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Review of the oceanography of Long Island Sound

By GORDON A. RILEY
Bingham Oceanographic Laboratory
and
Woods Hole Oceanographic Institution*

Summary—Long Island Sound is a shallow, semi-enclosed body of slightly brackish (23–31 ‰) water with an area of about 900 nautical square miles. Moderate tidal currents permit a small seasonal thermocline and slight vertical gradients in salinity, oxygen and nutrient salts. The major feature of non-tidal circulation is a two-layered transport system in which a freshened surface layer moves eastward out of the Sound and is replaced by a more saline inflow along the bottom. The latter contains more nutrients than the outflowing surface water, so that the transport system tends to accumulate and conserve nutrients. Freshwater drainage also makes a significant contribution of nitrate.

Phytoplankton concentrations are large, but the species composition is relatively limited. A large diatom flowering occurs in late winter, following an early winter minimum, with only minor fluctuations the rest of the year. There is sufficient mixing to prevent a large accumulation of nutrients in the bottom water, so that there is neither pronounced poverty in summer nor a big autumn flowering following destruction of the thermocline. Major limiting factors are the amount of effective light in autumn and winter and the nitrogen supply in spring and summer. Variations in light and temperature from one year to the next affect the winter species composition and the time of the flowering. Diatoms are largely replaced in summer by naked flagellates and other nannoplankton. During one summer when nitrate concentrations were higher than usual, diatoms were abundant and there was also an unusually large zooplankton crop. A causal connection is indicated but not well established.

The zooplankton consists of large numbers of small animals. Relatively few species are present. The dominants are two species of the copepod *Acartia* which alternate seasonally. Descriptive and experimental studies suggest that seasonal replacement is primarily a temperature-controlled competition rather than a direct, lethal temperature effect. Experiments show that the *Acartias* have high respiratory rates and low grazing rates compared with most other copepods that have been examined and possibly are able to achieve dominance only in waters sufficiently brackish to exclude more efficient oceanic species.

Preliminary studies of bottom fauna indicate a relatively large biomass, again consisting of large numbers of small animals. Fish eggs and larvae are abundant, and the Sound may be an important spawning and nursery ground. However, commercial fishery statistics show no indications of a large population of mature fish.

Total phytoplankton production is about the same as in the open coastal and bank waters off New England. Most of this production is utilized in the support of small animals which do not provide an adequate food supply for the efficient production of large carnivores.

INTRODUCTION

LONG ISLAND SOUND, like other New England waters, has been a source of interest and livelihood since colonial times, and its general features are well described in early expedition narratives. Scientific studies of its waters began a little more than a hundred years ago with a survey of the morphometry, character of the bottom, tides, and currents, jointly sponsored by the Navy and the predecessor of the present Coast and Geodetic Survey. The pertinent information was printed on a series of three excellent hydrographic charts in 1855. More thorough surveys of tides and currents were made

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during the late nineteenth and early twentieth centuries, and all available observations have been summarized by Le Lacheur and Sammons (1932).

The first oceanographic studies that may be regarded as modern in their general scope and outlook were begun in the 1870's under the able direction of Spencer F. Baird, U.S. Commissioner of Fish and Fisheries. For the waters from Cape Cod to New Jersey, and including Long Island Sound, we find in his reports during the ensuing years not only accounts of the fishes and their physical environment, but also monographs on the invertebrates (Verrill, 1873) and algae (Farlow, 1879), as well as other major works that are still in common use.

In 1935 the U.S. Fish and Wildlife Service established a laboratory at Milford, Connecticut, under the directorship of Victor L. Loosanoff. One of the most important contributions of this laboratory has been a thorough study of lamellibranch physiology and ecology by combined field and laboratory techniques. In addition, records have been maintained for fifteen to twenty years of temperature and salinity in the north-central part of the Sound, oyster spawning and setting, and other oceanographic matters of both practical and scientific interest.

In 1938 the Bingham Oceanographic Laboratory began a year's survey of plankton and associated environmental factors in the same area (Riley, 1941), and similar work was carried on during the summers of 1940, 1941, and 1950. A program of broader scope was instituted in 1952, consisting of weekly coverage of a grid of stations in the central part of the Sound for a two-year period, followed by a further expansion to coverage of the Sound as a whole at approximately monthly intervals. The latter work is still in progress.

The present paper reviews some of the work that has been done and attempts to extract some ecological generalizations that will be applicable to Long Island Sound in particular and perhaps in some cases to temperate littoral waters in general. For purposes of comparison it is pertinent to mention other work in nearby waters: a survey of temperature and salinity distribution by the Woods Hole Oceanographic Institution in the area from Woods Hole to the central part of Long Island Sound in 1946, a study of Block Island Sound from 1943 to 1946 and in 1949 by the Bingham Oceanographic Laboratory, and the work of Ryther (1954) and other Woods Hole staff members in the bays on the south shore of Long Island.

PHYSIOGRAPHY AND PHYSICAL OCEANOGRAPHY

Long Island Sound (Fig. 1) is a semi-enclosed body of water some 90 nautical miles long, with a maximum width of about 15 mi. and an area of 928 sq. mi. The maximum depth in the eastern end is about 100 m. There is little water of more than 35 m in the central and western basins, and the mean depth of the Sound as a whole is only 20 m. Free interchange with the waters of Block Island Sound occurs through a series of passes at the eastern end. In the west there is more limited interchange with the New York harbour and river waters.

The drainage basin is roughly eleven times the area of the Sound, and the annual volume of freshwater drainage averages 35% of the volume of the Sound. However, three-quarters of the river water enters the relatively open eastern end, where it is flushed out rapidly and has a minimal effect on the Sound as a whole.

Tidal interchange totals 8·6% of the volume of the Sound below mean low water, leading to currents of three knots or more in the eastern passes and a maximum speed

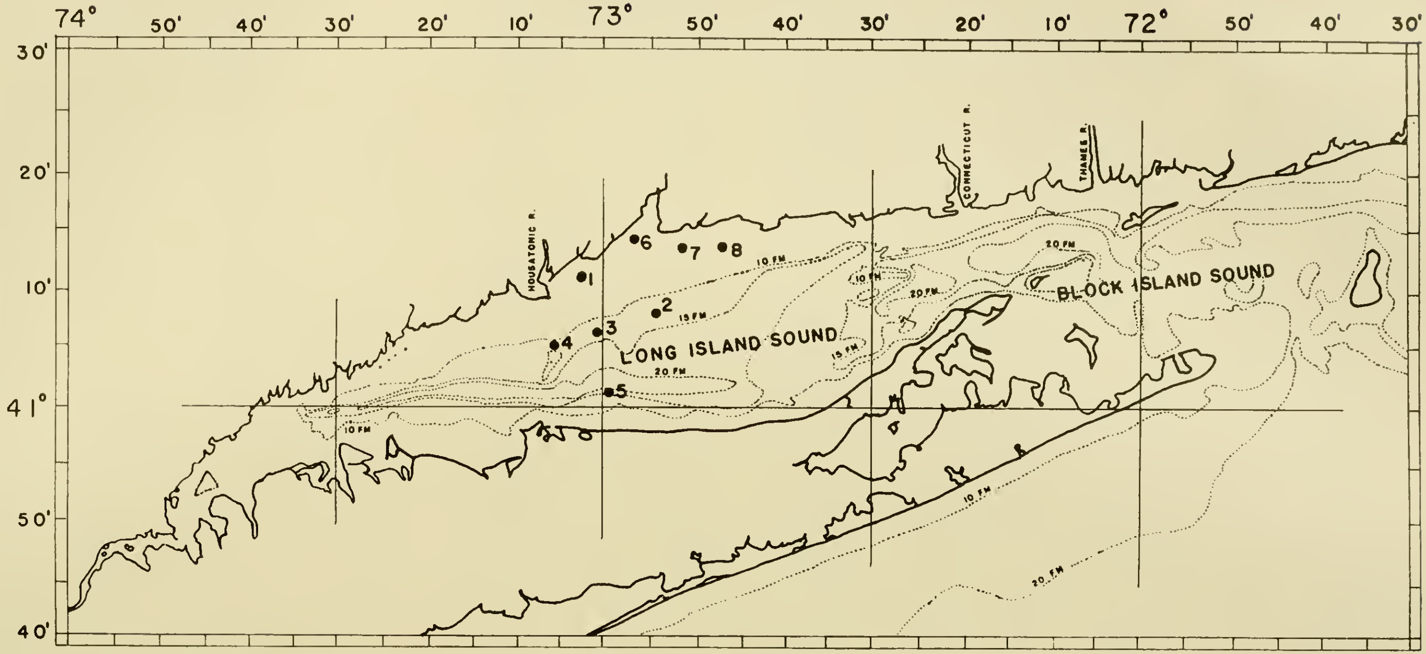

Fig. 1. Chart of Long Island Sound and adjacent waters. Depth contours at 10, 15, and 20 fm. in the Sound; 10 and 20 fm. elsewhere. Routine station positions of the 1952–54 survey in the central part of the Sound are shown as numbered dots.

of about one knot in the central and western basins. Many current stations, particularly in the eastern part of the Sound, show that the ebb is stronger than the flood in the surface layer, while the reverse is true at the bottom. Thus there is a tendency here, as in many other sounds and estuaries, for the surface layer to move seaward and to be replaced by saline water flowing in along the bottom. An analysis of the available current stations during the summer season (RILEY, 1955 A) indicates that this inflow through the eastern passes is of the order of 15–20 thousand m^3 per second. The bottom transport decreases rapidly as it moves west, approaching zero near the western end of the Sound. Clearly the slowing down is due to upwelling of bottom water and admixture with the surface layer, and current measurements demonstrate a corresponding augmentation of the eastward surface transport. The calculated mean rate of upwelling required to satisfy the principle of mass continuity is small, ranging from about 5 cm per month in the central and western part of the Sound to a maximum of 45 cm in the vicinity of the passes.

It would appear from current stations that about 1,100 m^3 sec enter the western end of the Sound from New York harbour and flow eastward as part of the surface layer. The latter is further augmented by freshwater drainage, amounting to about 300 m^3/sec in summer. Thus the surface outflow at the eastern end should exceed the inflow by about 1,400 m^3/sec, although the statistically derived transport estimates are not accurate enough to demonstrate this.

Complete current surveys are available only for the summer period. Analyses of salt balance (RILEY, 1952 A) indicated a seasonal variation correlated with freshwater drainage. Surface current measurements at Bartlett Reef Lightship in the eastern end of the Sound (LE LACHEUR and SAMMONS, 1932) showed a similar relationship, but farther west, at Cornfield Lightship, the seasonal variation was slight and was not clearly correlated with river outflow.

The distribution of temperature and salinity has been described by GALTSOFF and LOOSANOFF (1939) and RILEY (1952 A). Surface water temperatures have a seasonal range of roughly 3° to 19° in the eastern end of the Sound and 0° to 23° in the western portion. The total salinity range is about 23 to 31 $^{\circ}/_{\circ\circ}$, excluding occasional eddies of fresher water in the immediate vicinity of the rivers. The east–west salinity gradient is ordinarily about $5^{\circ}/_{\circ\circ}$, and there is a seasonal variation of 2 to $4^{\circ}/_{\circ\circ}$.

A two-year series of observations in the central part of the Sound (RILEY, 1955 A) at station positions shown in Fig. 1 serves to illustrate general features of the temperature and salinity cycles. There was a small thermocline in spring and summer, and the maximum difference between surface and bottom temperature was about 5° (Fig. 2). A slight salinity gradient was maintained throughout most of the year by the combined effects of freshwater dilution of the surface layer and inflow of saline water along the bottom. Differences in the seasonal cycles from one year to the next show obvious correlations with the meteorological variables included in Fig. 2.

SEASONAL CYCLES OF PLANKTON AND CHEMICAL FACTORS

The upper part of Fig. 3 shows the seasonal cycles of surface and bottom phosphate and nitrate as averages of analyses at inshore stations 1, 6, 7, and 8 (RILEY and CONOVER, 1955). Chlorophyll analyses included in the figure provide an estimate of the total phytoplankton population, and zooplankton catches obtained by oblique tows with a Clarke–Bumpus sampler are plotted as total displacement volumes.

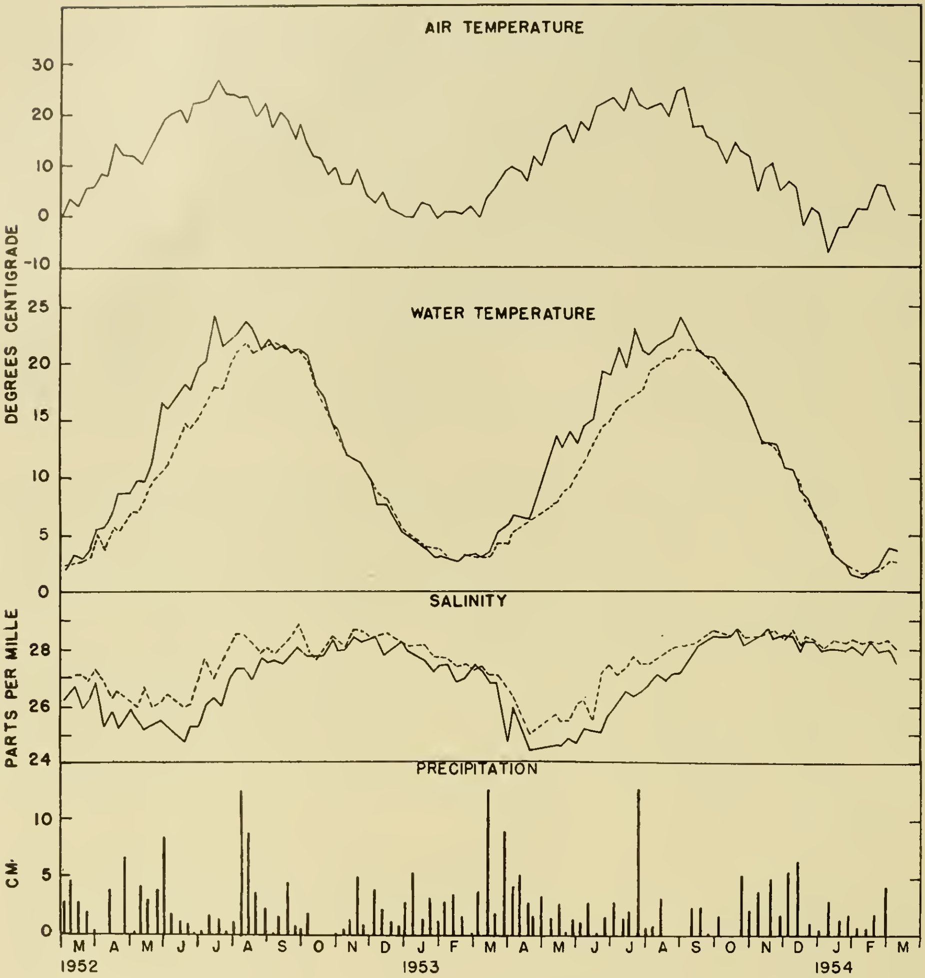

Fig. 2. Average temperature in °C and salinity in parts per mille at the surface (solid lines) and bottom (dotted lines) at offshore stations 2 to 5 (cf. Fig. 1). Weekly averages of air temperature recorded by the New Haven Weather Bureau and total precipitation in cm between successive dates of oceanographic observation.

The gross features of nutrient cycles are characteristic of temperate waters, but the proportions of nitrate–nitrogen and phosphorus are anomalous. During the winter maxima, the ratio of N:P by atoms has been of the order of 8:1, about half the value that might be expected in oceanic waters. The late winter flowerings of 1953 and 1954 almost completely exhausted the supply of nitrate in about three weeks but left a residuum of about 0·5 μg-at of phosphate-P in the water.

Most of the spring and summer analyses have shown little or no nitrate in any part of the water column. Harris (unpublished) has found small but significant quantities of ammonia, and this, together with organic nitrogen compounds, constitutes the main source of supply. Phosphate values during the same period generally have been within the range of 0·2 to 1 μg-at P per litre. Phosphate tended to increase gradually during the summer and more rapidly in autumn. Nitrate remained low

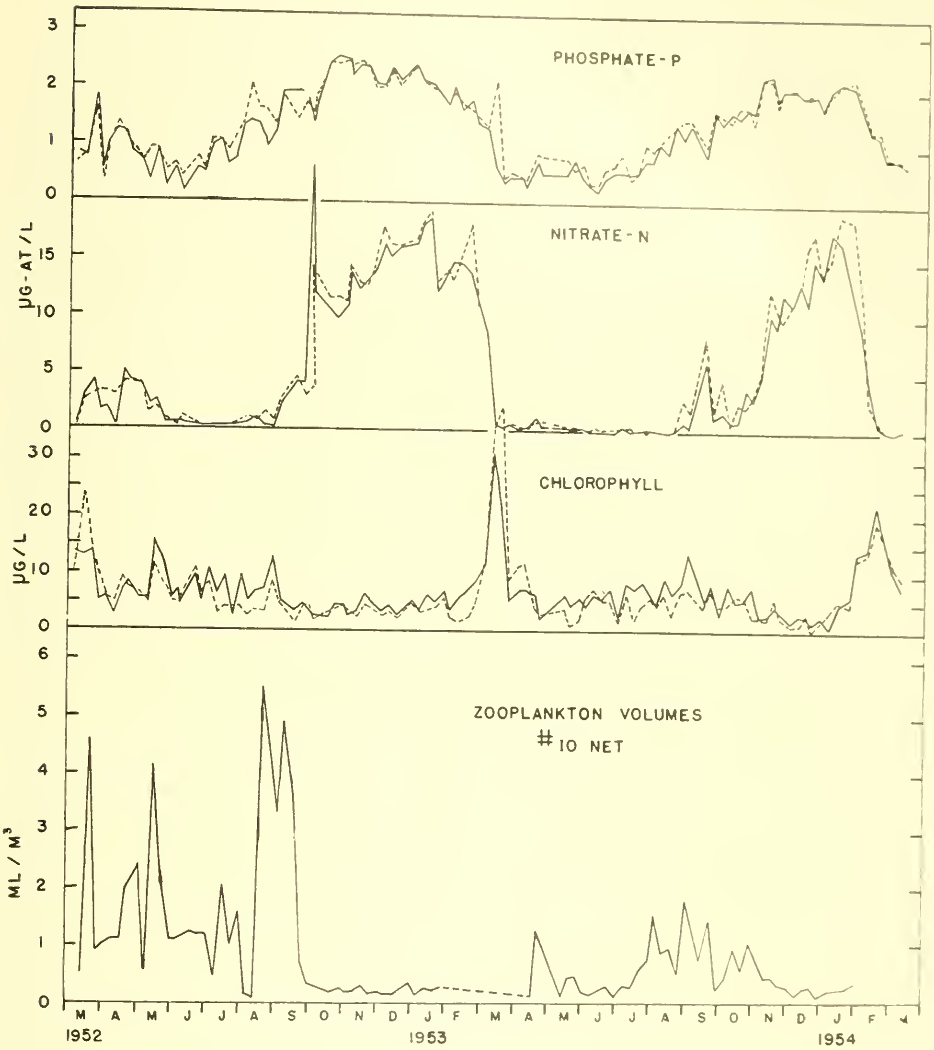

Fig. 3. Average phosphate, nitrate, and chlorophyll at the surface (solid lines) and bottom (dotted lines) at inshore stations 1, 6, 7 and 8. Zooplankton displacement volumes, also at inshore stations, are averages for the water column obtained by oblique tows with a No. 10 net.

until September. The autumn increase in nutrients was interrupted in October, 1953, presumably because of plant growth. While there was not a pronounced autumn flowering in the ordinary sense of the term, both phytoplankton and zooplankton crops were larger than in the autumn of 1952.

Phosphate and nitrate increased slightly from surface to bottom during most of the spring and summer. Stability was too slight to permit the accumulation of a large store of regenerated nutrients in the bottom water. It was reasonable, then, to find neither a pronounced summer period of phytoplankton impoverishment nor a marked flowering following destruction of the summer thermocline. It was common in autumn and early winter to find a significant reduction in phosphate and nitrate in the bottom water. The reason for this peculiar phenomenon will be discussed later.

The major diatom flowering occurred in late winter, as previously reported in Long Island Sound (RILEY, 1941) and some other littoral waters off the New England coast (BIGELOW, 1926; FISH, 1925). An early flowering in these latitudes requires that the phytoplankton be confined to a shallow stratum, since it is only in such an environment that the effective light intensity in winter exceeds the threshold necessary for active growth. Hence the flowering is likely to be early in shallow water and to begin later in the deeper water, frequently only after the establishment of vernal stability (BIGELOW, LILLICK, and SEARS, 1940; RILEY, 1942). In a particular location the time of the flowering may vary from year to year in accordance with variations in the amount of light available (ATKINS, 1928). However, in comparing the winters of 1953 and 1954 in Long Island Sound, there were no marked differences in incident radiation, and another explanation must be sought for the fact that the 1954 flowering was about three weeks earlier.

S. CONOVER (1955) found that the midwinter diatom population was dominated by two species, *Skeletonema costatum* and *Thalassiosira nordenskiöldii*, in about equal proportions. In 1953 *Skeletonema* dominated the flowering, achieving an average concentration of 36 million cells per litre at the stations sampled on March 9, as compared with one million cells per litre of *Thalassiosira*. In 1954 *Thalassiosira nordenskiöldii* rose to six million cells per litre on February 17, while *Skeletonema* achieved a peak concentration of nine million cells the following week. Considering the difference in size of the two species, *Thalassiosira* clearly dominated the early flowering period in 1954.

CONOVER conducted a series of experiments in 1954 in which natural populations were bottled and treated to a variety of conditions of light, temperature and nutrient enrichment. Table I shows a part of the data from the experiment of February 10 that is pertinent to the present discussion. It is apparent that *Thalassiosira* has an optimum growth rate at low temperatures and can tolerate low light intensities, while *Skeletonema* requires higher temperature and probably better illumination. Later experiments suggested that the critical temperature determining which species will dominate is between 2·4 and 3·7°C. The mean temperature in the Sound was 3·2° in February 1953, and 3·7° in March, and the corresponding means for 1954 were respectively 1·7 and 3·5°. CONOVER concluded that the lower temperature in 1954

Table I

Growth coefficients (fractional increase in cell number per day) of Skeletonema costatum *and* Thalassiosira nordenskiöldii *in two-day experimental exposures of natural surface water phytoplankton populations to normal seasonal temperature and surface light intensity, to reduced light, and to increased temperature*

Temperature °*C*	*Growth coefficients* *Skeletonema*	*Thalassiosira*
1·7	–0·021	0·058
1·7*	–0·025	0·015
5·0	0·144	–0·133
8·0	0·258	–0·163

* Average of four experiments at light intensities ranging from 1 to 24% of the surface value.

favoured the dominance of *Thalassiosira* and that its tolerance to low light intensity permitted a relatively early flowering. Contrariwise, physical conditions promoted dominance by *Skeletonema* throughout February and March, 1953, and toward the end of the 1954 flowering.

In 1955 the flowering was even earlier. The major growth took place during the last ten days of January, and the peak was attained early in February. The New Haven Weather Bureau reported that the percentage of sunshine in January, 1955, was the highest that has been recorded in 55 years of observation, so that an early flowering was not unreasonable. The temperature in the Sound was 3·1 to 3·3° at the beginning of the flowering, and *Skeletonema* was the dominant species. As the flowering progressed the temperature dropped to about 1°. At this writing, counts of the phytoplankton for this period have not been completed. Preliminary indications are that *Thalassiosira* gained in relative importance but was unable to achieve complete dominance.

Experiments by S. CONOVER (1955) showed that the 1954 flowering was terminated largely because of nitrogen deficiency. At this time and again in June, 1954, natural phytoplankton populations were enriched with phosphate, nitrate, iron, and manganese, singly and in combination. In all cases nitrogen was the one element that had a significant effect on the population as a whole, although individual species occasionally responded to other types of enrichment. Nevertheless, the percentage of nitrogen in the phytoplankton remained nearly constant through the year (HARRIS and RILEY,

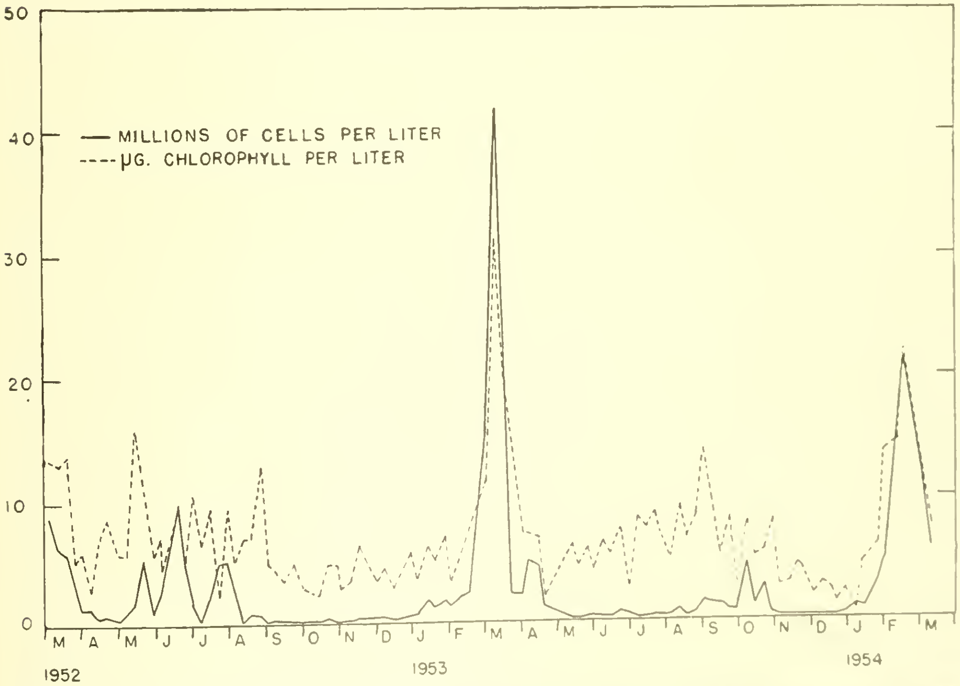

Fig. 4. Phytoplankton cell numbers and chlorophyll concentrations in the surface waters, plotted as the average of all values obtained at inshore stations.

1955), so that the deficiency obviously does not approach the extremity of laboratory cultures, in which the nitrogen content may be reduced to one-third normal (KETCHUM and REDFIELD, 1949).

It is beyond the scope of this paper to discuss seasonal succession in detail, but one other major feature is apparent in Fig. 4, which compares chlorophyll analyses with CONOVER's cell counts. The latter comprised mainly diatoms and armoured flagellates. In addition, occasional examinations of fresh material in summer have revealed two to five million naked flagellates per litre and many millions of small, unidentified *Chlorella*-like cells. These small species are believed to be largely responsible for the disparity between chlorophyll and routine cell counts in summer. Long Island Sound seems to resemble, to a much less extreme degree, the situation described by RYTHER (1954) in Great South Bay and Moriches Bay, Long Island, where there was an excessive summer dominance by " small forms ". These were shown by RYTHER's experiments to be favoured in their competition with diatoms by reduced salinity, high temperature, a low N:P ratio, and the presence of nitrogen primarily in forms other than nitrate. Similar environmental tendencies have been noted in Long Island Sound. It is perhaps significant in this connection that the slightly higher nitrate values during the summer of 1952 were accompanied by much larger quantities of diatoms.

In the locality described by Ryther, the nannoplankton appeared to have a distinctly toxic effect on shellfish. There is no evidence of a similar situation in the Sound. LOOSANOFF *et al.* (1947; 1953) have studied feeding rates and toxicity reactions of lamellibranchs, using a variety of nannoplankton species as food organisms. Their work indicates that the concentration of organisms required for toxic effects is well above the level of the population found in the Sound. On the other hand, R. CONOVER (1955) found that *Acartia*, the dominant genus of copepods in these waters, feeds much more effectively on diatoms than on nannoplankton. Hence the value of the latter as zooplankton food is somewhat questionable.

Quantitative aspects of the total zooplankton population, as depicted in Fig. 3, provide little material for generalization except that there is a minimal population in autumn and early winter, a larger but rapidly fluctuating crop in spring and summer, and a vast difference from one year to the next. Similar variability in the level of the summer population has been noted in previous studies during the summers of 1938 to 1941. There is no satisfactory explanation, although it may be argued on rather tenuous grounds that a causal relation exists between the relative abundance of nitrate, diatoms and zooplankton in 1952 as compared with their scarcity the following year.

According to DEEVEY (1955), copepods are the dominant zooplankton organisms in the Sound, the most important species being *Acartia clausi* and *A. tonsa*, with smaller but significant quantities of *Temora longicornis*, *Pseudocalanus minutus*, *Paracalanus crassirostris*, and *Oithona* spp. Several other copepods and three species of Cladocera occasionally constituted as much as 5% of the population, as did the larvae of various bottom invertebrates. In general, the species composition was quite limited, and several species that are common in the outer coastal waters and are known to have a wide salinity tolerance were unable to maintain significant numbers in the Sound.

R. CONOVER (1955) has made a descriptive and experimental study of the two species of *Acartia* with particular reference to problems of seasonal succession. *A. clausi* appeared in November or December and increased to a maximum in May of

102,000 per m^3 in 1952 and 62,000 in 1953. A rapid decline followed, and the species disappeared from the water in early August. *A. tonsa* appeared in June and increased to 82,000 per m^3 in August, 1952 and 46,000 in 1953. There was a more or less steady decrease during the autumn and early winter, a slight rise in early spring, and then virtual disappearance from the water. Thus *A. clausi* was dominant in winter and spring and was replaced by *A. tonsa* in summer and autumn, but both species persisted through almost the entire seasonal temperature range.

The data did not completely rule out the possibility that seasonal succession is controlled by direct, lethal temperature effects, but the form of the seasonal cycle suggested the more likely possibility of a temperature controlled inter-species competition. During the winter, when *A. clausi* was replacing *A. tonsa*, the latter was found mainly in the bottom waters. In laboratory experiments at low temperature, it was sluggish, but mortality was not excessive. The possibility of temperature-controlled competition was explored through the medium of grazing and respiratory experiments. The grazing experiments determined the quantity of water that each species could filter in a given length of time, and this, combined with the observed quantity of phytoplankton in the Sound, provided an estimate of total food intake. Respiratory experiments in turn determined how much of the food intake was required to satisfy immediate metabolic needs. In *A. tonsa* these two quantities were about equal during most of the winter. Only at the time of the flowering did the intake appear to be substantially larger than the requirement. *A. clausi*, on the other hand, was able to feed at a materially higher level than its rate of metabolic loss throughout the winter and hence was a favoured competitor for food at this season.

In summer *A. tonsa* was found in greatest abundance near the surface and *A. clausi* in the slightly cooler bottom layer, so that there was no close and immediate competition for food. Despite the preference for low temperature, *A. clausi* also remained a more effective feeder in summer than *A. tonsa*. Thus the summer succession involved a different mechanism, and one which has not been worked out in detail. But since adult *A. clausi* remained in the Sound for some time after immature stages disappeared, Conover concluded that the replacement was due either to failure of the animals to reproduce at high temperatures or to competition among the juveniles.

HORIZONTAL DISTRIBUTION OF PLANKTON AND NUTRIENTS

Maximum concentrations of both phytoplankton and zooplankton are ordinarily found in the western end of the Sound and in the shallow waters along the north shore. Here the average concentration of phytoplankton is about three times as large as in the eastern end of the Sound or in Block Island Sound and ten times the concentration in the outer coastal waters. Horizontal gradients in zooplankton and nutrients are similar but not so extreme.

Maximum concentrations are found in very shallow water, and the differences in the total population underlying a unit area of surface are not so marked. Ratios of the total populations in the Long Island and Block Island Sounds average about 1·5:1 for phytoplankton and 1:1 for zooplankton.

It has often been stated that inshore waters are very fertile and that this is primarily due to enrichment by freshwater drainage. However, it is apparent that there are no large regional differences in the total plankton population in southern New England waters, nor is there evidence of much difference in rates of production. Methods of measuring the latter are not accurate enough for precise estimates, but such information as is available (RILEY, 1952 B and 1955 C) indicates little difference between the Long Island and Block Island Sounds as far as phytoplankton productivity is concerned.

To be sure, Long Island Sound maintains a slightly higher concentration of nutrients, although again not necessarily a larger total stock per unit area. Two factors tend to maintain this higher concentration. First, freshwater drainage contains a highly variable but generally higher concentration of nitrate (but not phosphate) than Sound waters. Secondly, two-layered transport exchange creates a mechanism whereby the biological system automatically regulates the nutrient supply at a slightly higher level than in the outside waters. During most of the spring and summer, plant growth is sufficiently active to impoverish the nutrient supply in the surface layer. Part of the phytoplankton produced at the surface is utilized elsewhere in the water column, as is sufficiently evident from the existence of a bottom fauna. Thus the surface layer that is transported out of the Sound is relatively poor in total nutrient content, and the latter tends to be conserved and concentrated within the Sound as long as plant growth is sufficiently active to maintain a vertical gradient in nutrients.

During the autumn, when regeneration of nutrients exceeds utilization, very large concentrations have been found toward the western end of the Sound. These tend to be reduced as the season progresses by the combined effects of lateral diffusion and transport exchange. It has been common in autumn and early winter to find positive vertical gradients in nutrients, where rich western water overrides the inflowing bottom water. It was the frequency of this rather unusual type of vertical distribution that first focussed attention on the subject.

Preliminary calculations of enrichment by transport exchange have been made, using transport data mentioned earlier and the observed distribution of phosphate and nitrate. The amount of enrichment in the western half of the Sound during the spring–summer season was estimated to equal one-third of the amount of phosphate present at the time of the midwinter maximum and one-tenth of the nitrate stock. More accurate evaluation of this problem, and of the relative importance of river drainage, awaits the completion of work in progress on seasonal variations in the exchange rate and the distribution of total as well as inorganic nutrient stocks.

ORGANIC PRODUCTION

Two one-year series of measurements have been made of the photosynthetic rate of the surface phytoplankton in Long Island Sound (RILEY, 1941; S. CONOVER, 1955) using the light and dark bottle technique. The later work also included a few measurements at a series of depths from surface to near bottom. Another type of analysis has also been used to estimate the biological rate of change of oxygen and phosphate at various levels in the water column and on the bottom (RILEY, 1955 C). Having determined coefficients of vertical eddy conductivity from the vertical distribution and seasonal change in temperature, the coefficients were then applied to the observed distribution of oxygen and phosphate. This provided information on the rate of accumulation or depletion of the element at a given depth by vertical mixing. Any difference between the calculated rate and the observed change was then ascribed to biological processes. The oxygen and phosphate analyses agreed within narrow limits. The calculated net rate of change of oxygen in the surface layer was about 50% larger than the increase in experimental light bottles. The discrepancy may have been due to experimental error, since it is well known that bacterial growth is abnormally large in bottled sea water. However, there are also several possible sources of error in the physical oceanographic calculations, so that there is an uncertainty factor of at least 50% in the results of the productivity compilation.

The consumption of organic matter by the benthic community was estimated by physical oceanographic computation of the rate of transfer of oxygen downwards through the lower few metres of water and by the rate of upward transfer of phosphate from the bottom. An estimate of the rate of consumption by the plankton community could be obtained from the net rate of utilization of oxygen in the lower part of the water column, since the vertical distribution of plankton was relatively uniform. However, it was a minimal estimate because experiments showed a slight but significant amount of photosynthesis at depths of 15 to 20 m in summer. Dark bottle respiration averaged approximately twice the net rate of change in the lower water column. Experimental values were presumably too high, and therefore an intermediate value was chosen to represent the total oxygen consumption of the plankton community. Results are shown in Table II, together with somewhat similar estimates by Harvey (1950) for the English Channel.

Table II

Comparison of mean annual standing crops and organic production (grams organic matter per m²) in the English Channel (EC) and central Long Island Sound (LIS)

	Standing crop		*Daily production*		*Daily loss by respiration*	
	EC	LIS	EC	LIS	EC	LIS
Phytoplankton	4	16	—	3·2*	—	1·8*
			0·4–0·5†	1·07†		
Zooplankton	1·5	2	0·15	—	0·06	0·28
Pelagic fish	1·8	—	0·0016	—	0·025	—
Bacteria	0·04	—	—	—	0·013	0·46‡
Demersal fish	1–1·25	—	0·001	—	0·015	0·33
Epi- and in-fauna	17	19–38	0·03	—	0·2–0·3	
Bacteria	0·1	—	—	—	0·03	
Total consumption, exclusive of phytoplankton respiration					0·34–0·44	1·07

* Photosynthetic glucose production and loss of glucose by respiration.
† Production of phytoplankton of normal organic content in excess of respiratory requirement.
‡ Includes bacteria and microzooplankton. For further explanation of this item see text.

Data for the English Channel were obtained at a station in 70 m of water off Plymouth, as compared with a mean depth of 20 m in Long Island Sound. Nutrient concentrations were relatively low in the English Channel, although the total stock in the water column at the time of the winter maximum was about the same in both areas.

The Sound has a larger standing crop of phytoplankton and greater basic productivity. The zooplankton crop is only slightly greater. In this connection, R. Conover (1955) has pointed out that the dominant copepod *Acartia* is a relatively inefficient feeder, has a remarkably high respiratory requirement, and probably achieves great dominance only in waters that are sufficiently brackish to exclude the more efficient oceanic forms.

The estimate of zooplankton respiration is based on Conover's work, and the phytoplankton respiratory rate is a compilation of field and laboratory data by RILEY, STOMMEL, and BUMPUS (1949). When these items are subtracted from the total estimated respiration in the water column, the remainder, representing 0·46 g of organic matter consumed per day, is ascribed in Table II to bacteria and the fraction of small zooplankton that is not captured by the Number 10 net. While both of these elements of the population appear to be important, it is apparent that the method of calculation allows a wide margin of possible error in the estimate.

Consumption on the bottom in Long Island Sound appears to be about the same as HARVEY'S total, although collections of benthic invertebrates in the Sound (Sanders, in preparation) are larger. Later work in the English Channel by HOLME (1953) tends to reduce HARVEY'S estimate, so there is little doubt that the Sound has a larger total biomass. The number of animals is enormous, and the mean size of the individual is small compared with the English Channel.

WHEATLAND (1955) has demonstrated that the Sound is an important spawning and nursery ground for several species of fish. Little work has been done on adult fishes, but the commercial catch is small, and WHEATLAND'S examination of catch statistics indicated that the catch per unit effort is smaller than in the adjacent Block Island Sound.

In short, the high basic production in Long Island Sound is utilized by great numbers of small animals. Conversion to high-level food chain carnivores appears to be relatively inefficient.

GENERAL DISCUSSION OF FOOD CHAIN EFFICIENCY

Block Island Sound has a net production (excess of photosynthesis over respiration of the phytoplankton) estimated by RILEY (1952 B) at 285 grams of carbon per square metre of sea surface in a year, as compared with 205 grams in Long Island Sound. However, a considerable fraction of phytoplankton appeared to be lost by horizontal dispersal into the outer coastal region and the amount utilized *in situ* by the biological association was estimated to be only 150 grams. The annual fish production in Block Island Sound is about 50 to 100 lb. per acre wet weight (estimated from data in MERRIMAN and WARFEL, 1947). In terms of carbon content, this amounts to between 0·4 and 0·8% of the net phytoplankton production. From Table II it may be seen that Harvey's estimate of the combined pelagic and demersal fish production in the English Channel is 0·52 to 0·65% of the phytoplankton production. Hence both areas have about the same level of efficiency in food chain conversion, although Block Island Sound is more productive in the absolute sense.

Phytoplankton production on Georges Bank also nets about 150 grams of carbon per year (RILEY, 1944). Commercial fish catches have ranged from 7 to 33 lb. per acre, according to CLARKE (1946). Total production is probably more than twice the landings of table fish, so that the efficiency level is not very different from the figures listed for Block Island Sound and the English Channel.

A very different situation is found in such areas as the Sargasso Sea. Here the level of net production is uncertain, recent estimates varying from 30 g carbon per m² per year (STEEMANN NIELSEN, 1952) to 110 g (RILEY, 1953). According to RILEY, STOMMEL and Bumpus (1949), the total displacement volume of zooplankton underlying a square metre of sea surface is equal to the amount found on Georges Bank or in the Gulf of Maine and double the crop in southern New England coastal waters. However, its organic content is very low, and it was suggested that the zooplankton is a starved population, possibly with a low rate of production. The extended disposition of the plankton through a long vertical column in such waters requires the expenditure of a relatively large amount of energy in food capture and theoretically should lead to inefficiency in food conversion, with progressive attenuation of the higher members of the food chain. Quantitative information on the total fish population is lacking, but there is no evidence to indicate that it is a large one. Thus the basic production is roughly of the order of magnitude of that found in the English Channel, but it is largely dissipated at the plankton level.

It would appear that a high level of plant production is necessary but not sufficient for a thriving fishery. Block Island Sound and Georges Bank are probably superior to the English Channel at all levels of the food chain, but the English Channel appears to produce more marketable fish than Long Island Sound despite the high basic production of the latter.

Optimum efficiency of conversion seems to be characteristic of coastal and bank waters of moderate depth and salinity of 30‰ or more. A lesser degree of efficiency is probably to be expected in most deep oceanic waters. Two examples of brackish waters that have been examined, namely Long Island Sound and the Moriches–Great South Bay area, although productive in the basic sense also seem to be relatively inefficient in food chain conversions. The underlying reasons for this are not clearly understood, although some of the symptoms are obvious. There is a large proportion of nannoplankton existing in an environment which, according to Ryther's (1954) experimental studies, favours the dominance of such forms. They are not particularly good food for the large zooplankton which in turn would be the major source of food for larger animals. The brackish environment also apparently favours the dominance of zooplankton species that are inefficient feeders. Thus there exists in the water a relatively large quantity of unutilized phytoplankton and organic detritus. This in itself is a clear symptom of a low rate of turnover, and it probably promotes the dissipation of a major fraction of the energy of the system at low levels by bacteria and microzooplankton. It also tends to produce a bottom sediment of high organic content. The latter generally supports a smaller biomass than a mixed sand and mud bottom and one that is qualitatively less desirable for benthic carnivores. The mud bottoms in Long Island Sound have enormous numbers of nematodes and other microfauna which presumably have a high food requirement and rate of production but are of very limited value as food for groundfish.

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