Oceanography of Long Island Sound, 1952-1954
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OCEANOGRAPHY OF
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Volume XV

OCEANOGRAPHY OF
LONG ISLAND SOUND, 1952–1954

IX.   PRODUCTION AND UTILIZATION
OF ORGANIC MATTER

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ABSTRACT

The observed distribution of oxygen and phosphate was used to calculate the net biological rates of change of these elements on a seasonal basis. With the aid of experimental data and some arbitrary assumptions, the net changes were converted to estimates of total plant production and utilization of organic matter by various components of the marine association.

The total annual fixation of carbon by photosynthesis is estimated to be about 470 g/m². Over half of it is consumed in phytoplankton respiration. Of the estimated 205 g C/m² available for the remainder of the population, 26% appears to be used by that part of the zooplankton taken with a No. 10 net, 43% by microzooplankton and bacteria in the water column, and 31% by the benthic fauna and flora.

Although plankton concentrations are large, Long Island Sound does not appear to be superior in total productivity to adjacent open coastal waters. Comparison with Harvey (1950) indicates that phytoplankton production in Long Island Sound is at least twice as large as that in the English Channel, but it appears to be used less efficiently by the animal population.

INTRODUCTION

The 1952–1954 survey has been concerned primarily with descriptions of the standing plankton crop in the central part of Long Island Sound and of accompanying environmental characteristics of the water. Some information on the more difficult subject of biodynamics has been provided by experiments in the preceding papers of this volume and by a previous study of Long Island Sound (Riley, 1941). The distribution of nonconservative properties is also potentially useful in assessing the rates of production and utilization of biological materials. A preliminary analysis of the available information appears to be warranted, although the subject will need to be reexamined when the remainder of the survey has been completed.

Before taking up the problem in detail, some general principles should be discussed briefly. It is generally agreed that the local time change in oxygen, phosphate, or other nonconservative concentrations is the sum of: (a) a biological rate of change attendant upon plant growth; (b) an opposite change due to the katabolic activity of the biological association as a whole; and (c) a physical rate of change caused by admixture of water with a different concentration. The study of productivity requires isolating and measuring (a), (b), or both. Historically this has been accomplished in several different ways:

(1) During the spring flowering, phytoplankton growth is preeminent. Katabolic processes are at a low ebb, at least in the beginning. In shallow, turbulent water, where nutrients are reduced from surface to bottom, vertical diffusion effects may be ignored. Therefore, the observed change in a nonconservative concentration is a minimal but nearly accurate measure of phytoplankton productivity.

(2) The experimental technique of light and dark bottles aims at complete isolation. Enclosure in bottles eliminates (c). The light bottle measures (a) − (b). The dark bottle measures (b). Light + dark = (a). Against these theoretical advantages are opposed certain technical disadvantages. There are experimental errors, particularly with respect to growth of bacteria in enclosed samples. Sampling errors tend to be extreme, for the amount of experimental data that can be accumulated is a small fraction of the number of routine descriptive observations that can be obtained with an equal amount of effort.

(3) Physical oceanographic methods may be used to determine advection and diffusion coefficients, and these may be combined with observed gradients in nonconservative concentrations to evaluate (c). Then local time change − (c) = (a) − (b). The significance of this method from the standpoint of biodynamics depends upon the fact that (a) is generally much larger than (b) in the surface layer, while in deeper water (a) becomes negligibly small. Thus it may be possible to derive an estimate of total productivity, but the complex nature of the problem generally necessitates some arbitrary assumptions.

In this paper the net changes (a) − (b) of oxygen and phosphate will be determined for a series of depths in the central part of Long Island Sound according to method (3), using observed distributions of these elements and assuming that the coefficients of vertical eddy diffusivity are equal to the conductivity coefficients calculated in a previous paper in this series (Riley: PHYSICAL OCEANOGRAPHY). Further, it will be assumed that lateral transport and diffusion can be ignored. If this assumption introduces serious errors, the estimates will be modified later when the survey of the Sound as a whole has been completed.

ANALYSIS OF NET CHANGES IN PHOSPHATE

Allowing the simplifying assumptions listed above, the local time change in phosphorus P is given in differential form by

$$\frac{\partial P}{\partial t} = R + \frac{\partial}{\partial z} \cdot \frac{A}{\rho} \frac{\partial P}{\partial z}, \tag{1}$$

where A is the coefficient of vertical eddy diffusivity, z is depth, and R is the net rate of biological change, equivalent to (a) − (b) in the discussion above. Written in terms of finite differences,

$$\frac{\partial P_0}{\partial t} = R + \frac{1}{z}\left(\frac{A_z}{\rho} \cdot \frac{P_z - P_0}{z} - \frac{A_{-z}}{\rho} \cdot \frac{P_0 - P_{-z}}{z}\right). \tag{2}$$

Here P_0 is defined as the phosphorus concentration at a given depth; P_{-z} and P_z are the concentrations at a distance z above and below, respectively, the vertical axis being directed positively downward. A_{-z} and A_z are the corresponding average coefficients of eddy diffusivity for the distances z above and below P_0.

Equation (2) is suitable for determining the rate of change of phosphorus at intermediate depths. It is essential also to determine the rate of biological events in the immediate surface and bottom layers. For this purpose a flux equation is postulated,

$$F = -\frac{A}{\rho} \cdot \frac{\partial P}{\partial z}, \tag{3}$$

which is analogous to the heat transfer equation in the earlier paper on PHYSICAL OCEANOGRAPHY and which may be presented in finite difference form similar to equation (2). It provides a method for determining the amount of vertical movement of phosphate in unit time through a square centimeter of horizontal area, and any difference between the amount transferred and the observed change in concentration may be interpreted as a biological transformation.

In applying equations (2) and (3), the following data are available:

1. Average coefficients of eddy conductivity have been calculated for specific depth ranges and for periods of one to three months. The calculations cover all of the two-year survey period except the autumn seasons, when, for reasons previously discussed, the method was unsuitable.

2. The observed phosphate concentrations at the beginning and end of each time interval will be used to calculate the rate of change $\partial P_0/\partial t$.

3. Average vertical gradients during each time interval will be determined, using all available analyses except a few that show obvious and gross contamination.

As a numerical example of the method of utilizing these data, we shall estimate the biological rate of change of phosphate at the 5 m level at Sts. 2 and 4 during the period of May 21 to August 19, 1952, using mean values for the two stations. On May 21 the observed phosphate concentration at 5 m was 0.51 μg-at P/l; it increased to 1.00 μg-at P on August 19. During the entire period, the average vertical gradient in phosphate was 0.052 μg-at between 0 and 5 m and 0.209 μg-at between 5 and 10 m. The calculated mean coefficients of eddy diffusivity (conductivity) for the same depth ranges were 0.75 and 0.68 g cm^{-1} sec^{-1}, respectively. The time interval was 7.78×10^6 seconds. The density of the water was about 1.02. In accordance with the rest of the cgs notation, phosphate concentrations are multiplied by 10^{-3}. According to equation (2),

$$\frac{(1.00 - 0.51)10^{-3}}{7.78 \times 10^{6}} = R + \frac{1}{500}\left(\frac{.68}{1.02} \cdot \frac{.209 \times 10^{-3}}{500}\right.$$

$$\left. - \frac{.75}{1.02} \cdot \frac{.052 \times 10^{-3}}{500}\right)$$

$$R = -0.341 \times 10^{-9} \ \mu\text{g-at } P \ \text{cm}^{-3} \ \text{sec}^{-1},$$

or a net utilization of 0.03 μg-at P/l in a day.

Suppose that in a column of water 20 m deep, sampled at 5 m intervals, similar calculations are made for the 10 and 15 m levels. A rough numerical integration may then be made, the simplest way being to assume that the 5 m value is the average for the depth range of 2.5 to 7.5 m, etc. The whole water column may thus be accounted for, except the part above 2.5 and below 17.5 m. These require the use of equation (3). In the depth range between 0 and 5 m,

$$F = -\frac{.75}{1.02} \cdot \frac{.052 \times 10^{-3}}{500} = -.076 \times 10^{-6} \ \mu\text{g-at } P \ \text{cm}^{-2} \ \text{sec}^{-1}.$$

This is the average rate of upward (negative) movement between 0 and 5 m, and as in previous calculations of eddy conductivity, it is assigned to the midpoint in the stratum, namely 2.5 m.

During the same period, the surface concentration of phosphate increased from 0.30 to 0.99 μg-at P/l, which is equivalent to an increase of 0.022×10^{-6} μg-at P/sec. in a column of water 2.5 m long and with a cross section of 1 cm². The difference between the calculated flux into this column ($.076 \times 10^{-6}$) and the observed increase is assumed to represent net utilization of phosphate by the biological association. It amounts to about 0.02 μg-at P/l in a day.

Within this general framework, which is fixed by the nature of the problem and the available data, there is a choice as to whether each station should be treated individually or whether some attempt should be made to combine stations. The latter course seemed desirable in order to minimize effects of lateral movements, to average out sampling errors, and to obtain a single generalized result for the central part of the Sound. However, variations in the depth of water at the stations and in the depths sampled required a degree of individual treatment and later combination. Offshore Sts. 3 and 5 were similar in that the total depth of water was 25 to 28 m, and samples were generally taken at 0, 5, 15, and 25 m. One set of data was calculated for these two stations, using averaged observations.

The fact that some of the depth intervals were 5 m and others 10 required a slight alteration in the form of equation (2). A second set was obtained from Sts. 2 and 4, which were slightly shallower and were sampled at 0, 5, 10, and about 20 m. A third set comprised inshore Sts. 1, 7, and 8. St. 6 was too shallow to be usable.

Thus all three sets were available for average estimates of the net rate of change at 5 m and of the vertical flux between 0 and 5 m. Sts. 2 and 4 were used for the 10 m estimate, Sts. 3 and 5 for 15 m. All four offshore stations were averaged to determine vertical flux in a stratum 2.5 m above the bottom, and the latter was assumed for purposes of generalization to be at a depth of 20 m, since that is approximately the mean depth of the area under consideration.

TABLE I. Biological Rate of Change of Phosphate in μg-at P/Day in a Vertical Column of Water One Centimeter Square, Divided into Segments of 2.5 or 5 m (One-quarter or One-half Liter Each)

	0–2.5	2.5–7.5	7.5–12.5	12.5–17.5	17.5–20
Mar. 5–May 21, 1952	.000	−.013	−.009	−.001	.009
May 21–Aug. 19	−.006	−.009	−.012	.009	.033
Nov. 17–Feb. 10, 1953	−.008	.001	.004	.004	.000
Feb. 10–Mar. 16	−.008	−.057	−.023	−.026	.002
Mar. 16–May 18	−.012	−.004	.002	−.003	.016
May 18–Aug. 25	−.007	−.004	.005	−.002	.027
Nov. 18–Jan. 25, 1954	−.008	.001	.004	.004	.000
Jan. 25–Feb. 24	−.005	−.050	−.019	−.007	.000

Table I shows estimated net changes in phosphate in the water column and on the bottom. The method of calculation is such that the 17.5 − 20 m segment includes regeneration from one square centimeter of benthic surface at the base of the column. The early autumn periods are omitted from Table I because, as previously mentioned, eddy conductivity could not be determined and presumably had little application to the problem during these periods of extreme convective cooling. During late autumn and early winter, when temperature and phosphate gradients were slight and variable, calculations were possible but were subject to considerable statistical error. To reduce the error as much as possible, data for both years were combined.

Utilization of phosphate in the upper 2.5 m appeared to be relatively uniform throughout the year. Elsewhere there were marked seasonal variations. Maximum utilization occurred during the spring flowering periods, maximum bottom regeneration in summer. In autumn and early winter, utilization exceeded regeneration only in the upper 2.5 m.

An annual summation of net changes is presented in Table II. Each of the daily rates in Table I has been multiplied by the number of days in the period, and the products have been summed for the segments of the column in which net utilization exceeds regeneration and *vice versa*. Figures in parentheses are rough estimates for the autumn periods. First, it was assumed that the net changes in the upper 7.5 m during these periods were intermediate between the preceding summer season and the succeeding late autumn–early winter period. Second, the net change in the whole water column

TABLE II. SUMMATION OF NET CHANGES IN PHOSPHATE—µG-AT P/CM² OF SEA SURFACE

	Utilization		Regeneration		Difference	
	Depth	µg-at P	Depth	µg-at P	Calc.	Obs.
1952–3						
Mar. 5–May 21	0–17.5	−1.77	17.5–20	.69	−1.08	−.30
May 21–Aug. 19	0–12.5	−2.43	12.5–20	3.79	1.36	1.56
Aug. 19–Nov. 17	0– 7.5	(−.99)	7.5–20	(2.83)	(1.84)	1.84
Nov. 17–Jan. 25	0– 2.5	−.68	2.5–20	.77	.09	−.94
Jan. 25–Feb. 24	0–17.5	−3.90	17.5–20	.07	−3.83	−2.28
1953–4						
Mar. 5–May 21	0–17.5	−1.07	17.5–20	1.01	−.06	.00
May 21–Aug. 19	0– 7.5	−1.09	7.5–20	2.96	1.87	1.44
Aug. 19–Nov. 18	0– 7.5	(−.82)	7.5–20	(2.68)	(1.86)	1.86
Nov. 18–Feb. 10	0– 2.5	−.54	2.5–20	.61	.07	.10
Feb. 10–Mar. 16	0–17.5	−2.43	17.5–20	.00	−2.43	−2.32
Total						
1952–3	—	−9.77	—	8.15	−1.62	−.12
1953–4	—	−5.95	—	7.26	1.31	1.08
1952–4	—	−15.72	—	15.41	−.31	.96

is known by direct observation, so that by difference one can obtain the net change in the water column below 7.5 m.

During any one period, utilization and regeneration were seldom in balance, as may be seen in the next to the last column in Table II. When any such imbalance exists, it should result in a change in the average phosphate content of the water column. Furthermore, the accuracy of this calculated result is readily checked by comparing it with observed changes in phosphate concentration in the Sound. These are listed in the last column of Table II. The comparison between observed and calculated values is useful in gauging the internal consistency of the results.

NET CHANGES IN OXYGEN

Oxygen concentrations are susceptible to the same type of analysis of net changes. However, any attempt to estimate short-period biological effects in the surface layer is complicated by exchanges of oxygen through the sea surface. Thus Table III omits the upper 2.5 m of the water column. Otherwise the calculations duplicate the phosphate procedure described above.

Rather than attempt calculation of the rate of exchange of oxygen through the sea surface, the writer proposes a simpler alternative method for dealing with the upper 2.5 m. It seems likely that over a period of a year or two, the total production will approximately equal consumption, although an imbalance is likely to exist during

TABLE III. BIOLOGICAL RATE OF CHANGE OF OXYGEN IN MILLILITERS PER DAY IN A VERTICAL COLUMN OF WATER ONE CENTIMETER SQUARE, DIVIDED INTO SEGMENTS OF 2.5 OR 5 M. PARENTHESES INDICATE INTERPOLATIONS TO FILL GAPS IN THE DATA.

	2.5–7.5	7.5–12.5	12.5–17.5	17.5–20
Mar. 5–May 21, 1952	.019	−.004	−.014	−.040
May 21–Aug. 19	.028	.038	−.028	−.132
Aug. 19–Nov. 17	(.009)	(.005)	(−.028)	(−.082)
Nov. 17–Feb. 10, 1953	−.010	−.028	−.027	−.031
Feb. 10–Mar. 16	.064	.025	.015	−.028
Mar. 16–May 18	.014	.010	−.025	−.054
May 18–Aug. 25	.030	−.027	−.028	−.071
Aug. 25–Nov. 18	(.010)	(−.028)	(−.028)	(−.050)
Nov. 18–Jan. 25, 1954	−.010	−.028	−.027	−.028
Jan. 25–Feb. 24	.066	−.004	−.026	−.024

shorter intervals. If the figures in Table III are totalled, it becomes apparent that consumption was considerably larger than production in the water column below 2.5 m. Assuming that the difference is equal to production in the upper 2.5 m, an average value for the latter can be calculated. It is found to be 0.27 ml O_2/l in a day during the first year of the survey and 0.31 ml the second year. By way of comparison, a series of light and dark bottle experiments in the upper meter of water, mainly during the second year (see S. A. M. Conover in this volume), gave an annual mean of 0.31 ml/day for total photosynthesis and 0.20 ml for the net increase in oxygen. A few experiments at other depths or at otherwise reduced light intensity indicated that maximum photosynthesis occurred very near the surface at the time of the spring flowering but frequently at greater depths in summer. In view of these ambiguities in the comparison, the agreement

between experimental results and the physical oceanographic calculation is probably as good as can be expected.

OXYGEN PRODUCTION AND CONSUMPTION

Next an attempt will be made to determine not merely net changes in oxygen but total production and consumption. Table IV brings

TABLE IV. DAILY OXYGEN PRODUCTION AND CONSUMPTION—ml O_2/l

	Net change at 15 m	Experiments Phot. Resp.		Estimated Phyt. Resp.
1952–3				
Mar. 5–May 21	−.028	—	—	.047
May 21–Aug. 19	−.056	—	—	.115
Aug. 19–Nov. 17	—	—	—	.080
Nov. 17–Feb. 10	−.054	—	—	.030
Feb. 10–Mar. 16	.030	.42	.076	.060
1953–4				
Mar. 16–May 18	−.050	.53	.085	.048
May 18–Aug. 25	−.056	.33	.178	.110
Aug. 25–Nov. 18	—	.26	.200	.093
Nov. 18–Jan. 25	−.054	.11	.037	.014
Jan. 25–Feb. 24	−.052	.34	.048	.044

together pertinent information on this problem. First are listed the net changes in oxygen at 15 m, as determined by the physical oceanographic analysis. At this depth photosynthesis probably is negligibly small during the winter months, so that the calculated net change of about 0.05 to 0.06 ml O_2/day may be regarded as synonymous with total oxygen consumption. Also, these figures are probably applicable to the water column as a whole, since there are no marked or consistent vertical variations in the quantity of plankton.

The summer season presents a more difficult problem. In two sets of experiments performed in June 1953, at a series of depths, measurable photosynthesis occurred at 15 m or more. Moreover, one would expect respiration to increase in summer, so that the uniformity of the calculated net changes is suggestive of significant photosynthesis at 15 m throughout the summer season.

The respiratory experiments listed in the third column of Table IV are more or less in agreement with the calculated net changes in winter, but they are much larger in summer. The experimental method is open to criticism of course because of the likelihood of abnormal bacterial growth in the bottles. Thus the two types of measurements

tend to set maximum and minimum limits around the true value for oxygen consumption.

In a previous study of Long Island Sound (Riley, 1941) there was a series of 65 experimental determinations of oxygen production and consumption in light and dark bottles over periods of three or four days. The mean annual production was 0.33 ml/day, nearly the same as that in the present series. The consumption averaged 0.17 ml, as compared with an annual mean of 0.11 ml for the data in Table IV. It is problematical whether this higher value was the result of a longer exposure time or was due to the fact that most of the experiments were performed with inshore water containing relatively large amounts of detritus. A multiple correlation technique was used to estimate phytoplankton and zooplankton respiration and to eliminate unrelated bacterial effects. The statistical result was later shown by Riley, *et al.* (1949) to be in good agreement with the observed respiration of pure diatom cultures. It is also suitable for estimating phytoplankton respiration during the present survey provided a small correction is made for differences in the chlorophyll calibration (cf. Riley and Conover in this volume). The postulated relation between chlorophyll and respiration is shown in Fig. 1A. Applying observed temperatures and chlorophyll concentrations to this curve and averaging the results, we obtain the estimates in the last column of Table IV. It will be noted that these figures are lower than the experimental estimates of total respiration, but they are not markedly lower in the winter and early spring, when zooplankton and bacterial respiration are presumably at a minimum. It is also evident that the estimated phytoplankton respiration in summer exceeded the net change in oxygen at 15 m.

These figures will be used later to determine the proportion of photosynthetic production that is required for immediate use by the phytoplankton. Total respiration remains something of an enigma, but the body of evidence favors a compromise between calculated net changes and black bottle experiments. It will be assumed provisionally that (a) the mean annual respiration is 0.106 ml O_2/l/day as determined by experiment; (b) gaps in experimental data will be filled by substituting figures for the corresponding period of the following year; (c) the net change at 15 m will be adopted for any period when it exceeds the experimental value; and (d) during other periods the experimental data will be reduced by a constant
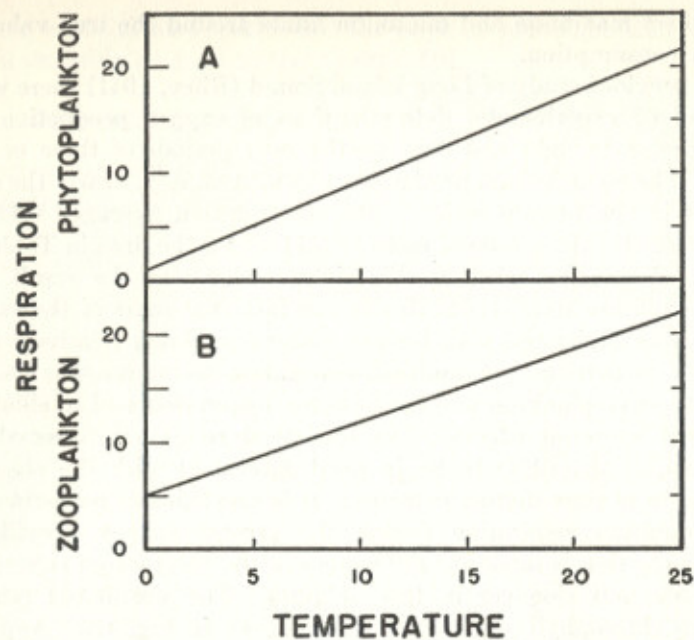
Figure 1. A. Coefficients of phytoplankton respiration. Daily oxygen consumption in microliters per microgram of chlorophyll. B. Zooplankton respiratory coefficients. Microliters of oxygen per day consumed by one milligram (wet weight) or one milliliter (displacement volume) of zooplankton.

fraction suitable for preserving the postulated annual mean. Numerical results will be presented later, but there are other problems to be discussed before the final summary is made.

In dealing with the 17.5 − 20 m stratum, an allowance will be made for respiration in the water, as in the rest of the vertical column. It will be assumed also that no photosynthesis occurs within this stratum. The difference between the net change for the whole stratum and the allowance for respiration in the water will then be allocated to bottom organisms.

Any treatment more detailed than a simple annual mean will also require further assumptions about net oxygen changes in the 0 − 2.5 m stratum: (a) The mean annual net changes are fixed at 0.27 ml O_2/l/day for the first year and 0.31 ml for the second, as previously estimated. Adding 0.11 ml for respiration, the figures for total photosynthesis are respectively 0.38 and 0.42 ml/l. (b) Assuming that

seasonal variations observed in experimental bottles are applicable to the problem, the latter (cf. Table IV) are systematically raised to adjust the annual means to the figures quoted in (a) above. Gaps in the first year's data are filled in with figures from the second year.

Results are shown in the first column of Table V. The remainder of this table is derived simply by adding the estimated respiration to the net change in oxygen, as given in Table III.

A balance sheet of production and consumption is presented in Table VI. The photosynthesis column is derived from Table V, and the method of estimating phytoplankton respiration has been

TABLE V. Estimated Daily Photosynthesis in ml O_2/l, Tabulated as Averages for the Depth Ranges Listed

	0–2.5	2.5–7.5	7.5–12.5	12.5–17.5
1952–3				
Mar. 5–May 21	.64	.09	.05	.03
May 21–Aug. 19	.40	.23	.25	.12
Aug. 19–Nov. 17	.32	.17	.15	.09
Nov. 17–Feb. 10	.13	.04	.00	.00
Feb. 10–Mar. 16	.51	.18	.10	.08
1953–4				
Mar. 16–May 18	.72	.09	.08	.01
May 18–Aug. 25	.45	.24	.12	.12
Aug. 25–Nov. 18	.36	.14	.06	.06
Nov. 18–Jan. 25	.15	.04	.00	.00
Jan. 25–Feb. 24	.46	.18	.04	.00
Means				
1952–3	.38	.14	.12	.06
1953–4	.42	.14	.07	.05
1952–4	.40	.14	.09	.06

explained. The difference between the two, listed as net production, represents material that is available for the production of phytoplankton cells and eventual nourishment of the animal population and bacteria. Zooplankton respiration is derived with reference to Fig. 1B, which is based on respiratory data for *Acartia* spp., the dominant copepods in the Sound (see R. J. Conover in this volume). Average zooplankton volumes (No. 10 net) and mean temperatures for each period are applied to the figure to obtain the respiratory estimates listed. The method of estimating the oxygen consumption by bottom fauna and flora has been explained. The difference between total oxygen consumption and the combined phytoplankton, zooplankton, and benthic fractions is listed in the table as "other" respiration. Nominally this category is assigned to bacteria and to small zooplank-

TABLE VI. BALANCE SHEET OF OXYGEN PRODUCED AND CONSUMED IN ml O₂/day IN A COLUMN OF WATER ONE SQUARE CENTIMETER IN CROSS SECTION AND EXTENDING FROM THE SEA SURFACE TO THE BOTTOM, AT A DEPTH OF 20 m (THUS TOTALLING TWO LITERS OF WATER)

	Photo-synthe-sis	Net Pro-duction	Water Column Phyt.	Zoopl.	Other	on Bottom	Total
1952–3							
Mar. 5–May 21	.246	.152	.094	.030	−.012	.026	.138
May 21–Aug. 19	.402	.172	.230	.052	.072	.088	.442
Aug. 19–Nov. 17	.283	.123	.160	.060	.070	.046	.336
Nov. 17–Feb. 10	.052	−.008	.060	.004	.048	.017	.129
Feb. 10–Mar. 16	.310	.190	.120	.018	−.034	.015	.119
1953–4							
Mar. 16–May 18	.266	.170	.096	.022	−.006	.040	.152
May 18–Aug. 25	.352	.132	.220	.022	.112	.027	.381
Aug. 25–Nov. 18	.223	.037	.186	.028	.026	.020	.260
Nov. 18–Jan. 25	.057	.029	.028	.004	.080	.014	.126
Jan. 25–Feb. 24	.230	.142	.088	.018	−.002	.011	.115
Means							
1952–3	.254	.117	.137	.036	.039	.042	.254
1953–4	.236	.096	.140	.020	.052	.024	.236
1952–4	.245	.107	.138	.028	.046	.033	.245

ton that escape the No. 10 net, but not without reservations. Discussion of this matter is relegated to a later section of this paper.

PHOSPHATE UTILIZATION AND REGENERATION

The calculation of net changes in phosphate was simple and straightforward compared with the oxygen analysis, but conversion to estimates of total utilization and regeneration requires further discussion and additional arbitrary assumptions. Phosphate regeneration differs from oxygen consumption in that it is primarily associated with animal and bacterial metabolism. There is little reason to believe that phytoplankton respiration is accompanied by significant amounts of phosphorus excretion except under relatively abnormal conditions. Examination of the tabular material indicates that phosphorus utilization is more nearly uniform with respect to depth than oxygen production and that considerable utilization occurs at depths where phytoplankton respiration exceeds oxygen production. Thus the net change in phosphate in deep water is even less reliable than oxygen as an indicator of the magnitude of katabolic processes.

There are no experimental data that can be used to set an accurate value for phosphorus regeneration. Nor is there a precise relation between oxygen consumption and phosphorus regeneration. The

normal O:P ratio by atoms appears to be between 250:1 and 300:1, but extreme variations have been noted (Riley, 1951). It will be assumed here that there is an atomic ratio of 300:1 between oxygen consumption, exclusive of phytoplankton respiration, and phosphorus regeneration. This is sufficient to equal four of the positive net changes in Table I. It slightly exceeds four others and is exceeded by only one. The estimate therefore appears to be of the right order of magnitude.

TABLE VII. ESTIMATED DAILY UTILIZATION AND REGENERATION OF PHOSPHATE IN μG-AT P/CM² OF SEA SURFACE

	Utilization 0–2.5	2.5–7.5	7.5–12.5	12.5–17.5	Total	Regeneration 0–20	Bottom	Total
1952–3								
Mar. 5–May 21	.001	.014	.010	.002	.027	.005	.008	.013
May 21–Aug. 19	.010	.015	.021	.000	.046	.036	.029	.065
Aug. 19–Nov. 17	.011	.013	.009	.005	.038	.038	.023	.061
Nov. 17–Feb. 10	.010	.003	.000	.000	.013	.015	−.002	.013
Feb. 10–Mar. 16	.008	.057	.023	.026	.114	.000	.002	.002
1953–4								
Mar. 16–May 18	.013	.005	−.001	.004	.021	.005	.015	.020
May 18–Aug. 25	.012	.014	.005	.012	.043	.040	.021	.061
Aug. 25–Nov. 18	.010	.006	.004	.000	.020	.016	.026	.042
Nov. 18–Jan. 25	.011	.005	.002	.002	.020	.025	−.003	.022
Jan. 25–Feb. 24	.006	.051	.020	.008	.085	.005	−.001	.004
Means								
1952–3	.0082	.0154	.0113	.0040	.0389	.0221	.0138	.0360
1953–4	.0110	.0119	.0044	.0053	.0324	.0217	.0145	.0362
1952–4	.0095	.0137	.0080	.0046	.0358	.0219	.0141	.0361
Mean O:P ratio (atoms)	760	230	185	−104	262		205	

Results of the calculation are shown in Table VII. The last line shows O:P ratios for the two-year period. The over-all ratio for production is normal. Values for individual depth ranges are aberrant, indicating a marked lag between net phytoplankton production and phosphate absorption.

DISCUSSION

In a previous study of Long Island Sound (Riley, 1941), experimental determinations of oxygen production at the surface were approximately the same as those in the present survey. On the basis of transparency data then available, it was estimated that the total photosynthetic production of carbon might be 10 to 15 times

the surface value, or some 600 to 1000 g C/m² in a year's time. That conclusion has not been borne out by the present work. The mean annual production for the two-year period just completed is estimated to be only 470 g C/m². Over half of this production appears to be utilized in phytoplankton respiration. Of the estimated 205 g C/m² available to the rest of the biological association, 69% appears to be used by pelagic organisms, the remainder by the benthic population. The phosphate analysis gives a slightly different pattern of utilization—61% by pelagic fauna and flora and 39% on the bottom.

The two physical oceanographic analyses and the experimental measurements that have been used in deriving these estimates exhibit a considerable degree of internal consistency. On the other hand, the methods have been indirect and involved, containing a number of assumptions that probably are not altogether valid. One major possibility of error lies in an assumption about the nature of turbulence. If coefficients of eddy conductivity are larger than eddy diffusivity, as some have claimed, then the biological rates of change are overestimated, particularly in spring and summer when maximum stability exists.

There also remains the question as to whether or not a reasonable set of assumptions has been made about the respiration of the plankton association. In carrying out the assumptions as stated, the final result was a production of about 88 g C/m² in excess of the demonstrable needs of the phytoplankton and No. 10 zooplankton catches. This excess was allocated in Table VI to "other" respiration in the water column, namely bacteria and microzooplankton. The observed numbers of tintinnids, early nauplii, etc., leave no doubt that this is a significant category. Nor is bacterial respiration likely to be negligible. Nevertheless, from the nature of the assumptions, it is possible that part of the 88 g of carbon constitutes error in the black bottle experiments.

Various aspects of the seasonal cycles and annual fluctuations warrant further attention. The spring flowering did not exhibit the excessive dominance over the rest of the seasonal cycle that is observed in some other waters. The rate of net oxygen production was more or less the same as the rest of the spring and summer season and constituted only 10 to 15% of the total annual production. The rate of phosphate utilization was approximately twice the highest value obtained at any other time in the year. However, the O:P

ratio was abnormally low, averaging about 150:1 for the total population, and this suggests that the phytoplankton was absorbing phosphate in excess of immediate needs, as it is known to do when the supply is abundant (Goldberg, *et al.*, 1951).

The calculated carbon production during the spring flowering exceeded demonstrable respiratory needs of the population by 34 g/m² in 1953 and 18 g in 1954. The state of anabolic dominance continued through the spring months until, by mid-May, nearly a third of the year's net carbon production existed in an unutilized state in the water column and on the bottom. It was then gradually used up during the remainder of the year, so that katabolic processes were dominant from mid-May until the onset of the next spring flowering. The same situation was found even more strikingly in the phosphate analysis (Table II), where the spring excess of utilization over regeneration was nearly 50% of the estimated net yearly utilization. Evidence of the same phenomenon in slightly varying form has been found in studies of the phosphorus cycle in the Gulf of Maine (Redfield, *et al.*, 1937) and in the English Channel (Armstrong and Harvey, 1950). There is no reason to regard it as abnormal, although the phenomenon may be exaggerated in shallow waters.

The spring zooplankton population did not expand in Long Island Sound as rapidly as it did in the English Channel and in some other areas that have been examined. The evidence pointed toward consumption of little more than a tenth of the flowering, which then terminated by rapid settling to the bottom. The reason for the failure of the zooplankton remains obscure. The obvious result was a summer and early autumn utilization of organic matter some 35% greater than the amount provided by current production. Such a system tends to smooth the adverse effects of fluctuations in available food. However, the long lag between production and utilization seems relatively inefficient from the standpoint of maximum use of the reservoir of nutrient elements.

Examination of the estimates of net oxygen production and phosphate utilization in Table VI and VII indicates that the spring flowering in 1953 was considerably more productive than that in 1954. This is not surprising, since cell counts and chlorophyll concentrations were also much larger. Of more ecological interest is the indication that the summer of 1952 was about 20 to 30% more productive than

the corresponding period in 1953. There was essentially no difference in the total standing crop of phytoplankton as indicated by chlorophyll concentrations. However, there were more diatoms and dinoflagellates in 1952 and possibly less naked flagellates and other forms not ordinarily included in cell counts. The one striking difference between the two summers was that the 1952 zooplankton volume averaged about two and a half times as much as the 1953 crop. Furthermore, the difference in net production between the two years approximately equalled the difference in the estimated food requirements of the zooplankton populations. In other words, the 1952 zooplankton increased sufficiently to use the extra production and keep the phytoplankton crop at the same general level.

The dominant species in the summer zooplankton population was *Acartia tonsa*. It is pointed out (see R. J. Conover in this volume) that this species appears to be particularly well adapted to feed on the larger phytoplankton forms and that both species of *Acartia* fed more effectively on diatoms than on natural populations of small summer flagellates. Thus the experimental work indicates that the species composition of the phytoplankton in 1952 was particularly favorable for the support of the larger members of the zooplankton population. It appears to be this, rather than the slight difference in productivity, that was primarily responsible for the vast difference in zooplankton crops.

In the waters of Block Island Sound, a relatively open body of coastal water east of Long Island Sound, a cursory one-year survey (Riley, 1952) has provided enough data for a rough comparison of the two areas. The ratio of annual mean surface phytoplankton concentration was 2.3:1, the larger value being in central Long Island Sound. The ratio of total crops was 1.5:1. Zooplankton displacement volumes (No. 10 net) were 1.5:1 on a volumetric basis and 1:1 in terms of quantity per unit area. With regard to oxygen production and consumption, the net utilization in the lower half of the water column in Block Island Sound totalled 41 ml/cm² in a year's time as compared with 36 ml in Long Island Sound. The net increase in oxygen at the surface appeared to be much larger in Block Island Sound (68 ml/year), and it was postulated that the excess of phytoplankton production over utilization was dissipated offshore by lateral diffusion. The total productivity of Block Island Sound was not determined. The correction factor for the respiration of

the plankton population is presumably smaller, and tentative estimates suggest that there is little difference in the total productivity of the two areas.

The extensive study by Harvey (1950) of production in the English Channel provides material for comparison of two quite different temperate water habitats. The area examined off Plymouth is deeper than Long Island Sound, averaging some 70 m. The nutrient and plankton concentrations are comparatively small, but it appears to be a remarkably efficient system with respect to both nutrient utilization and subsequent biological conversion.

TABLE VIII.   COMPARISON OF MEAN ANNUAL STANDING CROPS AND ORGANIC PRODUCTION (g organic matter/m²) IN THE ENGLISH CHANNEL (EC) AND CENTRAL LONG ISLAND SOUND (LIS).

	Standing Crop		Daily Production		Respiratory Loss	
	EC	LIS	EC	LIS	EC	LIS
Phytoplankton	4	16	—	3.2*	—	1.8*
			.4–.5†	1.07†		
Zooplankton	1.5	2	.15	—	.06	.28
Pelagic fish	1.8	—	.0016	—	.025	—
Bacteria	.04	—	—	—	.013	.46‡
Demersal fish	1–1.25	—	.001	—	.015	
Epi- and in-fauna	17	9	.03	—	.2–.3	.33
Bacteria	.1	—	—	—	.03	
Total, exclusive of phytoplankton respiration					.34–.44	1.07

* Photosynthetic glucose production and loss of glucose by respiration.
† Phytoplankton production in excess of respiratory requirement.
‡ In LIS this item also includes small zooplankton not sampled by the net.

Table VIII quotes part of the data from Harvey (1950: table 4) and compares it with the two-year averages from Long Island Sound. The method of arriving at the figures for Long Island Sound requires a few words of explanation. The mean standing crop of phytoplankton has a chlorophyll content of 6 μg/l. The chlorophyll content varies between 0.6 and 1.5% of the organic matter in surface net phytoplankton tows (see Harris and Riley in this volume), the latter figure applying primarily to a short period in winter and early spring. A reasonable average for the year is about 0.75%. Hence the standing crop of organic matter in a column of water 20 m deep appears to be about 16 g/m². However, Harvey used a conversion factor only half as large. If one or the other is in error, the ratio of abundance in the two areas might be only 2:1 instead of 4:1.

In the case of zooplankton, the organic content has averaged about 10% of the wet weight. This figure is applied to the mean annual

displacement volumes of No. 10 tows. Data on bottom fauna (see Sanders, in this volume) are measured dry weights less the weight of shells and other obviously nonorganic materials. A precise estimate of the quantity is not possible at this stage of the investigation, and the total population may be under-rated. There is an abundance of nematodes and other microfauna that has not been included in the measurements, and some of the largest animals have not been sampled adequately. Harvey's estimate may be a little large, since the recent survey by Holme (1953) gave an average value of 11.2 g dry weight/m^2.

Total photosynthesis and phytoplankton respiration are listed as glucose equivalents of oxygen data in Table VI. With regard to other data on production and respiration, one milliliter of oxygen is approximately equivalent to one milligram of organic matter of average carbon content. Therefore, the data in Table VI require no change except in the position of the decimal point. The figures for total oxygen consumption on the bottom in Long Island Sound properly include all three of Harvey's categories of bottom organisms. The pelagic fish constitute a blind spot in the Long Island Sound balance sheet. No allowance has been made for them in calculating total oxygen consumption, and if they utilize a significant amount of organic matter, the estimates of total production will need to be increased a corresponding amount.

These two bodies of water are not very different with respect to potential nutrient supply if the latter is rated in terms of the amount of essential elements underlying a unit area of surface at the time of the winter maximum. Long Island Sound has more phosphate and slightly less nitrate. In terms of nutrient concentrations, which are important in determining the rate of absorption, the Sound is superior. This, together with the efficiency of recirculation of re-generated nutrients in shallow turbulent waters, is presumably responsible for the high net production in the Sound.

The dominant members of the zooplankton population have been shown (R. J. Conover in this volume) to be relatively inefficient feeders with high respiratory requirements, and their inefficiency is reflected in a standing crop only slightly larger than the English Channel population, despite the large concentration of phytoplankton that is available. The latter appears to be mainly utilized by small organisms in the water column and by the benthic population. The benthic productivity is large, and the number of organisms is enormous,

since the fauna consists primarily of small herbivores and detritus feeders. Pelagic fish eggs and larvae are abundant (see Wheatland in this volume). The Sound may be an important spawning and nursery ground, but commercial fishery statistics indicate that the adult population is smaller than that in the open coastal waters to the east. In general, Long Island Sound appears to be relatively inefficient in the production of both groundfish and carnivorous invertebrate epifauna, as compared with both Block Island Sound and the English Channel.

The reasons for this inefficiency are not clear, although some of the symptoms are obvious: in spring an excessive plant growth that cannot be used immediately by the animal population and that probably is largely wasted in bacterial activity; in summer a heavy growth of small algae that appear not to provide adequate food for a mature zooplankton population. Possibly the Sound represents an intermediate point between a normal marine environment and the highly aberrant situation described by Ryther (1954) in Moriches Bay and Great South Bay, Long Island. There, excessive fertilization and reduced salinity promoted the growth of "small forms" which not only out-competed the larger phytoplankton species but also were useless or harmful to the animal population.

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