruction of the summer thermocline.

Significant quantities of nitrate appeared in the water column in September, and phosphate, which had increased slightly during the summer, rose more rapidly in autumn. In general, nutrient regeneration exceeded utilization, but with certain exceptions that are noted below.

By the end of September, diatoms had nearly replaced dinoflagellates once again. There followed, in 1952, a gradual decrease to a minimum population in late autumn. In 1953, a small flowering in September and October was accompanied by a reduction in nutrient concentrations and this apparently led to a temporary increase in the zooplankton stock. According to Riley (unpublished data), autumn flowerings have occurred occasionally in previous years; in 1954, although none was found in the central basin, a large one was found in a limited area in the shallow water at the western end of the Sound. In deeper waters off the New England coast, such as the Gulf of Maine, there is usually a late summer or early autumn flowering of fairly large magnitude (Bigelow, *et al.*, 1940). Apparently it comes soon after the seasonal temperature maximum, when the deepening and gradual destruction of the thermocline is beginning to bring nutrient-rich water to the surface. In Long Island Sound no such store of nutrients is available in the deeper water. There must be the preliminary step of a declining phytoplankton growth rate and an excess of regeneration over utilization before there can be a sufficient stock of nutrients to support a large flowering. This occurs in late September, and by then the light intensity may be inadequate to permit a flowering in the presence of strong vertical mixing. It is pertinent in this connection to note that Harvey, *et al.* (1935) considered light as the primary factor controlling the fall flowering in the English Channel. There, as in the Sound, the flowering was of uncertain occurrence and appeared late in the season.

In comparing environmental conditions, there were no pronounced differences from one autumn to the next. During the critical period from mid-September to mid-October, the estimated average radiation was 365 g cal/cm²/day in 1952, 415 in 1953, and 335 in 1954. Differences in vertical stability and in the amount of wind were essentially negligible. It is conceivable that the biological system was so deli-

cately poised that a mere 15% difference in radiation could determine the presence or absence of an autumn bloom. However, further work is needed to check this point.

Cerataulina pelagica and several species of *Chaetoceros* have been mentioned previously as distinctive elements of the early autumn population and as dominants in the early part of the 1953 flowering. As the season progressed, other species became dominant; in the later part of the 1953 flowering, *Paralia sulcata, Skeletonema costatum,* and *Thalassiosira decipiens* were the most important species.

During the remainder of the autumn and early winter there was a decrease in total population and a gradual change in composition to species more suited to the autumn environment. *Corethron criophilum,* one of the species typical of early fall, showed a distinct preference in experimental bottles for strong light, high salinity and temperature, and nutrient enrichment. The two most abundant late autumn species, *Paralia sulcata* and *Thalassiosira decipiens,* thrived in dim light, nutrient enrichment, and an intermediate range of temperatures. They did not grow well in experimental bottles at temperatures approaching the seasonal minimum, and in nature they were replaced at that time by the typical midwinter flora.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the aid of the senior investigator, Gordon A. Riley. Thanks are also due G. E. Hutchinson for his interest and advice. Acknowledgment is made to Victor L. Loosanoff, Director, and Herman R. Glas, skipper of the SHANG WHEELER, of the U. S. Fish and Wildlife Service Station at Milford, Connecticut for their help in carrying out the many phases of this project. The aid of my husband, R. J. Conover, was indispensible in the preparation of the manuscript. To Jack Fu, Charles Weems, and Frank Wong I extend thanks for help in preparing the data and drawings.

Parts of this paper, chiefly the spring flowering sections, were used in an expanded form as partial fulfillment of the requirements for the degree of Master of Science, Yale University. I sincerely appreciate this opportunity, made possible through the cooperation of G. A. Riley, Daniel Merriman, Director of the Bingham Oceanographic Laboratory, and the faculty of the Zoology Department, Yale University.

REFERENCES CITED

ATKINS, W. R. G. and P. G. JENKINS
1953. Seasonal changes in the phytoplankton during the year 1951–52 as indicated by spectrophotometric chlorophyll estimations. J. Mar. biol. Ass. U. K., *31:* 495–508.

ATKINS, W. R. G. and M. PARKE
1951. Seasonal changes in the phytoplankton as indicated by chlorophyll estimations. J. Mar. biol. Ass. U. K., *29:* 609–618.

BARKER, H. A.
1935a. Photosynthesis in diatoms. Ark. Mikrobiol., *6:* 141–156.
1935b. The culture and physiology of the marine dinoflagellates. Ark. Mikrobiol., *6:* 157–181.

BIGELOW, H. B.
1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish., *40* (2): 509 pp.

BIGELOW, H. B., L. C. LILLICK and MARY SEARS
1940. Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. Trans. Amer. phil. Soc., N. S. *31:* 149–191.

BRAARUD, TRYGVE
1945. Experimental studies on marine plankton diatoms. Norske Videnskaps-Akad., Oslo. I. Mat.-Naturv. Klasse, 1944 (10): 1–16.

BRAARUD, TRYGVE, K. R. GAARDER and J. GRØNTVED
1953. The phytoplankton of the North Sea and adjacent waters in May 1948. Rapp. Cons. Explor. Mer, *133:* 1–87.

CONOVER, S. M.
1954. Observations on the structure of red tides in New Haven Harbor, Connecticut. J. Mar. Res., *13:* 145–155.

FISH, C. J.
1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. U. S. Bur. Fish., *41:* 91–179.

GRØNTVED, J.
1952. Investigations on the phytoplankton in the southern North Sea in May, 1947. Medd. Komm. Havundersøg., Kbh., Plankton *5* (5): 1–49.

HARVEY, H. W.
1953. Synthesis of organic nitrogen and chlorophyll by *Nitzschia closterium.* J. Mar. biol. Ass. U. K., *31:* 477–487.

HARVEY, H. W., L. H. N. COOPER, M. V. LEBOUR and F. S. RUSSELL
1935. Plankton production and its control. J. Mar. biol. Ass. U. K., *20:* 407–441.

HENDEY, N. I.
1954. A preliminary check list of British marine diatoms. J. Mar. biol. Ass. U. K., *33:* 537–560.

HOAGLAND, D. R.
1948. Lectures on the inorganic nutrition of plants. Chronica Botanica, Waltham, Mass. 225 pp.

MARGALEF, R.
1954. Modifications induced by different temperatures on the cells of *Scenedesmus obliquus* (Chlorophyceae). Hydrobiologia, *6:* 83–94.

POOLE, H. H. and W. R. G. ATKINS
1929. Photoelectric measurements of submarine illumination. J. Mar. biol. Ass. U. K., *16:* 297–324.

RABINOWITCH, EUGENE
1952. Photosynthesis. Ann. Rev. Plant Physiol., *3:* 229–264.

RILEY, G. A.
1952. Hydrographic and biological studies of Block Island Sound. Phytoplankton of Block Island Sound, 1949. Bull. Bingham Oceanogr. Coll., *13* (3) : 40–64.

RODHE, W.
1948. Environmental requirements of fresh water plankton algae. Symbolae Botan. Upsalienses, *10* (1): 1–149.

STEEMANN-NIELSEN, E.
1937. The annual amount of organic matter produced by the phytoplankton in the Sound off Helsinger. Medd. Komm. Havundersøg., Kbh., Plankton *3* (3): 1–37.