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ASPECTS OF OCEANOGRAPHY OF LONG ISLAND SOUND

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Aspects of Oceanography of Long Island Sound

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Phytoplankton of Long Island Sound
1954-1955

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ABSTRACT

Three cruises in Long Island Sound in 1952 and 1953 and 17 more in 1954 and 1955 provided material for an analysis of phytoplankton populations and seasonal cycles. The mean annual surface concentration was 1.7 million cells/l in the shallow, nutrient-rich waters at the western end of Long Island Sound and decreased to 220,000/l at the eastern end. Main features of the seasonal cycle were diatom flowerings in late winter or early spring

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and in autumn. There were smaller May–June flowerings in which diatoms and dinoflagellates showed varying degrees of dominance. During the survey 105 identifiable species were found. These are listed with notes on seasonal and regional occurrence, times of flowering, and maximum observed populations. Seasonal cycles are described as to species associations and are discussed with reference to annual and regional variations and their relationship with other oceanographic variables. Regional preferences of individual species are classified in terms of frequency distribution in different parts of the Sound. Of the common and fairly abundant species, 15 were distributed approximately uniformly throughout the Sound, 11 were more common in the eastern end, and 8 in the western end. In the latter group littoral forms and dinoflagellates predominated. All species that were more common in the eastern end were diatoms, and most of them were clearly affiliated with the flora of adjacent coastal waters.

INTRODUCTION

Conover (1956) described phytoplankton taken in the central part of Long Island Sound during a two-year period of weekly collections from March 1952 to February 1954. In that period three cruises also provided material from the Sound as a whole, and 17 more such cruises were made from late March 1954 to early November 1955. These cruises were the basis for a descriptive account of the oceanography of the region by Riley (1959), which included temperature and salinity distribution, nutrients, and a quantitative treatment of the plankton as determined from chlorophyll analyses and zooplankton-displacement volumes. The present paper describes cell counts and species relationships as observed on the 20 cruises that obtained material from all of the Sound.

During 1954 and 1955 each cruise was divided into two parts. Starting in the central part of the Sound, trips were made alternately to the eastern and western ends at intervals of approximately two weeks. Thus a few stations in the central region had biweekly coverage, but most of the Sound was examined only once a month. About thirty stations were visited per cruise, but preserved phytoplankton samples were taken from only a third of them and only from the surface layer.

There are distinct limits to the conclusions that may be drawn from material that obviously is minimal from the standpoint of both spatial coverage and frequency of collection. In many cases certain patterns of seasonal succession or regional gradients have been observed during two or more years and can be regarded as having ecological validity. Precise comparisons of cell numbers, however, would have little significance. Many of the flowerings are of such short duration that the peak population cannot be accurately determined without more frequent sampling. Such limitations must be borne in mind in examining the results.

Although previous publications have described Long Island Sound in some detail, a brief review will help to fix attention on matters of ecological interest to be investigated in the present report and will also provide information useful in reading subsequent papers in this issue of the *Bulletin of the Bingham Oceano-*

graphic Collection. Fig. 1 is a chart of the area showing a typical cruise plan during the 1954–1955 survey and also the routine station positions occupied by Conover (1956) in studying the central region. The Sound may be divided into four areas of somewhat distinctive although intergrading oceanographic characteristics. The western narrows constitute a region of nutrient-rich and mainly shallow water west of about Long. 73° 35′ W. The main basin, extending from 72° 30′ to 73° 35′ W, is partially separated into central and western basins by points of land and a central shoal located between 73° 05′ and 73° 10′ W. East of 72° 30′ the Sound narrows and deepens to a maximum depth of about 100m in the Race, which is the largest of several passes connecting this area with more open waters to the east. Tidal currents are strong in the eastern narrows but become more sluggish west of Long. 72° 30′ W.

Riley (1959) reported that the mean annual concentration of chlorophyll was 11.8 μg/l in the westernmost area examined, and that it declined eastward to 1.7 at the Race. The east-west gradient in the total quantity of chlorophyll underlying a unit area of sea surface was not so extreme. Because of deeper water to the east and relatively uniform vertical distribution, the total phytoplankton in the eastern narrows achieved a level about half that of the western basin and narrows. General features of the seasonal cycle were similar in all of the Sound, although there were some differences in the timing of particular phases. For example, the major diatom flowering occurred in late winter in the central and western basins, but the peak was in April in the eastern narrows.

Conover (1956) found that total cell numbers were large in the central part of the Sound as compared with more open coastal waters of southern New England (Riley, 1952; Lillick, 1937), but the composition was somewhat limited as to number of species and differed in several important respects from that of adjacent waters. The present paper inquires further into these regional variations in cell number and species composition and attempts to discover whether there are sound ecological reasons for the observed differences.

The methods used in concentrating and counting the material and the terminology used in describing it are a continuation of Conover's previous work.

TOTAL CELL COUNTS

Table I shows the number of samples taken in each of the designated areas and the mean cell number in each group of samples. The east-west gradient is similar to that previously described by Riley (1959) in connection with chlorophyll concentrations. The remainder of the table shows maximum and minimum limits of variation in individual samples. The maxima are arranged in relation to three periods of the year when pronounced flowerings occurred. These were the winter diatom flowering (spring in the Race and eastern nar-

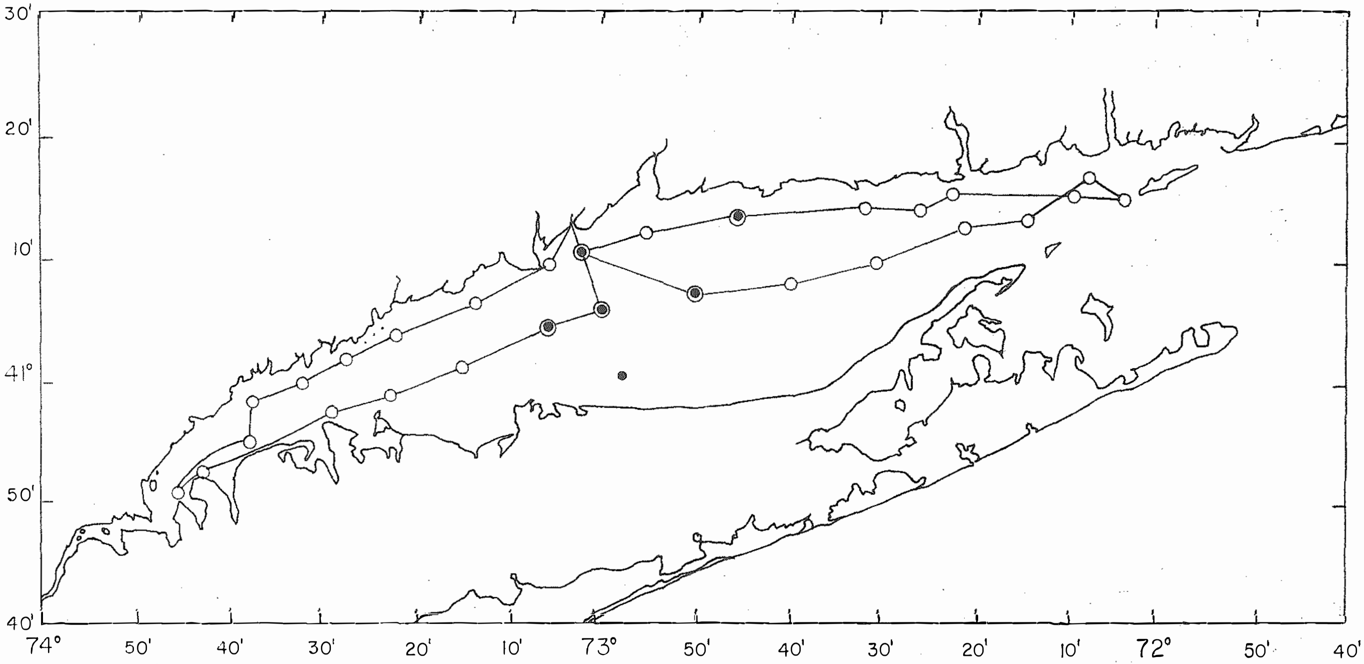

Figure 1. Chart of Long Island Sound showing positions of stations in the central basin that were sampled routinely in 1952 and 1953 (closed circles) and a typical sampling pattern during the 1954–1955 cruises (open circles).

TABLE I. MEAN CELL COUNT (thousands/l) IN DIFFERENT PARTS OF LONG ISLAND SOUND AND AT MAXIMUM AND MINIMUM LIMITS OF VARIATION.

	Race	Eastern Narrows	Central Basin	Western Basin	Western Narrows
Number of samples	16	32	98	49	17
Mean cell count	220	308	998	1,787	1,729
Minimum	31	46	22	17	87
Winter-spring maximum	720	750	14,100	11,300	7,320
May–June maximum	230	1,230	1,420	2,150	2,980
Autumn maximum	–	550	4,130	4,490	3,920

rows); a May–June flowering which, with certain exceptions to be noted later, was mainly a dinoflagellate bloom; and an early autumn diatom flowering. A more detailed picture of the seasonal cycle in three of the five areas is shown in Fig. 2, in which each point represents the average of all cell counts for a particular area and cruise. The logarithmic scale tends to minimize both seasonal and regional variations but is necessary in order to demonstrate essential details.

The most obvious feature in Fig. 2 is the winter flowering, which reached its peak in late January or early February 1955 in the central and western part of the sound. It was unusually early in 1955, presumably because of an unusual amount of sunshine in January. In the Race and eastern narrows the records indicate a gradual and unimpressive increase from December to April. The spacing of observations is far enough apart for an intervening maximum to have been missed. However, nitrate declined slowly and steadily during this period (Harris, 1959), suggesting a gradual growth of phytoplankton rather than a sudden and unrecorded increase and supporting the view that existing records are an essentially correct picture of events.

The eastern end of the Sound presents an anomalous situation. There is a fairly well documented theory (Bigelow et al., 1940; Riley, 1942, 1957) that the time of a flowering depends on the average amount of light within the euphotic zone, and that this is determined by a complex of factors including incident radiation, transparency of the water, depth, and vertical stability. Judging by other areas that have been observed, the relatively deep and turbulent waters of the eastern narrows probably could not support a flowering until April or May. However, this area is subject to seeding from earlier flowerings in Block Island Sound and the central part of Long Island Sound, and later examination of species composition will indicate a heterogeneous admixture of populations in the narrows. It will be noted in Fig. 2 that the April population in the eastern end of the Sound was small in 1954, and this was also the case during a cruise in April 1953. Thus there is little in present evidence to indicate that an April flowering is typical. Instead it is suspected that this area does not have a consistent flowering in the ordinary sense in

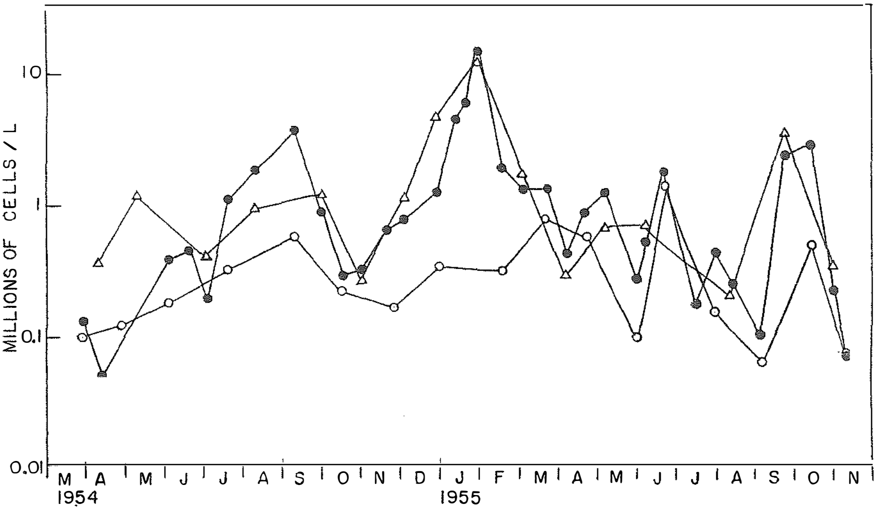

Figure 2. Logarithmic plot of seasonal variations in average cell numbers in the eastern narrows (open circles), central basin (closed circles), and western narrows (triangles), from March 1954 to November 1955.

either winter or spring. It seems likely that both the observed populations and the nutrient situation are mainly derived from adjacent waters and can be expected to vary from year to year.

Autumn diatom flowerings occurred throughout the Sound in September of both years and extended well into October in 1955. More extensive records in the central basin (Riley, 1967) have shown that an autumn flowering is not a consistent event, being slight or absent in 1952, 1953, and 1957. These were years when the water column was well mixed. In contrast, there was strong vertical stability due to freshwater drainage in 1954 and 1955. In 1956 the seasonal thermocline persisted into September, and again there was a flowering. A theory has been presented earlier (Riley, 1959) that light tends to be a limiting factor in these autumn flowerings, and that the presence of vertical stability ensures a flowering in the surface layer as soon as autumn regeneration of nutrients has progressed far enough to provide the necessary support for growth. In the absence of stability, the population is rapidly mixed through the vertical column and does not receive, on the average, enough light for effective growth.

Late autumn and early winter ordinarily is a period of pronounced poverty, but this was not so in 1954. Heavy autumn rains maintained a freshened surface layer throughout most of this period. The usual winter turbulence was reduced, and probably there was sufficient light for effective growth in the stable surface layer. In contrast, the cell counts during October and early November 1955 were more nearly typical of autumn conditions.

ACCOUNTS OF SPECIES

The total species list during the present phase of the survey differs little from that given by Conover (1956) for the central part of the Sound. There are additions or deletions of a few rare species, but these are of little interest except for maintaining records of geographical distribution.

As before, an arbitrary but useful distinction will be made between major and minor constituents. The former are defined as the species that constituted 5 % or more of the total cell count in one or more samples. These are marked with an asterisk in the species list. In addition, ten of the most important species are marked with two asterisks. There is no precise definition for this category, but in general it includes species that were either markedly dominant during a particular season or moderately abundant throughout the year and obviously were well suited to the full range of variations in the local environment.

The account is concerned only with present records. Comparison with earlier work by Conover (1956) will show major similarities and a few minor differences, but little would be gained by presenting a detailed comparison except for a few special cases in which variations from year to year have some bearing on ecological problems.

CENTRATE DIATOMS

Actinoptychus senarius was found in small quantities in about one-third of the cruises. There were no obvious seasonal or regional preferences.

Biddulphia aurita was found in small quantities in all parts of the Sound and at all seasons.

**Cerataulina pelagica* occurred in two-thirds of the cruises but was a dominant species only in May and October 1955. The largest observed concentration was 105,000 cells/l. Although it was present in all of the Sound, the maximum frequency was in the western half.

**Chaetoceros affine* was a minor dominant in October 1953, with scattered traces from January to March 1955.

**Chaetoceros compressum* was found in all parts of the Sound and in all seasons except late autumn and early winter. The largest observed concentrations of about 90,000 cells/l were in the western half in April 1954.

**Chaetoceros constrictum* was sparsely present in five sets of cruise observations in January, April, May, September, and December. Maximum concentration, in April 1953, was 16,000 cells/l.

Chaetoceros costatum was found only in two samples, early October 1952 and 1954.

**Chaetoceros curvisetum* was a dominant species in September and early October, 1952 and 1955, in the central and eastern part of the Sound. The largest observed concentration was 170,000 cells/l.

**Chaetoceros danicum* occurred in scattered samples in about half the cruises, mainly in spring and summer, but was a dominant species only in April 1953.

**Chaetoceros debile* was found in two-thirds of the cruises and was a moderately important species in the western half of the Sound, particularly from October 1954 to June 1955. The largest cell count was 360,000/l.

Chaetoceros decipiens was present in trace quantities during four spring and early autumn cruises.

**Chaetoceros didymum* occurred during a third of the cruises, with a maximum concentration of 15,000 cells/l in April 1953.

Chaetoceros gracile was present in a few samples in June 1952 and June–July 1955.

Chaetoceros laciniosum was found only in April 1954.

**Chaetoceros radians-C. tortissimum* are listed together because of difficulty in distinguishing them and the question as to whether they are valid species. They were common from January to midsummer, particularly in the western area, where a maximum cell count of 360,000/l was recorded in early July 1954.

Chaetoceros similis was present in minimal quantities from January to March 1955.

Chaetoceros subsecundum was found in a single sample in February 1955.

**Corethron criophilum* was a consistent but never abundant species from September to January. The largest recorded concentration was 16,000 cells/l.

**Coscinodiscus centralis pacifica* was present in a few samples in the autumn of 1952 and 1955.

Coscinodiscus excentricus was recorded in trace quantities at various times of the year, most commonly in the eastern end of the Sound.

**Coscinodiscus lineatus* was common in 1952 but subsequently was found only in April 1954.

Coscinodiscus perforatus cellulosa was sparsely present from June through December.

**Coscinodiscus radiatus* was another species found only in 1952 and the spring of 1954.

Ditylium brightwellii was found from February to June and in October, in the central and eastern part of the Sound.

Eucampia zoodiacus occurred in a few samples in October 1952 and May–June 1955.

Guinardia flaccida was found in October 1952 and in subsequent years in a few samples from February through July.

Hemiaulis sinensis occurred in a single sample in September 1955.

Lauderia borealis also was recorded but once, in April 1953.

***Leptocylindrus danicus* was present throughout the year in all parts of the Sound and deserves to be called a major dominant even though observed cell concentrations did not exceed 120,000/l. As in the earlier study (Conover, 1956), it has not been possible to make a clear distinction between *L. danicus* and *L. minimus*, and there is some doubt as to whether the latter is a separate species. The seasonal and regional distribution of both forms was about the same; the small form had a slightly lower cell concentration.

**Lithodesmium undulatum* was found mainly from September to December, but a few specimens were taken in April, 1954. It was abundant only in the western part, where slightly more than a million cells/l were recorded in October 1954 and 300,000 in September 1955.

Melosira italica was found in April 1953 during heavy flood conditions. This freshwater species apparently has some degree of viability in the sea.

Paralia moniliformis occurred in a single sample in September 1954.

***Paralia sulcata* was a year-round species with a peak population in autumn and early winter. The largest recorded concentration was 1.4 million cells/l in January 1955. October and November maxima of the order of 50,000 to 150,000/l occurred each year.

Rhizosolenia alata was observed in the eastern end of the Sound in April 1955.

Rhizosolenia calcar-avis was present in small numbers in June 1955.

***Rhizosolenia delicatula* is a year-round species throughout the Sound. Largest concentrations occurred in April or May and varied in different years from 45,000 to 430,000 cells/l.

**Rhizosolenia fragillissima* was taken in three-quarters of the cruises, but no blooms were found comparable to those described in earlier years of the survey. Maximum cell count was 49,000/l.

Rhizosolenia hebetata semispina occurred sparsely in March and April 1955.

**Rhizosolenia setigera* was commonly found from February or March until May or June and rarely at other times. Each year there were small April blooms which were generally of the order of 50,000 cells/l.

**Schroderella delicatula* was found only in late winter and early spring. The largest cell counts ranged from 63,000 to 256,000 cells/l in the different years and were found toward the end of the main diatom flowering.

***Skeletonema costatum* was the most important phytoplankton species in the Sound. It was taken on every cruise and also was a major constituent in one or more samples of every cruise. It dominated autumn and winter flowerings except in the eastern end, where it was partly replaced by offshore species. The maximum cell count of about 11 million/l is less than in Conover's previous account, but probably this is only because the sampling intervals were too far apart to record the peaks accurately.

***Thalassiosira decipiens* was found in at least minimal quantities in all but two cruises. It flowered in the late spring and autumn of 1954 and in the autumn of 1955. The maximum population was 1.5 million cells/l. It was reduced or absent in late summer.

***Thalassiosira gravida* was present during every cruise. It was most abundant from July to September and achieved a maximum concentration of 1.7 million cells/l in late July 1954.

***Thalassiosira nordenskiöldii* was a winter and spring form each year. The maximum cell count was 290,000/l.

**Thalassiosira rotula* occurred in all but four cruises. It was most common in the central and western part of the Sound in September. The maximum observed population was 770,000 cells/l.

PENNATE DIATOMS

**Asterionella formosa* is a remarkably euryhaline species. Although mainly a freshwater form, it was found at least in trace quantities in two-thirds of the cruises, in all parts of the Sound, and in concentrations of as much as 26,000 cells/l.

**Asterionella japonica* occurred in all but three cruises and achieved at least a slight degree of dominance in all months except July and August. Populations of 1–3 million cells/l were found in January and September 1955, with a considerably smaller peak in September 1954.

**Grammatophora marina* was recorded in scattered occurrences in about one-third of the cruises.

**Licmophora abbreviata* was found at only four stations, in spring and early summer.

Navicula distens was a minor constituent in four cruises at various times of the year.

Nitzschia closterium was present in half the cruises at various times but most consistently in spring and summer.

**Nitzschia delicatissima* barely qualified as a major constituent in the spring of 1953 and 1954 but was present in trace quantities in two-thirds of the cruises.

Nitzschia longissima was sparse at all times but occurred in a majority of the cruises.

Nitzschia pacifica occurred in two isolated samples.

***Nitzschia seriata* was primarily a January-to-June form, although not exclusively so. It was particularly important in the eastern end of the Sound, where it was the dominant species in March and April 1955. The maximum observed concentration was about one million cells/l. There is some misunderstanding as to the correct identification of this form. The specimens that have been examined seem to conform to the description of *N. pungens atlantica* as given by Cupp (1943), and this was the name used by Conover (1956). However, this form is almost certainly identical with a common species in other New England waters that has been called *N. seriata* by Lillick (1937), Riley (1952), and Smayda (1957). For the sake of uniformity, the latter terminology is used provisionally in the present paper.

**Plagiogramma vanheurckii* was found in March 1954 and February 1955.

Pleurosigma normani was never abundant but was found at various times of the year in eight cruises.

Rhabdonema minutum was found in October 1952 and April 1953.

Rhaphoneis amphiceros was recorded in June 1952.

Striatella interrupta appeared in a single sample in April 1954.

***Thalassionema nitzschioides* occurred in every cruise and achieved some degree of dominance in all seasons. The largest concentrations were in August and September 1954 and January to April 1955, the maximum being 870,000 cells/l.

**Thalassiothrix frauenfeldii* appeared sparsely in one-quarter of the cruises in winter and spring. In only one sample did it rate the designation of a major constituent.

DINOFLAGELLATES

Amphidinium crassum occurred in a few samples from the central and eastern part of the Sound in early April 1954.

Ceratium fusus was found in the Race in June 1952 and 1955, and in the central and western basins in early July 1954.

Ceratium lineatum was commonly found in early summer. A few specimens were taken in October 1952.

Ceratium tripos was seen in only two samples, both in the eastern part of the Sound in summer.

**Cochlodinium fauri* was taken in the western half of the Sound in April 1954.

Cochlodinium helicoides also was found only in the western half, in July 1954.

**Dinophysis acuminata* occurred in all but four cruises and was absent only from mid-November to February. It was taken throughout the Sound, but the largest cell count was only 10,000/l.

Dinophysis caudata was recorded only in October 1952.

Exuviella aperta occurred throughout the western half of the Sound in small numbers in July 1954.

**Exuviella apora* was an abundant species in June 1955, with a maximum cell count of three million/l. Smaller quantities were found during the remainder of the summer, and the species persisted as a trace until November. In 1954 there was one recorded occurrence in April and a small flowering in June with a peak concentration of 135,000 cells/l.

Exuviella baltica was found in small numbers in June 1952 and from April through June 1954. It was not seen in 1955.

**Glenodinium dinobryonis* occurred in June or July of each year but was a major constituent only in 1954, with a maximum cell count of 140,000/l.

Glenodinium lenticula was found only in June 1952.

**Glenodinium pilula* was a common but never abundant species (maximum 28,000 cells/l) except in late autumn and early winter. Although occasionally observed in the eastern end, it was mainly limited to the central and western basins.

Glenodinium rotundum made its only appearance in June 1952.

**Goniaulax cochlea* appeared in the Race and in the eastern narrows in late May 1955.

Goniaulax digensis was recorded in two samples in the western part of the Sound in June 1955.

**Goniaulax minima* was found in early July 1954 and in late May 1955, the maximum number being 110,000/l.

Goniaulax spinifera occurred as isolated traces in June and October 1954.

**Gymnodinium canus* was present in more than half the cruises and in all seasons except early winter. Maximum values of 10,000 to 17,000 cells/l occurred in early April 1953 and 1954.

Gymnodinium caput was found in a few samples from April to July 1954 and from September to November 1955.

Gymnodinium heterostriatum was recorded in a single sample in April 1954.

Gymnodinium variable was present as a trace in April of 1953 and 1954.

**Mesoporus globulus* was found from September to November 1955.

Mesoporus perforata appeared in a single sample in July 1954.

Peridinium breve occurred in about half the cruises, with no marked seasonal or regional pattern. In one year or another it was recorded in all months except October to December.

**Peridinium bulla* was found in June and October 1952, in April 1953, April to July 1954, and December 1954. The largest cell count was 61,000/l in early June 1954.

**Peridinium elongatum* was noted in June 1952, and from May to July and again in October 1954. Its maximum concentration of 32,000 cells/l coincided with that of *P. bulla*.

**Peridinium fimbriatum* occurred in half the cruises and at all times of the year but was a major constituent only in May and June, with peak abundance varying in different years from 26,000 to 46,000 cells/l.

**Peridinium globulus* was present in October 1952 and in March or April of subsequent years.

Peridinium grande was observed in a single sample taken from the eastern narrows in November 1954.

Peridinium granii was found in the eastern narrows in October 1952 and May 1955, and in a single sample in the western end in December 1954.

Peridinium hirobis was recorded only in March 1955.

Peridinium pellucidem occurred as a trace in January, April, and May 1955.

**Peridinium triquetum* was found on various occasions from March to October, with a maximum of 40,000 cells/l in June 1954.

***Peridinium trochoideum* was the most important member of the genus in the Sound. It was present in all but two cruises (October, December–January).

It flowered in June 1954 and was continuously abundant from March to the end of July in 1955. The largest cell count was about 600,000/l.

**Prorocentrum micans* was found in June 1952, April to July 1954, and July 1955. It was a major constituent only in early July 1954.

**Prorocentrum scutellum* was present each year from April or May until November, and it achieved the status of a major constituent in June or July and again in autumn. The largest cell counts were about 400,000/l.

**Prorocentrum triestinum* appeared in a few spring samples but was common only from July to November. Populations of half a million to a million cells/l were found in September 1954 and July 1955.

SILICOFLAGELLATES

Dictyocha fibula occurred in a single sample in March 1955.

Distephanus speculum was found in small quantities in two-thirds of the cruises. No seasonal or regional preferences were noted.

Ebria tripartita was present throughout the Sound in all but two cruises.

MISCELLANEOUS

Acanthoica quadrispina was recorded in May 1955. An unidentified *Euglena*-like form was found in small quantities in various parts of the Sound from June to September 1954 and from July to November 1955. An unidentified green alga attained the status of a major constituent in a single sample taken in April 1954.

A few centrate diatoms and a somewhat larger number of pennate forms were not identified. There were several unidentified species belonging to the following genera: *Coscinodiscus*, *Nitzschia*, *Dinophysis*, *Gymnodinium*, *Gyrodinium*, *Peridinium*, and *Prorocentrum.*

DISCUSSION OF THE SEASONAL CYCLE

The main body of the discussion will be concerned with seasonal events, as observed during the 1954–1955 survey, and particular attention will be given to the common and dominant forms. As far as possible the ecological reasons for succession will be explored, although it is apparent that field data are of limited value in analyzing the complex relationships involved.

The total material available on the subject includes not only the present information and the earlier work of Conover (1956), but also subsequent collections that were made in the central part of the Sound at intervals of two weeks to a month until 1960.

Thus the survey as a whole spans a period of eight years. During that time the pattern of seasonal succession has been consistent in its broadest generalities, but there have been many individual variations. One can never be sure whether such variations result from chance seeding by intrusion of adjacent water masses or from a response to small but significant variations in the environment. Conceivably the variations are as important as the more consistent events in providing information about the requirements of individual species. Hence the experience derived from the survey as a whole will be injected into the discussion wherever it seems appropriate. This will be done by examining the dominance of individual species at particular times in relation to deviations of radiation, temperature, and salinity from the eight-year average for the period in question.

MIDWINTER

Conover (1956) has described a late autumn period of poverty in the central basin, in which the sparse population is dominated by *Thalassiosira decipiens* and *Paralia sulcata*. These species gradually gave way in midwinter to others which were eventually to become the dominants in the late winter flowering.

It was pointed out above that conditions were unusual in the winter of 1954–1955, with appreciable stability in the water column and more active phytoplankton growth than usual. This growth was dominated by the same two species, which increased steadily from November to mid-January and attained maximum cell counts of more than one million/l each. Under these unusual environmental circumstances, *T. decipiens* and *P. sulcata* may be regarded as having initiated the winter diatom flowering. Other species that occurred in sufficient quantity to be ranked as major constituents in November and December were *Skeletonema costatum*, *Thalassionema nitzschioides*, and *Asterionella japonica.*

THE LATE WINTER FLOWERING

Skeletonema costatum, a major constituent in all winter flowerings that have been observed in these waters, occurred irregularly during the early winter. Most November and December samples contained less than 60,000 cells/l of this species. However, four stations, scattered in space and time, yielded counts of 150,000 to 485,000.

Skeletonema increased very rapidly during January 1955. On the 20th it outnumbered *Thalassiosira decipiens*, its nearest competitor, and by the end of the month it constituted 75 to 80% of the total cell count. *T. decipiens* and *Paralia sulcata* had decreased greatly by this time and were outranked by *Asterionella japonica* and, at some stations, by *Thalassionema nitzschioides.*

The end of January 1955 marked the peak of the flowering. The situation was different from most other years in that the phytoplankton began to decline while there was still an appreciable amount of nitrate in the water. The decline probably was due to heavy weather and a temporary reduction in radiation in February rather than nutrient depletion, and presumably an unusually early flowering is subject to this kind of inhibition. This was, in fact, one of the earliest flowerings that has been observed in the Sound.

By mid-February *S. costatum* had been reduced tenfold in the central part of the Sound. *A. japonica* had all but disappeared, and *T. nitzschioides* was the second-ranking species. *Thalassiosira nordenskiöldii* had increased rapidly to third rank in terms of numbers and possibly first rank in total volume.

Conover (1956) has studied the competition between *S. costatum* and *T. nordenskiöldii* and concluded that the latter has a superior growth rate at low temperature and with reduced radiation. This conclusion was based partly on experiments with natural populations and partly on observations of the natural trend of events in 1955 and earlier years. The winter of 1953 was unusually warm, and *S. costatum* was dominant. The 1954 flowering began with low temperature and dominance of *T. nordenskiöldii*, which was replaced by *S. costatum* later in the flowering as the temperature increased. The situation was reversed in 1955. The temperature decreased rapidly in January and early February, and the emergence of *T. nordenskiöldii* at that time in a different successional pattern strengthens the validity of the basic ecological theory.

With regard to other species relations, *S. costatum* and *T. nitzschioides* seem to be similar in most aspects of their behavior. Both species are present most of the time and have been major constituents every month of the year. Both are important in winter flowerings and in the early part of autumn flowerings, but *T. nitzschioides* is almost invariably of lesser importance than *S. costatum* and commonly is the third- or fourth-ranking species. Experimental evidence (Braarud, 1945; Riley, 1952; Conover, 1956) indicates that under most conditions *Skeletonema* has an inherently faster growth rate than *Thalassionema* and most other diatoms. However, *T. nitzschioides* has a broader tolerance to the full range of the environment than *Skeletonema*. When the temperature was above 20° and again in the fading light of late autumn and early winter, *Thalassionema* generally became more important.

Asterionella japonica is another species that achieves some degree of dominance in both autumn and winter flowerings. In one year or another, it has been a major constituent nine times between September and January. In seven cases out of the nine, radiation was above the seasonal average at the time the flowering developed, and in eight cases temperature was above the average. The early importance and subsequent quick disappearance of *A. japonica* from the 1955 flowering presumably were the result of early stability and a later increase in turbulence accompanied by decreasing temperature.

In the Race and eastern narrows the population was dominated from mid-February to April by *Nitzschia seriata*. This species is relatively more important in Block Island Sound than in Long Island Sound, and its success in the eastern narrows probably indicates both an influence due to exchange with offshore waters and an ecological similarity between the eastern part of the Sound and the offshore areas that favors the dominance of such species. Other dominants in this area in mid-February were *Thalassionema nitzschioides* and *Skeletonema costatum*. As the season progressed, secondary dominance was taken by *Schroderella delicatula* and then by *Leptocylindrus danicus*.

POSTFLOWERING PERIOD

The dominant species of the flowering remained as major constituents in March in the central and western areas, but the dominance was less clear-cut. *Chaetoceros debile*, *Schroderella delicatula*, and *Peridinium trochoideum* also became major constituents, and no single species was clearly superior at all stations. The March observations represented a state of transition from an unusually long and slow flowering to a postflowering reduction of both the total population and the number of individual species.

By early April the total cell counts had fallen to between 300,000 and 400,000 cells/l. Major constituents were *Chaetoceros debile*, *Leptocylindrus minimus* (?), *Rhizosolenia setigera*, *Skeletonema costatum*, *Nitzschia seriata*, *Thalassionema nitzschioides*, and *Peridinium trochoideum*. The last-named species was the most important one in the western basin and narrows. *N. seriata* and *T. nitzschioides* shared first rank in the central basin.

Seasonal succession during this period is extremely variable from year to year. *N. seriata*, which was dominant in the eastern narrows in 1955 and fairly important in the central region, was relatively insignificant in 1953 and 1954. *Chaetoceros compressum* was a strong dominant in 1954 but a mere trace in 1955. Other major constituents in 1954 were *Leptocylindrus minimus* (?), *Schroderella delicatula*, *Thalassiosira gravida*, *Plagiogramma vanheurckii*, and *Thalassionema nitzschioides*.

Considering the eight-year series as a whole, there were several species that achieved the status of major constituents toward the end of the winter flowering and had their greatest degree of dominance during the spring months. A total of eight species were major constituents at this time, for at least three of the eight years, and were never important otherwise. Of these, *Leptocylindrus* and *Rhizosolenia delicatula* were the most consistently important forms. Their behavior was strikingly similar. On every occasion when *Leptocylindrus* was a major constituent, *Rhizosolenia* was also, reaching its peak at the same time or slightly earlier or later. *Rhizosolenia*, however, was occasionally a major constituent when *Leptocylindrus* was not. On three occasions when one or both species flowered in March, radiation values during the period of increase were above the mean for the eight-year period. In nonflowering years most of the radiation values in March were average or below, and at such times the flora was dominated largely by the species that had been important in the late winter flowering. Dominance by these two species in April and May showed no consistent relationship with light, nor did variations in temperature or salinity appear to have any effect during any of the spring months.

Conover (1956) reported that in experiments early in the season, *Lepto-*

TABLE II. Relationship of Spring Dominants with Year-to-year Fluctuations in Radiation, Temperature, and Salinity. Numbers Indicate the Number of Years when a Given Species was a Major Constituent During the Seasonal Period in Question – in Association with Environmental Factors Above Average for the Period (+), Below Average (–), or Approximately Average (0).

	Season	Radiation			Temperature			Salinity		
		+	0	–	+	0	–	+	0	–
Lauderia borealis	April–May	3	0	0	0	0	3	0	0	3
Rhizosolenia setigera	April	3	1	0	0	2	2	1	2	1
Chaetoceros radians	January–March	2	2	1	2	0	2	5	0	0
Nitzschia seriata	March–June	4	1	0	1	1	3	0	3	2
Schroderella delicatula	March–April	3	1	2	2	1	3	1	2	3

cylindrus showed the greatest increase in bottles receiving the most light. Later in the season both *Leptocylindrus* and *Rhizosolenia* were inhibited by strong light. It would appear that both species have fairly narrow limits of light tolerance. Limitation by low light intensity might readily explain their presence or absence in March. No explanation has been found for their spotty occurrence in late spring and early summer. In a June experiment Conover found that $25\,{}^{0}/_{0}$ of the surface intensity was optimal for *Leptocylindrus*, but with a normal extinction coefficient of about 0.5, inhibition would be expected only in the upper 3m.

Chaetoceros compressum appears to be another species with a narrow range of optimum light intensity. Its dominance in March was associated with radiation values above the average level. On the one occasion when it was a major constituent in June, radiation was below average. In other months no consistent relation was found.

Five species of lesser importance are listed in Table II, with indications of the months when they were dominant and the kind of variations in radiation, temperature, and salinity that were associated with their periods of increase. Four of the five species show indications of a preference for strong light, and two or three appear to be favored by low temperature. There are also slight indications of salinity effects.

This group as a whole appears to have narrower limits of temperature and light tolerance than most of the species that were discussed earlier, although the temperature effects are not as clearly expressed as those of light. The observed seasonal distribution is most easily explained as a response to increasing vernal radiation, which is effective only during the brief period while the temperature is still relatively low.

May and June Blooms

Harris (1959) described small surges of ammonia production in late spring and early summer, which probably resulted from the bacterial decay of earlier flowerings and were followed by increases in phytoplankton as indicated by chlorophyll analyses. Thus the postflowering period of severe nutrient depletion gave way in May and June to small, sporadic flowerings in all parts of the Sound.

In early May 1954 there was a flowering in the western end in which *Skeletonema costatum* revived to primary dominance and other major constituents were *Chaetoceros radians-C. tortissimum*, *Leptocylindricus danicus*, *Rhizosolenia delicatula*, *Thalassiosira decipiens*, and *Thalassionema nitzschioides*. On June 1 and 2 the same species were important in the eastern end, and in the central basin they were still major constituents, although the total cell count had gone down and another group was reaching the status of major constituents, namely *Peridinium trochoideum*, *P. bulla*, *P. fimbriatum*, *P. elongatum*, and *P. triquetum*.

In mid-June and early July in the western half of the Sound *Chaetoceros radians-C. tortissimum* and *Thalassiosira gravida* were the only diatoms of any significance, and a dinoflagellate population was dominant. The most important species were *Peridinium trochoideum* and *Exuviella apora*, and major constituents at one or more stations also included *Dinophysis acuminata*, *Glenodinium dinobryonis*, *G. pilula*, *Goniaulax minima*, *Prorocentrum micans*, and *P. scutellum*.

The next year a similar *Skeletonema* flowering occurred in the central and western basins in early May. Other major species were *Leptocylindrus minimus* (?), *Nitzschia seriata*, and *Cerataulina pelagica*. *Peridinium trochoideum* became a first-order dominant in the eastern end of the Sound in late May, and ten other species, most of which have already been recorded as being important at this time of the year, were major constituents in one or more samples.

In early June 1955 *Peridinium trochoideum* was a strong dominant in the western half. Other major constituents were *Chaetoceros debile*, *Leptocylindrus minimus* (?), *Thalassiosira rotula*, and *Exuviella apora*. Later in the month *E. apora* had achieved dominance over *P. trochoideum* in the central basin. Both species were present in the eastern end, but *Skeletonema costatum* was found in large numbers (950,000 cells/l) in the eastern narrows and gave this area the largest cell count observed during the survey. Other major constituents were *Chaetoceros debile* and *Rhizosolenia delicatula*.

In summary, small flowerings were found in May and June, often but not necessarily in both months, for the small increases in nutrient supply which trigger the growth are quite variable in their occurrence. The May flowering tended to be dominated by diatoms and the June one by dinoflagellates, and there was also a regional difference in that dinoflagellates tended to be more important in the western half and diatoms in the eastern narrows. The diatom, *Skeletonema costatum*, and the dinoflagellate, *Peridinium trochoideum*, were outstanding dominants and strong competitors with each other. They were accompanied and occasionally outranked by a variety of other species, but these were less consistent in their appearance from year to year. Generalities about the requirements of individual species will be discussed later, because the spring and summer flora show a gradual transition that is best considered in terms of the full range of conditions prevailing between May and August.

SUMMER

July and August formed a period of small to moderate populations and no overwhelming dominance by any species, with the single exception of a flowering of *Thalassiosira gravida* in late July 1954. Other major constituents during the summer were *Skeletonema costatum*, *Thalassionema nitzschioides*, *Exuviella apora*, *Peridinium trochoideum*, and *Prorocentrum scutellum.*

The years 1954 and 1955 were typical with respect to the general character of species composition and the size of the total population. The latter achieves a more or less steady state during the summer. The rate of production is moderately high (Conover, 1956), but the phytoplankton supports a large zooplankton population at this time. The whole system is sufficiently in balance that variations in population level generally are less marked than in the little May–June flowerings.

Table III lists the most important species that have been found between May and August and shows the frequency of their dominance in relation to variations from average radiation and temperature during the eight-year survey. Certain indications of optimum light and temperature for particular species may be gleaned from this table, although the data are minimal for the purpose, and some care must be used in interpreting the results. If a flowering develops in association with a particular combination of light and temperature, it seems likely that the particular environment is favorable for the species in question. However, a species may become dominant without increasing materially, by virtue of decreases in other species. In this case there is no reason to think that the environment is particularly favorable; it is merely tolerated more readily than by other species which declined in numbers. *Thalassionema nitzschioides* is an example. Its apparently heterogeneous reactions to light and temperature make little sense ecologically except in terms of dominance at times when conditions were suboptimal for other species.

Cerataulina pelagicus was a major constituent five times in May and June. On one occasion radiation approximated the seasonal average during the development of the bloom; the other four times it was below average. In August and on one occasion in September when this species was a major constituent, the light intensity was above average. The data suggest a sharply defined light tolerance, the average May–June intensity being too high and the August–September too low. It seems odd that this species should attain its greatest degree of dominance in June when the light appears to be above the optimal level, rather than earlier in the season. Temperature is a possible limiting factor in midspring. The species was found in at least minimal amounts every month

TABLE III. Relationship of Late Spring and Summer Dominants with Year-to-year Fluctuations in Radiation and Temperature. Numbers Indicate the Number of Years when a Given Species was a Major Constituent During the Seasonal Period in Question – in Association with Environmental Factors Above Average for the Period (+), Below Average (–), or Approximately Average (0).

Radiation	May			June			July			August		
	+	0	–	+	0	–	+	0	–	+	0	–
Cerataulina pelagicus	0	0	2	0	1	2	0	0	0	1	0	0
Skeletonema costatum	1	2	2	2	0	2	3	0	0	2	0	2
Thalassiosira gravida	1	1	0	2	0	1	2	0	1	2	1	2
Thalassionema nitzschioides	0	0	3	0	0	2	3	0	1	3	1	2
Peridinium trochoideum	2	1	0	1	3	1	3	1	1	0	0	0
Prorocentrum scutellum	0	0	0	1	0	0	4	1	0	1	2	1
P. triestinum	0	0	0	0	0	0	3	1	0	0	0	1
Exuviella apora	0	0	0	2	0	0	2	2	0	1	0	0
Temperature												
Cerataulina pelagicus	0	1	1	1	0	2	0	0	0	1	0	0
Skeletonema costatum	3	0	2	1	0	3	3	0	0	4	0	0
Thalassiosira gravida	1	0	1	1	0	2	2	1	0	2	1	2
Thalassionema nitzschioides	1	0	2	0	0	2	2	1	1	3	1	2
Peridinium trochoideum	2	1	0	1	2	2	1	1	3	0	0	0
Prorocentrum scutellum	0	0	0	1	0	0	3	1	1	1	1	2
P. triestinum	0	0	0	0	0	0	2	0	2	1	0	1
Exuviella apora	0	0	0	2	0	0	1	0	3	1	0	0

except December, but vigorous growth occurred only when the temperature was above 10°.

Peridinium trochoideum, unlike most of the other dinoflagellates, commonly appeared in early spring, although it was seldom an important dominant until May or June. The table suggests that average light intensity is optimal in June, and an intensity higher than average is favorable in May and July. Despite the ability of this species to exist under a wide range of temperature conditions, optimal growth occurred within a fairly narrow range. The table suggests that a temperature higher than average was favorable in May and one lower than average in July.

That maximum vertical stability is found in the Sound from May to July also is believed to be ecologically important to *P. trochoideum* and other dinoflagellates. Reduction of vertical turbulence makes it easier for dinoflagellates to maintain a position in the vertical column that is optimal with respect to light and temperature. Diatoms, on the other hand, require a moderate amount of turbulence to maintain a position near enough to the surface for effective growth.

Riley (1967) reported an instance in which detailed sampling of the vertical column during a June flowering of *P. trochiodeum* revealed that 90% of the population was congregated in a one-meter stratum centered around a depth of 3m. This is indicative of narrow preferences for light or temperature or some optimal combination of the two. It also reveals, incidentally, that the surface sampling program described herein is probably very poor in its quantitative delineation of total dinoflagellate populations.

The light intensity at the depth where *P. trochoideum* was swarming was about one-quarter of the surface intensity. There appears to be an avoidance of full surface sunlight despite indications in Table III that high radiation values are required by this species for active growth. Possibly the length of daylight may be more important than high intensity. Little attention has been given to the effect of day length on common planktonic species, and it may be important.

The three other dinoflagellates in the table also were favored by higher-than-average radiation during the first month when they achieved dominance. They tended to replace *P. trochoideum* in late June or July, and high temperature favored their early dominance. They were largely replaced by diatoms in late July or August. The period of maximum dinoflagellate abundance spanned the period when radiation was at its yearly peak, and the temperature was rising from about 10 to 20°.

Thalassiosira gravida and *Thalassionema nitzschioides* were the most consistently successful diatoms at temperatures above 20°. *Skeletonema costatum* was less important than at most other seasons and frequently was, at best, the third-ranking species. Probably it was near the upper limit of temperature tolerance, but even so it was better able to survive than the dinoflagellates. This led to a paradoxical situation in which *Skeletonema* was a major constituent only when the temperature was above average but lost dominance to the dinoflagellates when the temperature was slightly lower.

AUTUMN FLOWERINGS

A major autumn flowering began in September of both 1954 and 1955. *Skeletonema* was the early dominant in all cases except at a single station in the central basin in 1954, where it was slightly outranked by *Prorocentrum triestinum*. Other major constituents in the early stages of the flowerings were *Thalassiosira gravida* and *T. rotula* in 1954 and *T. rotula Asterionella japonica*, and *Cerataulina pelagicus* in 1955.

By the end of September, *Skeletonema* was losing its clear-cut dominance. A total of some ten species were major constituents in one year or both. Their relative importance varied markedly from one area to another, but in general the most important, aside from *Skeletonema*, were *Asterionella japonica*, *Thalassiosira decipiens*, and *Paralia sulcata*. The last two emerged as dominants toward the end of October 1954 and continued so into midwinter. In 1955 *A. japonica* had brief dominance in mid-October, with lesser quantities of *S. costatum*, *Leptocylindrus danicus*, and *Chaetoceros curvisetum*. At this time

T. decipiens and *P. sulcata* declined to mere traces, but they recovered in late October and were emerging as dominants in early November when the survey ended.

In the earlier study of the central basin, autumn growth was slight in 1952 and 1953. As stated before, the flowerings of 1954 and 1955 are believed to have been due primarily to more favorable physical conditions, particularly the maintenance of stability. The nutrient supply was minimal at the onset of the flowering. The maximum observed nitrate was 5 μg-at N/l, and most stations had considerably less. Rapid regeneration must have been going on in the bottom water, however, because the supply of nitrate increased as the flowering progressed.

Looking at the data as a whole, it is apparent that the sequence of autumn species has been nearly the same in flowering and nonflowering years. Each flowering has begun with early dominance by major summer constituents and the persistence of some minor ones, which ordinarily would be disappearing at that time. There is then a gradual shifting of dominance to more typically autumnal species.

Asterionella japonica, an important constituent in 1953 and 1955 but not in 1952 and 1954, is properly regarded as one of the autumn group. This species obviously has wide tolerance to variations in temperature and light, but it is found sparsely if at all in August in these waters, which presumably are close to the limits of its temperature tolerance. In the cooler waters of the Gulf of Maine, it is present and sometimes flowers in August (Lillick, 1940). *Thalassiosira decipiens* is more or less similar to *A. japonica* in its seasonal distribution, and *Paralia sulcata*, the other late autumn dominant, is present throughout the year but is never abundant at other times.

The autumn flowering would appear to be at first the result of a prolongation of the physical conditions of summer combined with an improvement in nutrient supply. This combination permits the increase and continued dominance of typical summer species. The autumn flora achieves dominance eventually, but its appearance probably is delayed by a flowering. In nonflowering years *P. sulcata* and *T. decipiens* frequently become important in early October, as contrasted with late October or early November in flowering years.

The differences from one year to another in mid-autumn dominants can largely be explained by a hypothesis that their relative dominance is controlled by the amount of light available. It is suggested that with moderately good illumination, *A. japonica* has a higher growth rate than *T. decipiens*, and that the latter is superior to *P. sulcata*. Under conditions of poor illumination, however, the series is reversed. This would account for the fact that *A. japonica*, if present at all, takes early precedence over *T. decipiens* in bloom years, and the latter readily dominates *P. sulcata* until later in the autumn. In nonflowering years, however, *P. sulcata* quickly dominates the mid-autumn scene (mainly by default, for all cell counts are small), while the other species are absent or grow very slowly.

In discussing the effects of light limitation in autumn and the tolerance of autumn dominants to reduced light intensity, it should be pointed out that temperature also may be important through its effect on respiration. In analyzing environmental factors associated with autumn and winter flowerings, Riley (1967) found that the amount of light required to initiate an autumn flowering was much higher than that required in winter. This did not appear to be due to differences in species composition, because *Skeletonema costatum* was one of the first dominants in both flowerings. Nor was there an indication of light adaptation, for the statistically computed photosynthetic coefficients are virtually the same in both cases. The cause appears to be a greater loss of phytoplankton material in autumn by plant respiration and by the grazing effect of zooplankton. The late autumn dominants obviously can grow effectively at a lower light intensity than *Skeletonema* can tolerate, but it remains an open question whether this is because of more efficient photosynthesis or a lower respiratory rate.

REGIONAL COMPARISON

Earlier sections of this paper have noted regional differences in Long Island Sound with respect to tidal currents, depth of water, and nutrient supply. The western end represents an almost estuarine condition, enclosed and nutrient-rich although not extremely reduced as to salinity, while the eastern end is more nearly representative of open coastal conditions.

By ordinary monographic habitat definitions, the flora is a mixture of mainly temperate and boreal species of littoral and neritic and even oceanic tendencies. By way of checking these designations and further exploring species ecology, the distribution of individual species will be examined for evidence of preferences for one part of the Sound or another.

Group 1 in Table IV shows the frequency distribution of certain species that seem to be rather uniformly distributed in all parts of the Sound. This group includes most of the major dominants, which suggests that the most successful species are likely to be those well adapted to the full range of environmental conditions in these waters.

Group 2 shows some species with markedly higher frequency in the eastern end of the Sound. Most of these probably are derived from open coastal waters, and in most cases their capacity to grow in the Sound is limited. Perhaps they could maintain themselves in the eastern end more effectively if the transport exchange were less vigorous. However, the fact is that only *Nitzschia seriata* achieved really important status, and for only a short period.

Group 3 consists of species with a higher degree of frequency in the western end, although none was limited to this area. Some of the dinoflagellates in the group undoubtedly are littoral and brackish-water species that thrive in the shallow bays and estuaries opening into the western basin and narrows. It was

TABLE IV. Percentage Frequency of the Listed Species in Various Parts of Long Island Sound, Expressed as the Number of Samples in Which the Species was Taken in a Given Area in Relation to the Total Number of Samples Taken. Criteria for Grouping are Discussed in the Text.

	Race	Eastern Narrows	Central Basin	Western Basin	Western Narrows
Group 1					
Chaetoceros compressum	31	28	27	24	29
C. didymum	6	0	7	2	0
C. radians-C. tortissimum	19	9	20	10	35
Corethron criophilum	6	16	19	14	12
Coscinodiscus perforatus cellulosa	19	25	17	12	18
Leptocylindrus danicus	38	53	38	22	53
Paralia sulcata	63	63	60	65	53
Skeletonema costatum	75	88	76	69	94
Thalassiosira decipiens	69	38	41	37	82
T. gravida	62	53	64	59	64
Asterionella formosa	44	41	27	28	18
A. japonica	37	25	40	29	18
Thalassionema nitzschioides	87	91	80	80	76
Dinophysis acuminata	6	31	31	43	24
Peridinium trochoideum	63	62	55	53	59
Group 2					
Chaetoceros affine	6	12	4	6	0
C. curvisetum	0	16	5	2	0
C. danicum	31	22	11	0	0
Coscinodiscus centralis pacifica	0	12	6	0	0
C. radiatus	6	28	18	14	0
Ditylium brightwellii	6	25	8	0	0
Navicula distens	19	12	6	2	0
Nitzschia seriata	44	37	22	16	12
N. delicatissima	44	22	11	10	6
Pleurosigma normani	6	25	11	2	6
Thalassiothrix frauenfeldii	6	9	5	0	0
Group 3					
Chaetoceros debile	12	16	16	23	53
C. constrictum	0	6	6	4	12
Lithodesmium undulatum	0	3	7	14	29
Exuviella apora	6	9	15	26	6
E. baltica	0	3	5	6	12
Glenodinium pilula	19	0	19	37	29
Peridinium globulus	6	3	7	10	23
P. triquetum	6	3	14	12	29

common in summer to find populations of red tide dimensions in some of these bays, and nearby Sound waters were discolored by the effluent. Probably most of these forms had a marginal existence at best in open waters.

Table IV lists only the common and fairly abundant species. Some of the others are listed below with similar indications of areal preference or lack of it. However, the validity of the grouping is less secure in the case of the less common species.

Found mainly in the eastern end:

- *Rhizosolenia alata*
- *R. calcar-avis*
- *Amphidinium crassum*
- *Ceratium tripos*
- *Goniaulax cochlea*
- *G. spinifer*

Found in the western end:

- *Rhizosolenia hebetata* f. *semispina*
- *Cochlodinium fauri*
- *C. helicoides*
- *Exuviella aperta*
- *Goniaulax digensis*

Distributed throughout the Sound:

- *Rhizosolenia fragillissima*
- *R. setigera*
- *Schroderella delicatula*
- *Thalassiosira nordenskiöldii*
- *T. rotula*
- *Grammatophora marina*
- *Nitzschia longissima*
- *N. closterium*
- *Gymnodinium canus*
- *Peridinium breve*
- *P. bulla*
- *P. elongatum*
- *Prorocentrum scutellum*

Many of the major constituents in Long Island Sound are also important in other New England waters. It seems desirable to examine these other areas briefly to find out whether a comparison will throw any light on the ecological requirements of the species in question. Most of these waters have a distinctly higher salinity than Long Island Sound and are deeper and more oceanic in character. The winter temperature regime is similar throughout the entire region, but maximum summer temperatures range from a little more than 10° in the northern part of the Gulf of Maine to about 25° in Long Island Sound. Moreover, light is expected to be more strongly limiting in the deep and turbulent waters of the Gulf of Maine.

Most of the information on the Gulf of Maine was obtained from an unusually complete and quantitative survey published by Bigelow et al. (1940) and Lillick (1940). Other reference material for this area was obtained by Bigelow (1926), Burkholder (1933), and Braarud (1934). Most of these earlier works were based on qualitative net hauls and hence did not give an accurate picture of total species composition. However, they are useful for evaluating the degree of dominance of some of the species over a period of years.

Fish (1925) described a series of net collections in Woods Hole Harbor. Lillick (1937) enumerated the phytoplankton in water samples taken in open coastal waters south of Woods Hole. Riley (1952) described a similar survey in Block Island Sound. Data from these three papers are used to evaluate the phytoplankton of southern New England coastal waters.

Study of the seasonal cycles of species that occur in these three major areas shows that there are several distinct behavioral types, some of which appear to have ecological significance. These may be summarized as follows:

A. Three of the Long Island Sound dominants were found in every New England area eleven to twelve months of the year, and each had peaks of abundance at approximately the same time in all three areas. They were *Skeletonema costatum*, *Thalassionema nitzschioides*, and *Paralia sulcata*. *Skeletonema* is the most important. It is a first-ranking species in Long Island and Block Island Sounds and in some of the inshore waters of the Gulf of Maine. In deeper waters it is less successful, perhaps because of its cobalamin requirement. In this connection, it would be desirable to determine the cobalamin requirements of some of the offshore dominants. Some that might profitably be tested are *Thalassiosira nordenskiöldii* and the various *Chaetoceros* spp. that dominate the spring flora in the offshore waters of the Gulf of Maine.

B. Several species varied in numbers or duration from one area to another, but peaks of abundance occurred at about the same time in each area. In areas of lesser dominance, they tended to appear later and die out sooner than in the area of greatest abundance. When they were present only as a minor species for a short time, this time corresponded with the peak of abundance in the area of greatest dominance. They tended to be present most or all of the year in the area of greatest dominance, although a few were distinctly limited as to season. Evaluation of ecological significance is difficult because there are no pronounced differences to analyze. In general these are well-adapted species with broad tolerances, and the majority had their peaks during the usual periods of optimum growth, that is, the diatom flowerings of spring and autumn or the period of dinoflagellate growth in spring and early summer.

The species in this group are:

Cerataulina pelagicus
Chaetoceros radians
Leptocylindrus danicus
Nitzschia longissima
Thalassiosira gravida
Thalassiosira rotula
Peridinium trochoideum
Distephanus speculum
Ebria tripartita

C. A few species were similar to group B except that the peaks of abundance did not coincide closely. There were no obvious ecological reasons for the differences. These were *Chaetoceros curvisetum*, *C. decipiens*, and *Prorocentrum scutellum*.

D. This group, consisting of *Chaetoceros compressum*, *Guinardia flaccida*, *Lauderia borealis*, *Rhizosolenia delicatula*, and *R. setigera*, comprised spring and summer forms in the deepest and most open areas where they were found, while in shallower areas the inception or peak population occurred earlier in the spring or later in the autumn. This type of variation is to be expected when a species is inhibited by low light intensity. Incident radiation varies little from one area to another, but the complex of light, turbulence, and depth of water, which determines the amount of light received by any one organism, is more favorable in shallow water. In southern New England waters there is also the possibility of inhibition by high temperature.

E. Several species had peak populations in the Gulf of Maine in summer, generally late summer, while in southern New England waters they flowered in late spring or early summer and again in September or October but were reduced or absent during the period of greatest abundance in the Gulf of Maine. This group is believed to have an upper limit of temperature tolerance that is exceeded in late summer in the southern part of the region. The following species are included:

Asterionella japonica
Chaetoceros debile
Nitzschia seriata
Rhizosolenia fragillissima
Thalassiosira decipiens

F. *Thalassiosira nordenskiöldii* behaved similarly except that it exhibited no autumn peak in southern waters. Probably this species was less tolerant of high temperature than group E. *Nitzschia seriata* is a somewhat intergrading form which is found in southern coastal waters in autumn but not in the slightly warmer waters of Long Island Sound.

G. *Chaetoceros affine* and *Corethron criophilum* were found at all seasons, although somewhat spottily, except in Long Island Sound where they were largely limited to summer and autumn. Conover (1956), noting that they were never found when the salinity was less than 27 ‰, suggested that stenohaline tendencies were responsible for their exclusion in spring and early summer. Since that time *C. affine* has achieved a slight degree of dominance in spring on two occasions when the salinity was about 26.5 ‰, which is unusually high for this season. *C. criophilum* did not. Neither species was successful during two autumn seasons when the salinity was abnormally low.

H. Several species were found in one area or another during all months of the year, thus demonstrating wide tolerance of the environment, and yet they never occurred in appreciable numbers. That they won a place in the list of major constituents was largely a matter of default. When conditions were particularly unfavorable for other species, these constituted a significant fraction of the total population. Their so-called peaks were scattered and occurred at seemingly unlikely times such as mid-autumn, mid-winter, or the spring postflowering period. The species include *Grammatophora marina*, *Prorocentrum micans*, and a number of others that have been major constituents at the 5 % level but were not regarded as important enough to receive special attention in the present analysis. Several other species of similarly slow growth and minimal abundance, but with more consistency in the time at which their peaks occurred, have been put into categories A and B.

I. Four species of some importance in Long Island Sound have not been reported in any of the New England areas. These are *Schroderella delicatula*, *Exuviella apora*, *Goniaulax minima*, and *Prorocentrum triestinum*. There is little to be said about them except that their limitation to the Sound suggests a requirement for reduced salinity, abundant vitamins, or some other factor peculiar to its waters.

There is no reason to doubt that the total array of factors governing regional distribution and seasonal succession is complex. In order to put the foregoing analysis into proper perspective, it is necessary to consider what are some of the most likely factors. They may be listed as follows:

1. Various effects of light, temperature, and salinity as described above.

2. General nutrient level. Experiments with natural populations by Conover (1956) indicated that some of the autumn dominants require a moderately high level of enrichment for effective growth. The possible role of nutrients in the competition between diatoms and dinoflagellates needs further study. In theory, the ability of phytoplankton to absorb sufficient nutrients will vary with the size of the cell and its movement in relation to the medium, either by passive sinking or active swimming (Munk and Riley, 1952). Some species therefore are expected to be more effective than others when nutrient concentrations are low, but verification of theory in terms of direct observation largely remains to be established.

3. Qualitative aspects of the nutrient supply. Ryther (1954) experimentally demonstrated the importance of different kinds of nitrogen sources in determining seasonal succession of phytoplankton in Great South Bay, Long Island. In Long Island Sound Conover (1956) showed that nitrogen was usually the most important limiting factor. Certain species responded strongly to other kinds of enrichment, however, and this suggests that the requirements for particular elements are by no means the same in all species. Algal nutritionists in recent years have proven that auxotrophy is widespread. They have not worked extensively with common planktonic forms, but many of these may have auxotrophic tendencies, and variations in the abundance of various organic substances in sea water may affect distribution and succession.

4. Chemical competition. It is well known that some species of phytoplankton secrete organic metabolites that may stimulate or inhibit the growth of other species. Unfortunately, most of the information on this subject is anecdotal and unspecific as to the nature of the substances involved. The possible importance of such substances has been postulated frequently but has never received serious attention.

The present analysis has indicated the importance of light and temperature in controlling some major aspects of seasonal succession and regional distribution. To a lesser extent salinity also appeared to be important. The importance of other possible factors cannot be evaluated at the present time. It must be conceded that they may at times modify or over-ride physical effects, and there are enough unexplained variations in seasonal cycles to make this view tenable. An analysis of physical factors is therefore only a small part of the solution of the problem. It is a logical first step in that it reveals certain probabilities that can be tested experimentally, and this in turn opens the way for experimental work on the more subtle problems of nutrient relationships.

REFERENCES

BIGELOW, H. B.

1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. (1924), *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. Part I. Numerical distribution. Trans. Amer. phil. Soc., *31*: 149–191.

BRAARUD, TRYGVE

1934. A note on the phytoplankton of the Gulf of Maine in the summer of 1933. Biol. Bull., Woods Hole, *67*: 76–82.

1945. Experimental studies on marine plankton diatoms. Avh. norske VidenskAkad., 1944 (10): 16 pp.

BURKHOLDER, P. R.

1933. A study of the phytoplankton of Frenchmans Bay and Penobscot Bay, Maine. Int. Rev. Hydrobiol., *28*: 262–284.

CONOVER, S. A. M.

1956. Oceanography of Long Island Sound, 1952–1954. IV. Phytoplankton. Bull. Bingham oceanogr. Coll., *15*: 62–112.

CUPP, E. E.

1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Instn Oceanogr., *5* (1): 238 pp.

FISH, C. J.

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

HARRIS, EUGENE

1959. The nitrogen cycle in Long Island Sound. Bull. Bingham oceanogr. Coll., *17* (1): 31–65.

LILLICK, L. C.

1937. Seasonal studies of the phytoplankton off Woods Hole, Massachusetts. Biol. Bull., Woods Hole, *73*: 488–503.

1940. Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. Part II. Qualitative composition of the planktonic flora. Trans. Amer. phil. Soc., *31*: 193–237.

MUNK, W. H., and G. A. RILEY

1952. Absorption of nutrients by aquatic plants. J. Mar. Res., *11*: 215–240.

RILEY, G. A.

1942. The relationship of vertical turbulence and spring diatom flowerings. J. Mar. Res., *5*: 67–87.

RILEY, G. A.
1952. Phytoplankton of Block Island Sound, 1949. Bull. Bingham oceanogr. Coll., *13* (3): 40–64.
1957. Phytoplankton of the north central Sargasso Sea, 1950–52. Limnol. & Oceanogr., *2*: 252–270.
1959. Oceanography of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *17* (1): 9–30.
1967. The plankton of estuaries. *In* Estuaries. Horn-Shafer Co., Baltimore. (in press).

RYTHER, J. H.
1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. Biol. Bull., Woods Hole, *106*: 198–209.

SMAYDA, T. J.
1957. Phytoplankton studies in lower Narragansett Bay. Limnol. & Oceanogr., *2*: 342–359.

Transport and Mixing Processes in Long Island Sound

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ABSTRACT

After a preliminary discussion of qualitative aspects of water movements, transport exchange is calculated according to the salt balance method. The necessary data include salinity measurements throughout Long Island Sound at approximately monthly intervals and freshwater drainage during the intervening periods. From these it is possible to calculate the average transport into and out of the Sound between successive cruises. The total exchange rate varied seasonally from about 9 to 60 thousand m³/sec, with a minimum in early spring and a maximum in early summer. The rate of exchange increased with an increase in vertical stability and with westerly winds; it decreased when there was excessive freshwater drainage. These factors were mainly responsible for the observed seasonal variation.

The salinities observed during 1954 and 1955 were averaged and arranged in a simplified east-west profile. The pattern of salinity distribution is the result of the interaction of freshwater drainage, currents, and turbulent mixing. All of these factors, except horizontal tur-

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bulence, have been measured or computed. Therefore it is possible, with certain simplifying assumptions to be explained later, to calculate coefficients of horizontal eddy diffusivity between successive points on the profile. The coefficients ranged from 0.8 to $6.7 \times 10^6 \mathrm{cm}^2/\mathrm{sec}$. If these values are correct, horizontal diffusion is a minor but significant factor in determining salinity distribution. It appears to be approximately one-quarter as important as advection in the central and western parts of the Sound and somewhat less in the Sound as a whole. Horizontal diffusion appears to be severely reduced in the eastern end by the presence of horizontal density gradients, despite the fact that tidal forces are strong in the eastern narrows. In this respect horizontal mixing differs from vertical mixing and nontidal currents, both of which are correlated with the tidal excursion.

INTRODUCTION

Previous studies of the physical oceanography of Long Island Sound (Riley, 1952, 1956, 1959) include descriptive accounts of morphometry and temperature and salinity distribution, a compilation of available current measurements, and preliminary estimates of transport exchange based on considerations of salt balance. The exchange computations in Riley (1952) were based on a minimal quantity of data, and the problem needs to be reopened now that more extensive observations have been obtained. The present analysis is based on a series of data collected between March 30, 1954 and November 9, 1955. Two-day cruises were made at intervals of two or three weeks, going alternately to the eastern and western ends of the Sound. Thus a few stations in the central basin had approximately biweekly coverage, and the remainder were visited at intervals of a month or slightly more.

A brief descriptive account of the temperature and salinity distribution was given in Riley (1959), together with information on cruise patterns. The present paper contains further descriptive details that bear upon problems of water exchange, and it uses the salinity data to compute exchange rates according to the salt balance method.

ACKNOWLEDGMENTS

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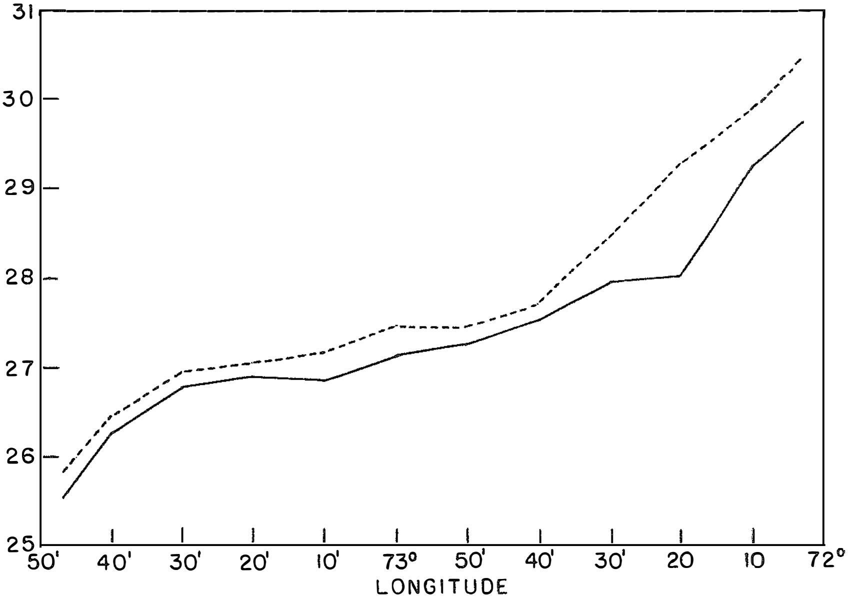

Figure 1. East-west gradients of salinity in Long Island Sound, at the surface (solid line) and bottom (dotted line). All 1954 and 1955 observations averaged by 10′ ranges of longitude.

QUALITATIVE ASPECTS OF MIXING AND TRANSPORT

Fig. 1 shows the salinity of surface and bottom water averaged for the whole period of the investigation. Marked freshening occurred at the western end of the Sound, which is connected by a narrow channel with harbor and river waters in the vicinity of New York City. The surface water was freshened by the outflow of the Connecticut and Housatonic Rivers, which have their outlets at Long. 72° 24′ W and 73° 04′ W, respectively. The higher salinity of the easternmost bottom water approaches that of the adjacent and more seaward waters of Block Island Sound.

The reason for the general form of the curves in Fig. 1 is not immediately obvious. Tidal currents are strong in the constricted eastern and western ends and relatively weak in the central basin. If horizontal mixing were a simple function of tidal speed, one would expect the salinity gradients to be weak in the ends of the Sound and stronger in the central part, the opposite of the observed situation. Part of the reason for this is suggested by the profiles of average density distribution shown in Figs. 2 and 3. A pattern of sloping isopycnals extending from surface to bottom is found throughout the year in the ends of the Sound. There is little horizontal layering except in the central area in summer. The vertical scale in the figures is, of course, greatly ex-

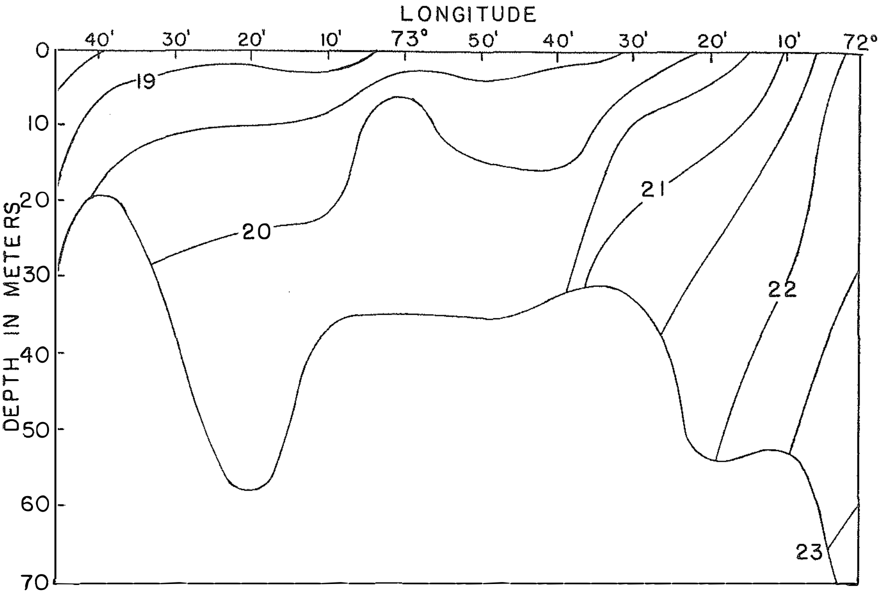

Figure 2. East-west profile of mean density distribution, May to July, 1954 and 1955.

aggerated, so that what appears to be a steeply sloping isopycnal surface may actually have a grade of only 5 m/km; nevertheless, the existence of this system probably has an important bearing on the character of the mixing processes. Mixing probably takes place most readily along the surfaces of equal density, and mixing normal to these surfaces will be reduced by stability of the water. In most oceanographic situations stability affects only vertical diffusion, but in the present case both the vertical and horizontal components are likely to be affected.

A transport pattern has been demonstrated (Riley, 1956) in which the surface water has a net movement eastward and out of the Sound and is replaced by a westward bottom flow of more saline water. These movements are readily demonstrated by current measurements, but this does not result in a simple two-layered system, as is evident in Figs. 2 and 3, which, as already mentioned, show little horizontal layering except in the central part of the Sound in summer.

In the eastern end of the Sound a given isopycnal will move several kilometers westward on the flood tide and will tend to penetrate farther along the bottom than at the surface. There is a tendency during the ebb for the upper part of the isopycnal to be carried farther toward the east. Thus the transport pattern would tend to transform sloping isopycnals into horizontal surfaces. The fact that this does not happen must mean that there is a close balance between the transport effect and certain opposing processes that tend to increase the slope

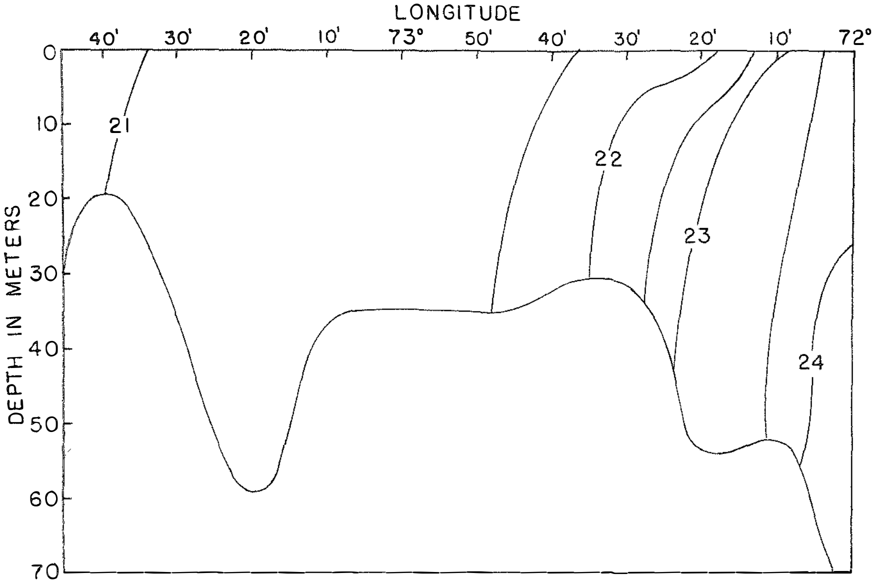

Figure 3. East-west profile of mean density distribution, October to March, 1954 and 1955.

of the isopycnals. One such process is, of course, vertical mixing, and another is vertical advection, whereby part of the water in the lower layer is continually lost by entrainment into the eastward-moving surface layer. The existence of this phenomenon is indirectly evident from current measurements, which show a decline in the mass transport of the lower layer as it moves westward and a corresponding increase in the eastward-moving surface layer.

The density structure in the central part is more indicative of a horizontal layering of water masses than is that in the eastern end, particularly in summer. The transport pattern is weaker, but the tides, which are presumed to be the cause of vertical turbulence, also are weaker. Stability due to surface warming in summer further reduces turbulent mixing, and a semblance of a true two-layered system is set up. Direct current measurements are insufficient to describe the transport in detail, and salinity observations suggest that the exchange may be quite variable. There are occasional rather sudden increases in the salinity of the bottom water, suggesting massive intrusions of saline water from the eastern end, flowing into the central basin and spreading westward along the bottom. These are commonly associated with westerly winds, and the implication is that an easterly wind drift in the surface layer is compensated by a westward inflow along the bottom.

As indicated earlier, seasonal warming does not have a very significant effect on the density structure in the eastern end of the Sound. Nevertheless, vertical salinity gradients are sometimes extreme. When the Connecticut River is in flood, a thin and stable surface layer of markedly reduced salinity extends from the mouth of the river to the eastern passes 9 to 12 miles away. Under these conditions of relatively slight vertical mixing, the bottom inflow of saline water appears to be reduced. It would seem that the relatively unmixed river water flows out by reason of its hydraulic head and does not enter into the development of transport exchange.

Thus the general pattern of exchange is modified in various ways by seasonal warming, by winds, and by freshwater drainage. These will be dealt with quantitatively in a later section as well as a quantitative analysis of the relations between advection and mixing processes in determining the general features of salinity distribution. However, this cannot be done without some ambiguity as to the meaning of the results, since there is no way to compute mixing coefficients in an entirely acceptable form in this kind of system. What has been done is to compute coefficients of vertical eddy conductivity by standard methods. Then, assuming that these numbers can be applied to diffusion problems, they are combined with data on advection and salinity distribution to determine the coefficients of horizontal eddy diffusivity required to bring the whole system into balance. This is a conventional approach except for the question of what the coefficients of vertical eddy conductivity really mean. There seems little doubt that they contain both vertical and horizontal components. With sloping isopycnals of the type described, part of the mixing could take place along isentropic surfaces. The results might therefore include both vertical conductivity in the conventional sense and an exchange between surface water at a given locus and bottom water some 10 to 15′ of longitude to the west. The results obtained, although ambiguous, have an important bearing on the general problem of processes which maintain the isopycnals in a sloping position. The balance is most readily maintained if the opposing processes are both essentially controlled by the same forces. The amount of transport depends primarily upon the tidal excursion. The amount of mixing presumably depends upon shearing stresses that also should bear a relation to tidal velocities and associated advective exchange. Fig. 4 shows that mean coefficients of "vertical" eddy conductivity are in fact related to the tidal excursion, which adds support to the concepts developed here.

EARLIER DATA ON TRANSPORT

Riley (1952) computed transport by two methods. One was a series of dynamic computations based on observations in the vicinity of the eastern passes. It was expected that the results, ranging from 7 to 20×10^3 m^3/sec for bottom inflow, would be maximal because of possible frictional retardation. Later calculations to be presented here are more or less in agreement. Transport also was computed from data then available on salinity and freshwater

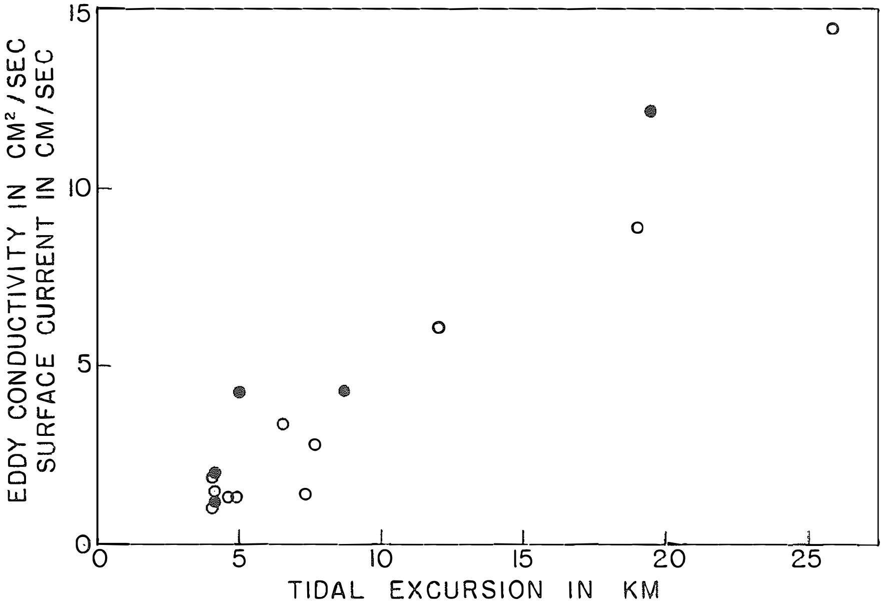

Figure 4. Relationship of coefficients of eddy conductivity (annual means), shown as dots, measured nontidal surface current shown as circles, and tidal excursion.

drainage. Results ranged from 3 to 12×10^3 m^3/sec, which seems slightly too small in the light of present information. Moreover, an earlier conclusion that transport exchange varies in proportion to freshwater drainage is not borne out in the present analysis.

Compilation of current measurements (Riley, 1956) indicated that the inflow at the bottom and the outflow at the surface were both of the order of 15 to 20×10^3 m^3/sec, and the transport in both layers gradually decreased westward. There is no reason to doubt the general validity of these results, although it has become apparent that transport is highly variable and cannot be fully described by averaging a few current measurements.

Data now at hand are suitable for a more definitive account of mean transport as determined by the salt balance technique. This requires compilation of freshwater drainage data for the period in question, and other analyses, already referred to, require computation of coefficients of vertical eddy conductivity. These matters will be taken up briefly before proceeding to the salt balance calculations.

FRESHWATER DRAINAGE

Three major drainage basins provide the Sound with fresh water. They are, in order of importance, the Connecticut River basin, with a drainage area of

11,250 square miles (statute), the Housatonic River basin (1,950 square miles), and the Thames River (1,470 square miles). Smaller rivers in Connecticut, the New York mainland, and on Long Island drain an area of 1,150 square miles. Thus the entire drainage area is 15,820 square miles, or about 13 times the area of Long Island Sound.

Nearly 80% of the river drainage enters the Sound near the eastern end and does not significantly affect the central and western parts. The eastern end therefore exhibits seasonal fluctuations in surface salinity, vertical salinity gradients, and runoff-induced transport to a much more marked degree than the remainder of the Sound.

Present estimates are based on data from the Water Supply Papers of the U. S. Geological Survey. These papers contain daily measurements of runoff from most of the larger rivers that drain into the Sound and give estimates of the areas drained. Figures for the total drainage area were obtained from the Connecticut Office of the U. S. Geological Survey.

The total drainage into the Sound was computed as follows: A. For each drainage basin, (1) flow rates for the large rivers draining directly into the Sound were obtained at the gauging station closest to the mouth; (2) contributions from tributaries entering the main stem below that station were added directly; (3) the area from which runoff under items (1) and (2) was obtained was subtracted from the total drainage area of the basin under consideration, and runoff from the remaining area was assumed to be similar in nature and magnitude to runoff from the areas of the gauged lower tributaries. B. In the entire area drained, 275 square miles were unaccounted for by adding the areas of all measured basins. This represents a coastal area containing streams too small to warrant examination by the U. S. Geological Survey. For purposes of computation this area was assumed to be distributed in a narrow strip along the coastline, and the assumptions made about its drainage were the same as in A3.

In order to facilitate treatment of the results in various types of additional calculations, both the north and south shores of the Sound were divided into ten segments, each 10′ of longitude in length, ranging from 72°05′W at the eastern end to 73°45′W at the western end. To compute the drainage into these segments, items A1 and A2 were added directly to the appropriate segments, and A3 and B were distributed evenly along the coastline. Errors in the original figures and in the assumptions have led to an uncertainty of about 7% in the results. Detailed results will be introduced later in connection with transport computations. These will consist of a summation of daily runoff for the periods between successive cruises in each of the 10′ segments. In addition, a few generalities are given here.

Table I lists runoff rates for the entire drainage basin averaged by seasons for most of a four-year period, of which the last two years are of particular interest in connection with the present survey. Mean annual rates were of the

TABLE I. TOTAL FRESHWATER DRAINAGE IN M³/SEC, SEASONAL AND ANNUAL MEANS.

	January –March	April –June	July– September	October– December	Annual Mean
1952..........	1,200	1,700	300	430	910
1953..........	1,620	1,450	180	470	920
1954..........	850	1,370	560	980	950
1955..........	870	1,130	750	–	–

order of 920 m^3/sec, corresponding to a total annual freshwater inflow of about 2.9×10^{10} m^3. This is about half the volume of the Sound between 72°05′ and 73°45′W. Because of the concentration of drainage in the eastern end, however, enough fresh water enters areas 1 and 2 (72°05–25′W) to replace their volume 2.5 times annually, while the remainder of the annual runoff is equivalent to only 12% of the Sound volume west of area 2.

Maximum runoff generally occurred during April and May, preceded by secondary peaks in December to February. In most of the data accumulated by the U. S. Geological Survey, minimum flow rates have occurred in early autumn, and the data shown here for 1952 and 1953 exemplify a typical seasonal variation. In 1954 drainage was low during the first six months but unusually high during the last six, so that the annual mean was normal. This pattern was repeated in more exaggerated form in 1955, in which spring runoff was extremely subnormal but was balanced later by floods accompanying hurricanes. Although the survey was conducted during a period that was not quite typical, sufficient variation was observed to get an adequate analysis of climatic effects.

VERTICAL EDDY CONDUCTIVITY

Temperature data obtained during the 1954 and 1955 cruises were used to compute coefficients of vertical eddy conductivity. The Sound was divided into five zones determined by longitude: Section I contained all stations from Long. 72°03′ to 72°25′W; Section II 72°25′ to 72°45′; thence by intervals of 20′ of longitude to Section V, which terminated in the western part of the Sound at 73°45′W. Each section included from three to seven stations which were occupied routinely on each cruise.

Average temperatures were determined for a series of depths for all stations in each zone. Differences in temperature from one depth to the next were also averaged. The method of averaging individual gradients was used in preference to obtaining gradients from the averaged temperatures at successive depths, because differences in the total depth of water at individual stations produced artificial irregularities in some of the average temperatures.

Coefficients of vertical eddy conductivity were then computed from the temperature change between successive cruises and from the average vertical

TABLE II. COEFFICIENTS OF VERTICAL EDDY CONDUCTIVITY IN AREAS I to V AS DEFINED IN THE TEXT. AVERAGE VALUES FOR THE PERIOD BETWEEN THE TWO DATES AT THE HEAD OF EACH COLUMN.

Area	Depth (m)	1 IV 27 IV 1954	27 IV 2 VI	2 VI 23 VII	23 VII 10 IX	18 XI 28 XII	28 XII 18 II 1955	25 III 22 IV	22 IV 27 V	27 V 24 VI	24 VI 29 VII	29 VII 2 IX	2 IX 13 X
I	2.5	9.1	3.0	1.3	0.51	70.	–	3.6	5.6	3.8	9.8	1.6	1.8
	5.0	5.5	2.7	1.4	0.43	42.	91.	5.2	12.5	6.4	9.7	2.4	3.8
	7.5	5.9	3.4	1.7	0.27	85.	31.	26.	14.6	6.4	9.3	3.1	5.0
	10.0	6.4	3.9	1.3	0.32	–	21.	–	20.	9.3	9.3	2.5	4.1
	12.5	7.2	4.2	1.2	0.40	91.	16.	–	16.5	6.4	7.8	2.6	4.7
	15.0	11.0	4.7		0.49	94.	19.	–	14.8	7.6	8.2	2.4	4.4
	20.0	22.	4.4		0.44	62.	16.	–	26.	14.	4.8	1.4	2.6
	25.0	34.	3.8		0.17	25.	11.	–			2.9	1.1	1.7
II	2.5	1.4	0.48	1.5	0.25	–	55.	1.3	3.2	1.8	2.1	0.11	3.6
	5.0	1.6	0.50	1.4	0.17	54.	–	1.4	1.2	0.95	1.9	0.07	2.4
	7.5	2.5	0.51	2.3	0.16	61.	–	1.8	0.89	0.70	2.0	0.10	3.0
	10.0	3.5		2.1	0.15	26.	22.	1.5	1.8	1.0	1.1	0.09	3.8
	12.5	4.0			0.10	8.0	11.	1.3	8.2	1.3	0.55	0.05	2.3
III	2.5	1.0	0.29	0.42	0.17	–	–	1.4	0.81	0.43	0.69		5.9
	5.0	0.68	0.32	0.40	0.14	–	–	1.4	0.44	0.16	0.23		2.7
	7.5	0.29	0.17	0.58	0.22	8.0	5.5	2.3	0.19	0.10	0.13		2.1
	10.0					4.0	7.4						1.4
		13 IV 11 V 1954	11 V 2 VII	2 VII 13 VIII		3 XII 21 I 1955	21 I 31 I	4 III 6 IV	6 IV 6 V	6 V 7 VI	7 VI 12 VII	12 VII 9 VIII	9 VIII 22 IX
IV	2.5	3.7	0.74	0.42		25.	20.	0.96	0.86	0.64	0.67	0.97	0.88
	5.0	1.2	0.51	0.29		11.	–	0.68	0.88	0.51	0.29	0.50	0.57
	7.5	0.74	0.50	0.29		2.6	7.5	0.97	0.93	0.39	0.15	0.31	0.37
	10.0	0.68	0.53			0.80	2.5	1.3	0.90	0.29	0.09	0.18	–
	12.5							1.0	0.54	0.23			
V	2.5	5.5	0.71	0.38		7.0	0.65	0.85	1.2	0.49	0.38	2.0	–
	5.0	2.3	0.51	0.35		4.5	0.25	0.77	1.1	0.34	0.19	0.62	0.05
	7.5	1.1	0.71	0.54		3.5	0.18	1.0	1.0	0.27	0.08	0.21	–
	10.0	0.72	0.50	0.36		3.7	0.25	1.8	1.0	0.34			–
	12.5					3.2	0.15	1.0	0.56	0.22			–

gradients, using methods described by Riley (1956). Results are shown in Table II. This material will be used later in transport calculations. Most of the results were usable for this purpose, although negative results indicated that convection rather than conductivity was mainly responsible for the vertical flux of heat at certain periods in autumn and winter. Such periods are indicated by dashes in Table II, since there is no point in including patently meaningless negative numbers. Seasonal variations were large, with minimum values in summer, as expected. Regional variations also were noted, with maximum coefficients in the eastern end of the Sound where tidal currents are strong. Mean annual values compiled from the table are related to tidal currents as illustrated in Fig. 4.

SALT BALANCE CALCULATIONS

Fig. 5 is a schematic diagram of salt balance. T is the bottom transport in m³/sec into the eastern end of the Sound, T' is a small and slightly significant net transport into the western end, F represents fresh water entering at many points. The sum of all these sources of water must equal the outflow. The salinity of the water is denoted by S_1, S_2, S_3, and the salt content per unit volume by $\rho_1 S_1$, etc. The sum of the products of transports and their salt content will determine the degree of salt balance. The rate of change of salt in the water mass as a whole may be indicated for convenience as an average

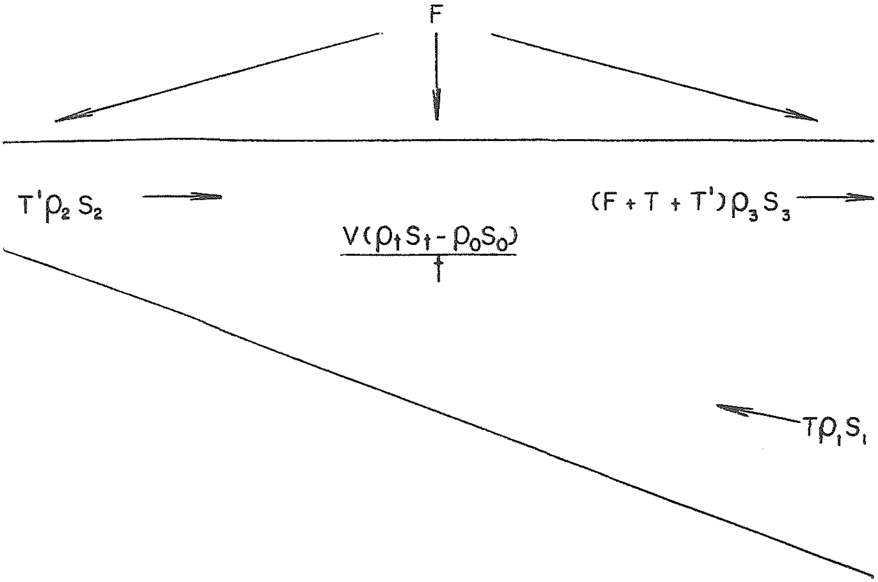

Figure 5. Schematic diagram of transport and salinity balance. For further explanation see text.

change between one cruise and the next. Thus $\varrho_0 S_0$ is the average salt per unit volume during any one cruise, and $\varrho_t S_t$ is the salt content during a second cruise t seconds later. This rate of change multiplied by the total volume of the Sound V gives the total change in salt content. Thus, the general equation for salt balance is

$$\frac{V(\varrho_t S_t - \varrho_0 S_0)}{t} = T\varrho_1 S_1 + T'\varrho_2 S_2 - (F + T + T')\,\varrho_3 S_3. \qquad (1)$$

Solving for T, which is of particular interest at the moment,

$$T = \frac{V(\varrho_t S_t - \varrho_0 S_0)}{t\,(\varrho_1 S_1 - \varrho_3 S_3)} + \frac{T'(\varrho_3 S_3 - \varrho_2 S_2) + F\varrho_3 S_3}{\varrho_1 S_1 - \varrho_3 S_3}. \qquad (2)$$

In applying this equation, F is the freshwater drainage previously referred to. Since there is an uncertainty of about 7 % in drainage computations, several second-order simplifications can be made without serious loss of accuracy. They are as follows:

(1) Rainfall on the surface of the Sound and evaporation are assumed to cancel each other, and hence are not included. Rainfall is about 12 % of freshwater drainage from the surrounding basin. Mean annual precipitation is about 115 cm. The total annual evaporation probably is very nearly the same. The seasonal cycles of rainfall and evaporation are slightly different, but correction for these differences is too small to warrant the effort.

(2) The transport T' into the Sound from the west was estimated by Riley (1956) to be about $1.1 \times 10^3\,\text{m}^3/\text{sec}$. This value, based upon direct current measurements, will be used throughout. There is no assurance that T' is in fact a constant, but no estimates of the degree of variation are available. The total T' is of the order of 2 to 14 % of later estimates of transport at the eastern end of the Sound, and its variations are assumed to be insignificant.

(3) Variations in density ϱ also are fairly small, particularly since the analysis compares successive cruises, thus minimizing seasonal temperature changes. The error is slight if a mean density $\bar{\varrho}$ is substituted into equation (2), taking the place of the individual ϱ's. When this is done, the $\bar{\varrho}$'s cancel, and numerically equivalent values are obtained by direct use of salinity differences.

(4) Finally, a factor that may not be entirely negligible is inherent in the scheme that has been outlined. This scheme assumes that advection is the only process significantly effecting interchange of salt. Horizontal salinity gradients are such that horizontal eddy diffusivity also will transfer salt into the Sound. If a significant part of the transfer is effected by eddy flux, the estimates of volume transport will be too large. Discussion of the magnitude of this error is relegated to a later section.

For purposes of computation, the main body of Sound waters was divided into ten areas by drawing arbitrary north-south lines at 10′ intervals of longitude, the same pattern of division as the one previously used in computing freshwater drainage. Area 1 extended from 72°05′ to 72°15′, and so on to area 10, which terminated at 73°45′W. Within each area an average vertical salinity curve was obtained for each cruise, and the salinity in successive intervals of 5 or 10m depth was multiplied by the planimetrically determined volume of water occupying each depth interval. All areas were then added together, and the final volumetric summation was used, in accordance with simplifying assumption (3), to determine the rate of change of salt content in equation (2).

There was a technical difficulty in that cruises covering areas 1–6 alternated with cruises in areas 6–10. Some sort of interpolation was necessary in order to estimate the salinity change in the whole Sound during a given interval. Fig. 6 shows a reasonable degree of agreement between the salinity in area 6 and the volumetric summation (VS) of salinities in areas 6 through 10. This can be expressed by the regression equation,

$$VS = (2.3 S_6 + 0.65)\, 10^8, \tag{3}$$

where S_6 is the mean salinity in area 6. Each determination of salt balance in the Sound as a whole will therefore be based on the computation of areas 1 through 5 plus an estimate of areas 6–10 derived by application of equation (3) to observed salinities in area 6. The ratio of observed VS (eastern half) to

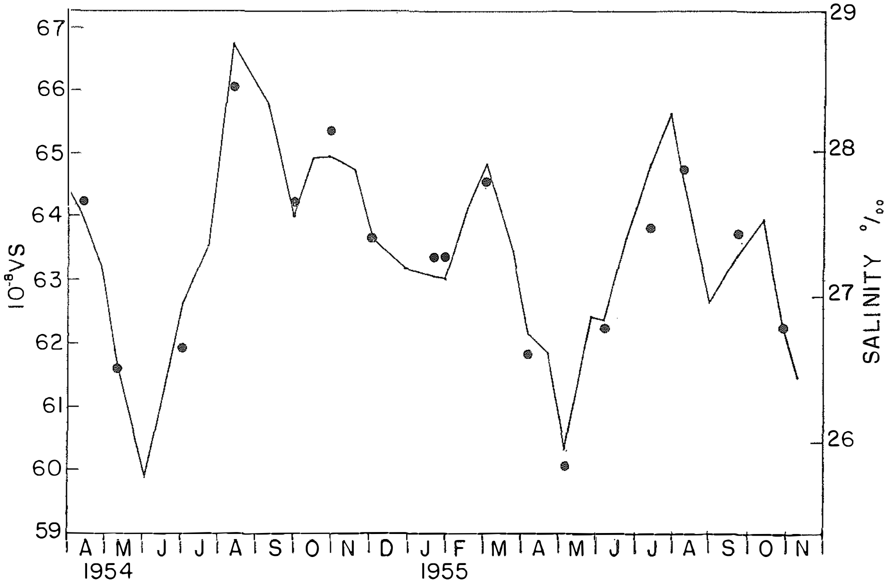

Figure 6. Average salinity in the central part of Long Island Sound (solid line) compared with total salt content in the western half (dots).

statistically interpolated VS (western half) is about 3:1, so that statistical error is minimized by the volumetric relations of the situation.

The evaluation of S_1, S_2, and S_3 presents further difficulties. There are sampling problems in that the average salinities observed on two successive cruises are hardly expected to be a faithful representation of the average value throughout the intervening period. The designation of a correct TS_1, TS_2, and TS_3 is also difficult since it implies some knowledge of vertical variations in transport velocity as well as in salinity distribution. Most observations suggest that the transports are strongest near the surface and bottom. Hence the analysis will utilize near-bottom salinities for S_1 and the 0–5 m stratum for S_3. Each value is an average, for both cruises, of areas 1 and 2 and a station in the Race, a pass just to the east of area 1. S_2 is derived from a single station just west of area 10.

As a sample calculation, data for the first two cruises are as follows:

March 30–April 1, 1954 $VS_0 = 16{,}600 \times 10^8$
April 26–27 $VS_t = 15{,}957 \times 10^8$
$t = 22.5 \times 10^5$ sec
Mean $S_1 = 30.43\,^0/_{00}$
„ $S_2 = 26.05\,^0/_{00}$
„ $S_3 = 28.33\,^0/_{00}$
$F = 1.75 \times 10^3\ \mathrm{m^3/sec}$

Applying the data to equation (2),

$$T = \frac{-643 \times 10^8}{22.5 \times 10^5 \times 2.01} + \frac{(1.1 \times 10^3 \times 2.28) + (1.75 \times 10^3 \times 28.33)}{2.01}$$

$$= 10^3\,(-14.1 + 1.2 + 24.7) = 11.8 \times 10^3\ \mathrm{m^3/sec}.$$

The results as a whole are shown in Fig. 7*A*. There is a seasonal trend of sorts, in which minimum values are obtained during the spring period of maximum drainage, and summer values tend to be large. However, there is always some doubt as to the validity of an analysis, such as the present one, that involves small differences between large numbers. Independent verification is needed, and perhaps the most satisfactory criterion is an examination of relationships with factors that might affect the transport T and thus control its seasonal cycle.

In examining these relationships, we first refer again briefly to the schematic diagram in Fig. 5, in which the net transport out of the Sound at the surface was defined as the sum of the freshwater drainage F, the inflow at the western end T', and the net bottom transport into the Sound at the eastern end T. In the sample calculation above, $T = 11.8 \times 10^3\ \mathrm{m^3/sec}$, and $F \times T' = 14.6 \times 10^3$. Thus the net transport into the Sound at the bottom is equal to 80 % of the surface outflow, and in most of the other computations it is also a large pro-

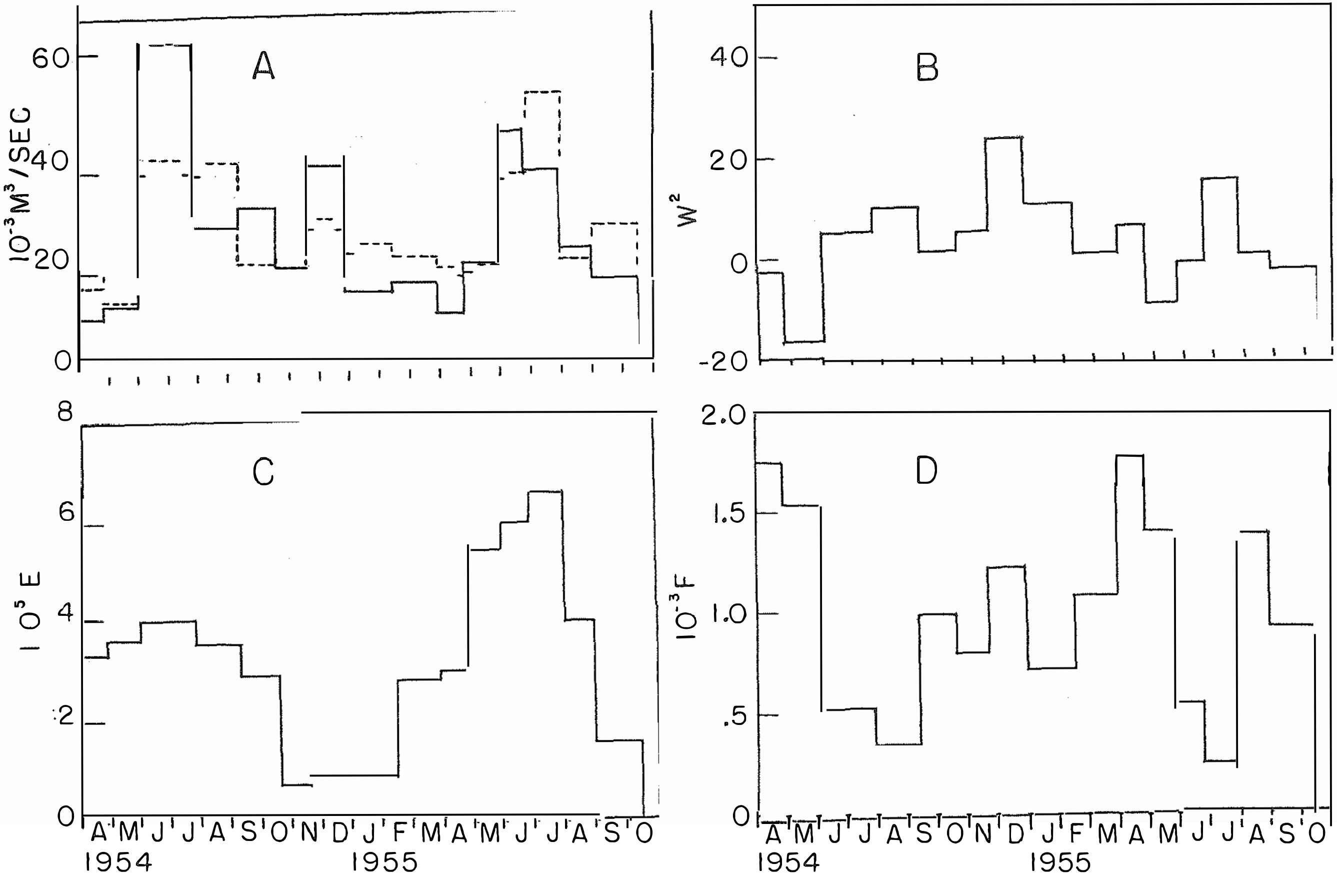

Figure 7. Computed transport and associated variables shown as average values between successive cruises. *A.* Solid line, transport computed from salt balance equation; dotted line, statistically derived values obtained from application of equation (5). *B.* Mean-squared wind speed; positive values, westerly component; negative ones, easterly component. *C.* Stability. *D.* Freshwater drainage in thousands of m³/sec.

portion of the total. To a large degree, the two transports vary together. From the earlier qualitative discussion, a physical inter-relation was also apparent in that surface outflow is augmented by gradual entrainment and removal of water from the inflowing bottom layer.

Dynamically, too, there appears to be a close inter-relation. The evidence for this will come out of further examination, but the inplication is that although certain processes operate primarily on the bottom layer and others on the surface layer, they have a similar effect in augmenting the volume transport of both layers. Thus, insofar as the two transports operate together in controlling salt balance, it is convenient to refer to the whole system as a transport exchange.

One factor that obviously operates on the surface layer is wind stress, but indirect effects on the bottom layer are readily observable. This was particularly apparent during an earlier period in the survey when observations were made at more frequent intervals than in later years. A two-year series of weekly observations was obtained in the central part of the Sound from March 1952 to March 1954. During each summer there was a rapid and irregular increase in the salinity of the bottom water following the usual spring minimum. This increase could be accounted for only by transport from the eastern end of the Sound, and the irregularity suggested discontinuous, or at least highly variable, movement.

The increase in salinity was slower in 1953 than in 1952. This provides an important clue in that the usual pattern of prevailing southwesterly winds was lacking in the summer of 1953, and easterly winds were more common from the first of July until mid-August. Vectorial weekly averages of wind speed and direction have been computed for the summer months of both years. Fig. 8 shows these averages, as well as the relationship between wind and changes in bottom salinity during the week in question. The graph leaves little doubt that westerly winds accelerate transport exchange, for logically the immediate effect of the wind is to increase the easterly movement of surface water out of the Sound, and the observed indraft of saline bottom water is an indirect effect.

There are no continuous current records available to document the character of the flow that has been suggested. Such current stations as have been made merely confirm the possibility of great variability in tidal movement and residual drift.

Density structure (Figs. 2 and 3) and salinity profiles (for example, see Riley, 1956, Fig. 11) suggest that horizontal layering by massive intrusions of saline water could be typical of much of the central and western basins in summer. However, there is no evidence of the existence of such phenomena in the eastern and western narrows where, as indicated earlier, the interrelationships between tidal currents and vertical mixing maintain the isopycnal surfaces in a permanently sloping condition. This implies that vertical mixing is insufficient to maintain the necessary balance of processes in the central and

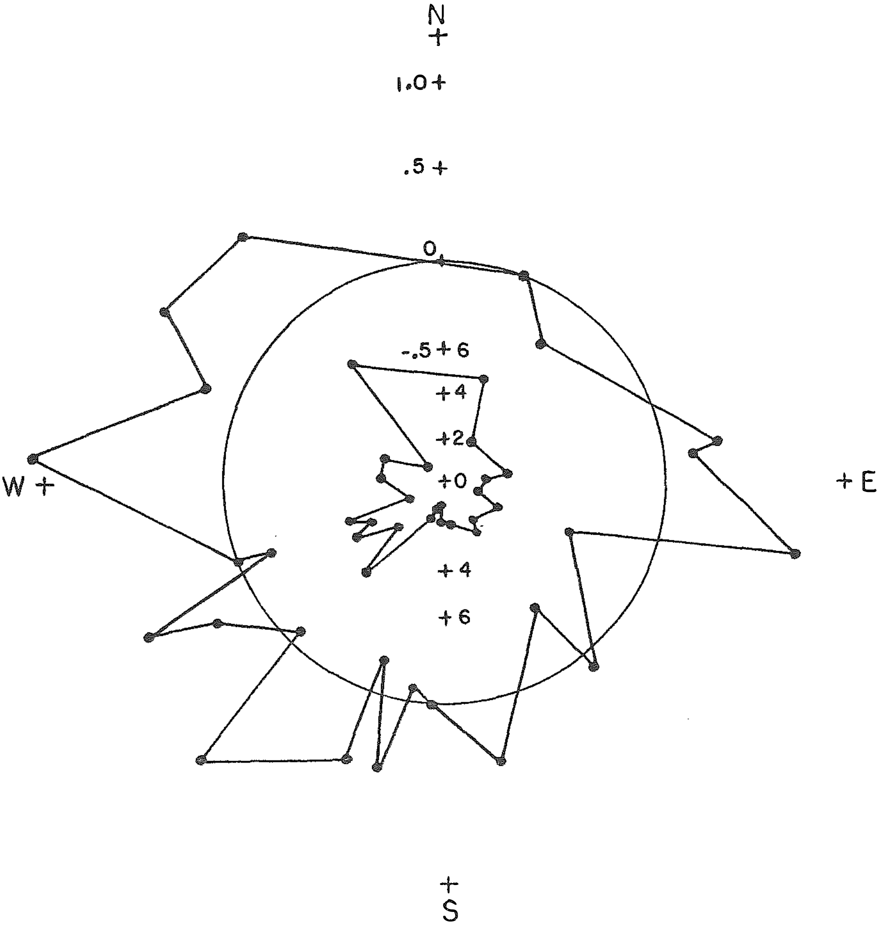

Figure 8. Wind versus salinity increase in the central part of Long Island Sound in late spring and summer of 1952 and 1953. Inner figure, vectorial weekly mean wind velocity in mph. Outer figure, weekly change in bottom salinity in relation to mean wind direction.

western basins in summer but is barely able to do so in winter. There is the further implication that weak tidal mixing in these basins is insufficient to prevent the development of thermal stability in summer to a degree that will have a critical effect on the transport pattern. Finally, the saline intrusion itself will increase vertical stability.

Clearly there is a complex array of phenomena involved, and there is no intention of dealing with the problem exhaustively here. Nevertheless, the relationship between transport and vertical stability will be examined statistically because intuitively horizontal layering should facilitate intrusion of saline water along the bottom.

Freshwater drainage also has a marked effect on vertical stability in the eastern end of the Sound, and transport computations here suggest an opposite relationship, namely that the transport of the bottom layer is reduced during periods of maximum freshwater drainage. This is a somewhat different kind of problem, however, in that excessive drainage produces a discontinuity layer of much greater stability than that associated with seasonal warming. Strange as it may seem, the stability is strong enough so that the situation approaches the one described by Cameron and Pritchard (1963) as a non-tidal model, in which salt water is entrained in the surface layer, but the latter is not mixed appreciably into the underlying water. The relationship of this kind of system with transport also will be examined statistically.

These various possible factors are shown in Fig. 7*B*, 7*C*, and 7*D*. The effect of wind stress is expressed as mean-squared wind speed and is reduced to east-west components during the periods between successive cruises. The westerly component is given as positive and the easterly one as negative. The stability E is approximated in each area according to the formula,

$$E = \frac{10^{-3}\,\Delta\sigma_t}{z}, \tag{4}$$

where $\Delta\sigma_t$ is the difference in density between surface and bottom, and z is the total depth of water in meters. The values so obtained were then averaged for areas 3 through 8, which constitute the main basins of the Sound where the hypothesis of a relationship between stability and transport particularly warrants examination. Data on total freshwater drainage are used to examine possible relations of this factor with transport, but as indicated earlier, most of the drainage is concentrated in the eastern end of the Sound, where the postulated relationship is believed to be particularly important.

The relationship of these factors with calculated transport T was then examined statistically. The multiple regression equation was

$$T = 42 \times 10^4 E + 0.79\,\overline{W^2} - 10.9\,F + 19.4, \tag{5}$$

where $\overline{W^2}$ is the mean-squared wind. The other symbols have already been defined. Fig. 7*A* compares transport as derived from this equation with the earlier computation. Although the number of observations is minimal for statistical purposes, the multiple correlation coefficient of .75 appears to be significant (P = ca. .001). The average of all observations is 26.4×10^3 m^3/sec, which is slightly more than the results obtained by direct current measurements.

Theoretically, the transport scheme that has been used here should be applicable not only to the Sound as a whole but also to the fraction lying west of any chosen longitude, provided the amount of freshwater dilution is known. The latter cannot be determined precisely, however, because there is no assurance that the only dilution is from rivers draining into the area. It is possible for a significant amount of fresh water to move in from the east on some occasions. As a case in point, it would be desirable to determine the transport exchange between the eastern narrows and the central basin. The analysis would comprise areas 3–10. The Connecticut River flows into the Sound just east of area 3; its waters have a generally eastward movement, but there is some flood tide flow into area 3, and occasional eddies of fresh water have been observed even farther west.

Two analyses were made of areas 3–10 on the basis of arbitrary assumptions, the first that half the outflow of the Connecticut River moves westward into the areas being analyzed and the second that there is no westward movement. The first assumption yielded an average transport value of 26.6×10^3 m^3/sec for the two-year period. This is almost certainly too large, for it equals the total calculated transport into the eastern passes. Results of the second analysis averaged 12.4×10^3 m^3/sec. This agrees closely with direct current measurements, but there are reasons for thinking that the correct value is somewhat larger. Aside from the observed fact that some Connecticut River water moves into the area, three negative results were obtained during periods of flood. This means that the postulated freshwater supply was insufficient to produce the observed reduction in salinity. In short, the two analyses serve only to set maximum and minimum limits for the rate of bottom transport into this area.

A further analysis has been made of the western half of the Sound (areas 6–10). The Connecticut River is 25 miles east of area 6, and no rivers of any consequence lie between. Hence an estimate of drainage does not present a critical problem. Both horizontal and vertical salinity differences, however, are smaller in the central part of the Sound than in the eastern narrows, so that sampling errors tend to be large. Since the observations now under consideration are less complete than those from the earlier program of weekly collections from 1952 to 1954, it is desirable to include these earlier observations in the analysis. There are two possible ways of utilizing them: (a) to compile an average seasonal pattern of vertical salinity differences ($S_1 - S_3$) and combine these averages with the 1954–55 data on drainage and rate of change of salinity in the western half of the Sound; (b) to utilize observed salinity differences and drainage for 1952–1955 and, accepting equation (3) as a suitable means for determining the rate of change of salinity in the western half of the Sound, calculate the transport for the whole period, and thus fill in the gaps in that part of the necessary information. Results obtained by methods (a) and (b) are presented in summary form in Table III. Item (c) is a computation based entirely on 1954–55 data. No serious discrepancies are indicated, but there is no high degree of agreement either.

Direct current measurements (Riley, 1956), mainly in spring and summer, indicated a net transport in the bottom layer of 2.3×10^3 m^3/sec at Long. 73°W, a considerably smaller figure than the calculated transport in the table. Two possible reasons can be given for the lack of agreement. The one having to do

TABLE III. Estimates of Average Bottom Transport T into Area 6 (Long. 72° 55′–73° 05′W) Based on Three Methods Described in the Text (Thousands of m^3/sec).

	(a)	(b)	(c)
Spring and summer	4.2	7.8	8.7
Annual mean	8.4	9.0	11.9

with horizontal eddy diffusivity will be discussed in the next section. The other is concerned with the apparently intermittent nature of the transport exchange. The variability of this exchange has been evident in all the analyses, and it seems likely that the influxes of bottom water may occur quite rapidly, for the 1952–53 survey showed some marked salinity increases between one week's sampling and the next. If these larger movements take place quickly and are soon finished, they would be observed less frequently than the weaker currents during a program of direct current measurements.

Transport into the western half of the Sound was examined with respect to the same group of environmental factors that was used in the earlier analysis of total transport. In view of the large sampling errors, it was desirable to use computation (b) described above, since 35 sets of data were obtained by it in contrast to 15 in the other two. The resulting equation,

$$T = 2 \times 10^4 E + 0.13\,\overline{W^2} - 23.0\,F + 12.0,$$

is similar in form to the one that was obtained in the study of transport into the Sound as a whole, although the relative importance of individual factors differs considerably. The stability relationship in particular is relatively insignificant. In conclusion, the statistical analysis does not invalidate hypotheses that transport exchange is accelerated by westerly winds and impeded by excessive freshwater drainage. The postulated effect of stability is significant in the overall analysis but is unimportant in the western half of the Sound. There seems to be little doubt that thermal stability facilitates the pouring of saline bottom water into the central basin in summer, but more general conclusions about stability effects are unwarranted.

CALCULATIONS OF HORIZONTAL EDDY DIFFUSIVITY

It was pointed out earlier that equation (1) is an oversimplification in that all exchange of salt is assumed to depend upon transport, and possible effects of horizontal eddy diffusivity are ignored. Salinity gradients are such that diffusion always tends to increase the amount of salt in the Sound; if this eddy flux of salt is significant, the advective flux via bottom transport will be overestimated. The present section will attempt to evaluate the relative importance of advection and diffusion in the Sound. Inevitably such calculations require simplification and arbitrary assumptions, but there will be various ways of checking the validity of the results.

A general equation for the rate of change of salinity S at any given point on an east-west profile of the Sound may be written

$$\frac{\delta S}{\delta t} = \frac{d}{dx} \cdot \frac{A_x}{\varrho} \cdot \frac{\delta S}{\delta x} + \frac{\delta}{\delta z} \cdot \frac{A_z}{\varrho} \cdot \frac{\delta S}{\delta z} - v_x \frac{\delta S}{\delta x} - v_z \frac{\delta S}{\delta z} - KS, \qquad (6)$$

where the horizontal and vertical axes of the profile are represented by x and z, respectively, and are directed eastward and down. Coefficients of horizontal and vertical eddy diffusivity are denoted by A_x and A_z, respectively; similarly the advective velocities are shown as v_x and v_z. K is a coefficient of dilution indicating the rate of addition of fresh water at any given point.

For convenience the Sound will be represented as a two-layered system shown in Fig. 9*A*. The division between the two layers is taken arbitrarily as the midpoint between surface and bottom. This does not deviate significantly from the depth of minimum net velocity. Current measurements indicate that the transition between the two layers occurs at about 10m in most of the central basin and increases to about 15m between Long. 72° 20′ and 72° 30′W. The situation in the extreme ends of the Sound is more problematical.

In this figure, a series of points is laid out at 10′ intervals of longitude and at the midpoints of the upper and lower strata. At each point it is assumed that the salinity exists in a steady state such that $\delta S/\delta t = 0$ in equation (6). It is further assumed that freshwater drainage is mixed uniformly into the upper layer at the point where each river enters the Sound. Thus K values for the upper layer can be calculated from drainage data and the volume of Sound water in the area in question; in the lower layer $K = 0$.

Although the Sound seldom exists in a steady state condition, an average observed over a considerable period may be treated as a steady state problem. The average salinity of surface and bottom waters previously shown in Fig. 1 can then be fitted into the pattern of local concentrations in Fig. 9*A*, and mean drainage data during the same period be used to determine dilution coefficients.

At each point in the pattern, the salinity is assumed to be uniform in the upper half of the upper layer and in the lower half of the lower layer. Thus any gradient that exists is between the two points, as illustrated in Fig. 9*B*.

Bottom currents are derived from measured values (Riley, 1956, Fig. 10). Surface currents are obtained by adding bottom transport, the average freshwater drainage, and an estimated $1.1 \times 10^3 \text{m}^3/\text{sec}$ of water coming into the western end and moving east. To convert total transport to current velocity, it is assumed that half of the cross-sectional area of the Sound at any given point is occupied by each transport system. This is of course a drastic over-

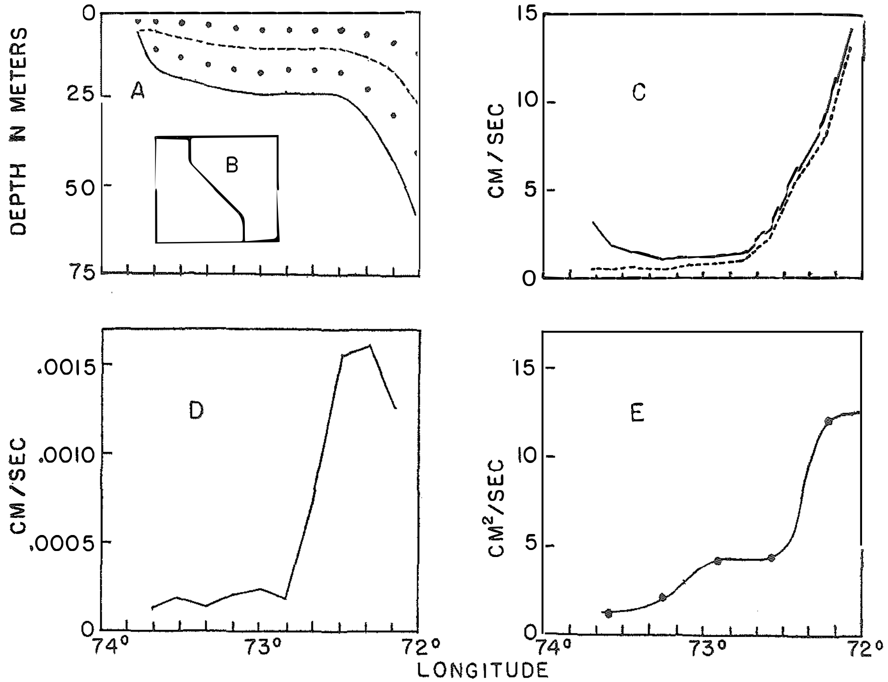

Figure 9. *A*. Diagram of profile for computation of horizontal eddy diffusivity. For explanation see text. *B*. Postulated form of vertical salinity gradient. *C*. Mean eastward current in the surface layer (solid line) and westward current in the bottom layer (dotted line). *D*. Estimated rate of upwelling. *E*. Average coefficients of vertical eddy conductivity.

simplification of the true velocity profile. Mean current estimates so obtained are shown in Fig. 9*C*.

The westward decrease in transport and current velocity must be accompanied by upwelling in order to preserve continuity of mass. The average rate of upwelling is readily determined from the decrease in transport from one point to the next and the area of the Sound between successive points. Calculated values are given in Fig. 9*D*. Fig. 9*E* shows average coefficients of vertical eddy conductivity from an earlier part of the paper. It will be assumed that these data and interpolated values taken from the smooth curve can be used to represent vertical eddy diffusivity. As indicated earlier, this is not entirely justified. If the computed coefficients contain both vertical and horizontal components, due to mixing along sloping isopycnal surfaces, this is a perversion of the usual meaning of the equation. A_x will be a true A_z plus a certain proportion of A_x which represents the horizontal component of mixing along surfaces of equal density. The A_x calculated from the equation will be the remaining horizontal component, and this is essentially mixing across the density surfaces. The first type is a free movement in the sense that there are no density barriers, but the slope of the surfaces limits the range of the movement to a few miles. The second type probably is inhibited by density barriers in the same way that vertical stability reduces vertical diffusion, but it is the only possible means for extensive horizontal turbulent interchange.

Rewriting equation (6) in finite difference form, with due regard for simplifications and boundary conditions that have been postulated, the equation for a point in the surface layer is

$$\frac{A_x(S_x - S_0)}{\varrho x^2} - \frac{A_{-x}(S_0 - S_{-x})}{\varrho x^2} + \frac{A_z(S_z - S_0)}{\varrho z^2} - \frac{v_x(S_x - S_{-x})}{2x} - \frac{v_z(S_z - S_0)}{z} - KS_0 = 0, \quad (7)$$

where S_0 is the salinity at any given point; S_x and S_{-x} represent the salinity at adjacent points x distance to the east and west, respectively; and S_z is the salinity in the bottom layer. A_x, v_x, etc., are average eddy coefficients and current velocities, respectively, for the intervening distances. An analogous equation can be written for the bottom layer.

Numerical values can be assigned to all terms in equation (7) except A_x and A_{-x}. A final simplifying assumption is introduced at this point, which may or may not be correct but seems reasonable in the light of the previous discussion. Since qualitatively it appears that horizontal eddy diffusivity, or at least that part of it so designated in the present analysis, is reduced by horizontal density barriers, it is postulated that within the limits of density variation found in the Sound,

$$A_x = \frac{C}{\Delta_x \sigma_t},$$

where C is a constant, and $\Delta_x \sigma_t$ is the change in density from one point in the pattern to the next (see Fig. 10). The first two terms in equation (7) can then be written

$$C\left[\frac{S_x - S_0}{\varrho \Delta_x \sigma_t x^2} - \frac{S_0 - S_{-x}}{\varrho \Delta_{-x} \sigma_t x^2}\right],$$

and C can be solved by a least squares fit, combining equations for all points in both layers. It is found that $C = 6.12 \times 10^5$. Computed values for A_x are shown in Fig. 10.

The results do not have a high degree of statistical validity (P = ca. .1), but the most likely alternative assumption, namely a constant A_x, gives much worse results.

Other considerations need to be introduced in order to decide whether the results are internally consistent. This will in a sense be the same sort of analysis and will use the same data, but it will combine data in such a way as to reduce sampling errors to a minimum.

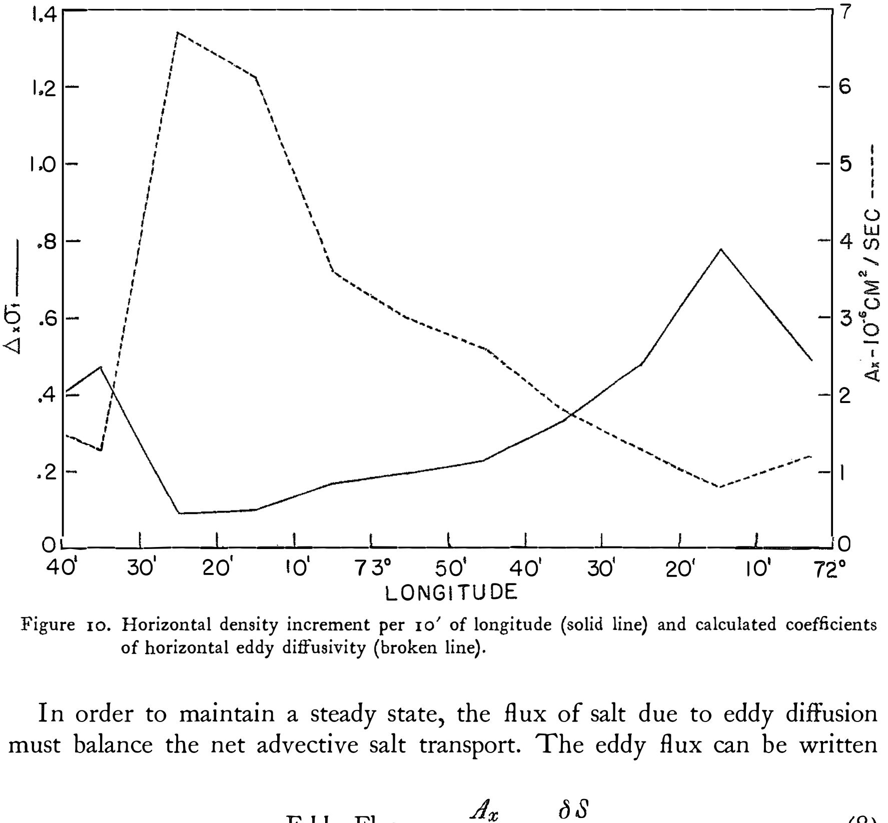

Figure 10. Horizontal density increment per 10′ of longitude (solid line) and calculated coefficients of horizontal eddy diffusivity (broken line).

In order to maintain a steady state, the flux of salt due to eddy diffusion must balance the net advective salt transport. The eddy flux can be written

$$\text{Eddy Flux} = -\frac{A_x}{-\varrho} \cdot yz \cdot \frac{\delta S}{\delta x}, \qquad (8)$$

where yz is the cross-sectional area of the Sound at any given point, and the other terms are as previously defined. In the western half of the Sound,

$$\text{Eddy Flux} = -3 \times 10^6 \cdot 4.8 \times 10^9 \cdot \frac{0.32 \times 10^{-3}}{28 \times 10^5} = -16.5 \times 10^5 \text{ g/sec.}$$

The negative sign indicates a westward flux that must be balanced by a net eastward transfer of salt by advective processes. A transport balance sheet will be prepared. It utilizes mean salinities and freshwater drainage data averaged for the period of the investigation, a generalized value of 1.02 for ϱ, a figure for bottom transport into the western half of the Sound that is derived from direct current measurements, and a similarly derived estimate of surface transport into the Sound at the western end. The balance sheet obtained is as follows:

$$\begin{array}{llllll}
(T) & 2.3\times10^3\,\mathrm{m^3/sec} & \times1.02\times27.44\,^0/_{00} & \times10^3 & = & 644\times10^5\ \mathrm{g\ salt/sec.} \\
(T') & 1.1\times10^3 & \times1.02\times25.57 & \times10^3 & = & 287\times10^5. \\
(T+T'+F) & -3.44\times10^3 & \times1.02\times27.11 & \times10^3 & = & -951\times10^5. \\
 & & & \text{Net loss} & = & 20\times10^5\ \mathrm{g/sec.}
\end{array}$$

The net advective loss of salt from the western half of the Sound is nearly in balance with the calculated gain by diffusion, the difference being only about 20 $^0/_0$. In the Sound as a whole, a similar computation leads to an estimated gain by eddy diffusion of 65×10^5 g/sec and a net loss by transport of 87×10^5. Again the eddy coefficients are slightly too small for perfect balance; however, if the coefficients were as large in the eastern end as the maximum value in the central basin, the eddy flux would be more than 400×10^5 g/sec. This result supports the earlier postulate that horizontal eddy diffusivity, or at least that component under consideration here, is reduced in the presence of horizontal density gradients.

Although the average effect of transport must be a net removal of salt from the Sound, there must be many times when this is not so. It is pertinent in this connection to consider observed changes in total salt content in relation to possible shifts in this balance. In the western half of the Sound, the total salt content is about 640×10^{12} g. The estimated mean eddy flux of salt into this area would be equivalent, in a month's time, to 0.67 $^0/_0$ of the total salt content, or a salinity increase of about 0.18 $^0/_{00}$. During periods in spring and summer when freshwater drainage was minimal and salinity was increasing, the average increase between cruises was 0.78 $^0/_{00}$, or roughly four times the mean eddy flux. Probably this is due primarily to transport rather than an increase in diffusion, although this is by no means certain. Tentatively one might suppose that advective transfer might be three or four times as important as diffusion in this area. In the Sound as a whole, with a total salt content of about 16×10^{14}g, the estimated eddy flux at the eastern end could produce a monthly increase in salinity of 0.11 $^0/_{00}$. Thus the importance of eddy diffusion in the Sound as a whole is somewhat less than in the western half.

DISCUSSION

Pritchard (1952) postulated that horizontal eddy diffusivity is relatively insignificant in estuaries. Other investigators studying the flushing rates of estuaries (Ketchum, 1954, and other papers by the same author; Barlow, 1955) have tended to deal with total exchange by salt balance methods without attempting to distinguish between advection and diffusion. Much of their work, however, contained an implicit assumption that eddy diffusivity was negligible, because otherwise it would not have been valid for them to apply results based on salt balance to other variables that have quite different horizontal gradients. In the present case, eddy diffusion is less important than advection but is not negligible, particularly in the consideration of nutrient distribution (Harris, 1959). If the hypothesis is correct that horizontal eddy diffusion is inversely proportional to horizontal density differences, categorical statements should not be made about the relative importance of turbulence without considering the density structure. Some of the bays and estuaries described by the authors cited have strong density gradients, and their treatment of the problem probably was valid. However, the matter needs to be examined in a wider variety of circumstances.

In the present case, the treatment of seasonal variations in transport by the salt balance method was oversimplified, because effects of horizontal eddy diffusivity are too large to be ignored. The discrepancy between calculated transport and measured currents is expected to be largest in the western half of the Sound. The difference between the results of salt balance computations (Table III) and observed currents has been discussed, and the question arises as to whether the discrepancy can be resolved by proper consideration of diffusion effects. The original transport equation is readily modified to include a term for eddy flux by combining equations (2) and (8). Extensive application of such an equation would not be justified, because knowledge is lacking about possible seasonal variations in eddy diffusivity. Calculations have been made on a mean annual basis, however, using values for eddy diffusivity from Fig. 10. In the Sound as a whole, the recalculated advection (bottom transport T) averaged $24.6 \times 10^3\,m^3/sec$, a relatively insignificant reduction from the previously estimated mean transport of 26.4×10^3. In the western half, there was a distinct reduction of the annual mean from 8.4 to $3.5 \times 10^3\,m^3/sec$. The latter figure is only slightly larger than the estimated bottom transport into the western half of the Sound derived from measured currents ($2.3 \times 10^3\,m^3/sec$ at Long. 73° W). There is no great discrepancy between the two kinds of transport computations when proper allowance is made for diffusion effects.

Present results agree in order of magnitude with previous estimates of both advection and diffusion in Long Island Sound, but in several respects there are modifications of earlier points of view. The relationship of horizontal turbulent mixing and density structure was not suspected, and the effects of wind on transport had not been analyzed. There is one direct contradiction in that the earlier analysis (Riley, 1952) suggested an increase in transport exchange during periods of excessive freshwater drainage, while present work indicates the opposite. The earlier conclusion, based on minimal data and a severely simplified method of calculating salt balance, is withdrawn.

REFERENCES

BARLOW, J. P.

1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. Biol. Bull., Woods Hole, *109*: 211–225.

CAMERON, W. M., and D. W. PRITCHARD

1963. Estuaries. *In* The Sea. M. N. Hill *et al.*, Eds. Interscience Publ., New York, *2*: 306–324.

HARRIS, EUGENE

1959. The nitrogen cycle in Long Island Sound. Bull. Bingham oceanogr. Coll., *17* (1): 31–65.

KETCHUM, B. H.

1954. Relation between circulation and planktonic populations in estuaries. Ecology, *35*: 191–200.

PRITCHARD, D. W.

1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. J. Mar. Res., *11*: 106–123.

RILEY, G. A.

1952. Hydrography of the Long Island and Block Island Sounds. Bull. Bingham oceanogr. Coll., *13* (3): 5–39.

1956. Oceanography of Long Island Sound, 1952–1954. II. Physical oceanography. Bull. Bingham oceanogr. Coll., *15*: 15–46.

1959. Oceanography of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *17* (1): 9–30.

A Drift Bottle Study in Long Island Sound

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ABSTRACT

During a period of 13 months, 746 bottles were set adrift from a station in the western third of Long Island Sound. Recoveries totaled 47 °/₀. Data on direction and speed of drift are discussed with respect to the effects of wind and nontidal circulation. Results indicate that transient currents set up by winds are more important than tidal effects in determining surface water movements.

INTRODUCTION

This study constitutes the first serious attempt to examine surface currents in Long Island Sound on a year-round basis. The only other drift bottle experiments in the area were conducted during a limited period in early autumn by Prytherch (1929). Previous studies of tidal currents and residual drift were based largely on summer measurements by LeLacheur and Sammons (1932) and Riley (1952, 1956).

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[1] The first author began this study as a project for a junior high school science fair and continued the releases and tabulation of results for a year longer. The second author, who is now at the Institute of Oceanography, Dalhousie University, Halifax, is largely responsible for the preparation of the paper.

The drift bottle study began in March 1959 and continued until early April 1960. The number liberated during any one month ranged from about 45 to 90, except in August 1959 when there were no releases. Bottles were put out along the Connecticut shore at points that varied slightly from time to time but in general were between Long. 73°16′ and 73°18′ W.

METHODS

Large-mouth, screw-cap bottles were ballasted with dry sand so that they floated nearly awash. A stamped, self-addressed postcard inserted in each explained the project and asked for the position and date of recovery. The bottles were thrown into the water from the beach during ebb tide, so that the current tended to carry them offshore, thus minimizing immediate beaching. Ordinarily two to five bottles, occasionally as many as seven, were released at a time, and this was done 15 or 20 times each month.

RESULTS

Out of 746 bottles released, 349 recoveries were reported by June 1960. Four replies were discarded because their information appeared to be a hoax, while a few others failed to give complete information. Also, as is common in drift bottle work, the elapsed time between release and recovery was occasionally so long that the results had little meaning. More than 90% of the recoveries, however, were usable in the data analyses.

Fig. 1 is a chart of Long Island Sound showing the number of bottles found on specified segments of the shore line. In addition to those illustrated, two landings were reported outside the Sound: one recovery was made at Westport, Massachusetts, well to the eastward, and one at New York, just west of the narrows at the extreme left of the chart. Fig. 1 also shows the limits of tidal excursion near the point of release and the calculated residual tidal drift as determined by Riley (1952) from tidal data published by the U.S. Coast and Geodetic Survey.

Slightly more than half the landings occurred within a few miles of the launching site. The next largest group was found on the Long Island shore southeast of the point of release, and altogether about 100 were concentrated along the Long Island coast between 72°50′ and 73°30′ W. Smaller numbers were found east of 72°50′, and Table I, which lists returns by months, shows that these all occurred between January and June. About an equal number landed in the western narrows beyond 73°30′ W. The eastern Connecticut shore was very sparsely represented.

Table I shows a slight seasonal variation in the percentage of recoveries,

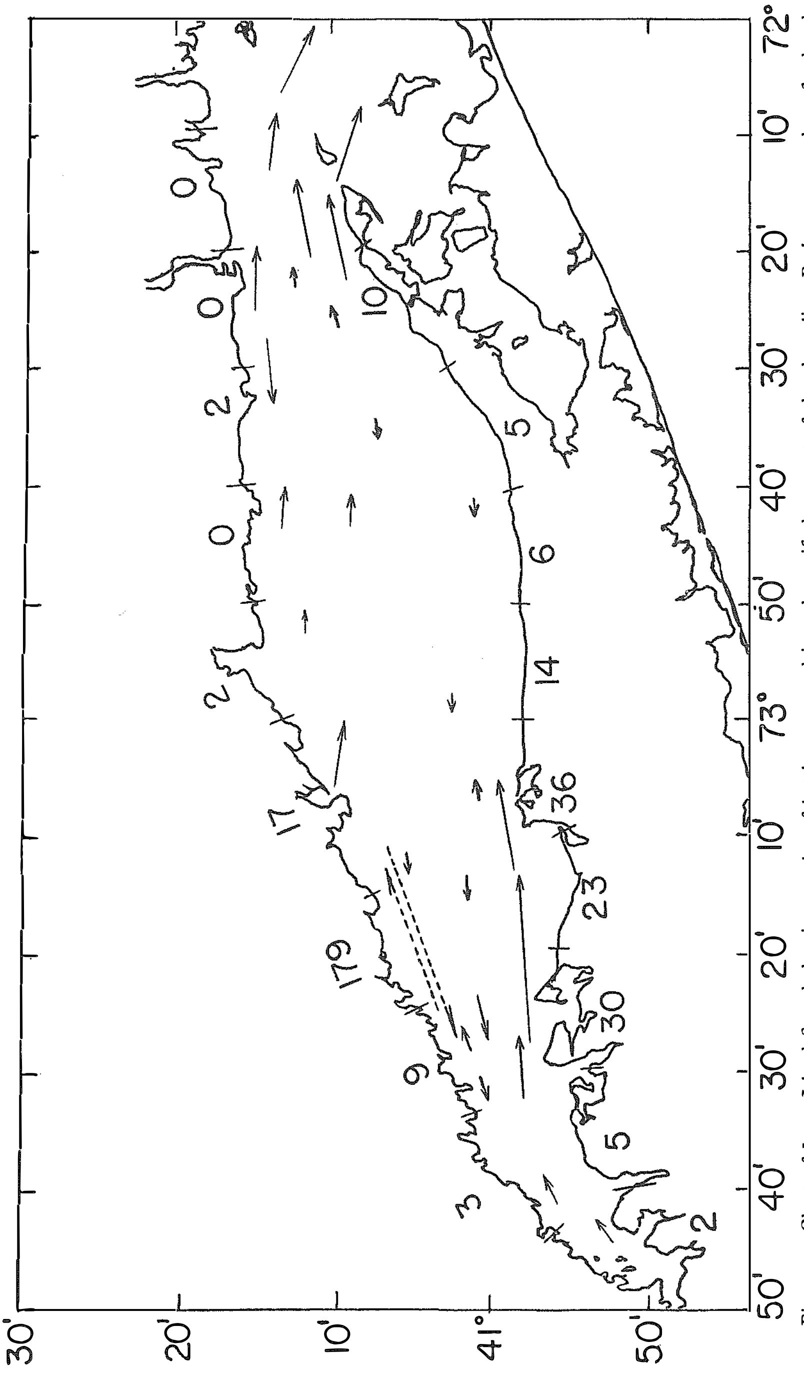

Figure 1. Chart of Long Island Sound showing number of bottles recovered in each specified segment of the shore line. Broken arrows show flood and ebb tide excursions near the point of release of the bottles. Solid arrows indicate residual tidal drift in various parts of the Sound.

TABLE I. MONTHLY RECORD OF DRIFT BOTTLE RECOVERIES FROM THE SEGMENTS OF SHORE LINE OF LONG ISLAND SOUND. DATA FOR MARCH AND APRIL INCLUDE BOTH 1959 AND 1960.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Long Island shore:												
East of 72° 20′	–	–	–	–	1	–	–	–	–	–	–	–
20′–30′	1	2	4	2	1	–	–	–	–	–	–	–
30′–40′	2	–	1	2	–	–	–	–	–	–	–	–
40′–50′	–	–	1	1	1	3	–	–	–	–	–	–
50′–00′	8	2	–	1	–	1	–	–	–	1	–	1
73° 00′–10′	6	8	15	1	–	1	–	–	–	2	2	1
10′–20′	3	–	9	–	–	3	–	–	4	–	–	4
20′–30′	2	–	7	1	–	–	–	–	6	–	10	4
30′–40′	–	–	2	1	–	–	–	–	–	–	–	2
40′–50′	1	–	–	–	–	–	–	–	–	–	–	1
50′+	–	–	1	–	–	–	–	–	–	–	–	–
New York-Connecticut shore:												
72° 30′–40′	–	–	1	–	–	–	–	–	–	1	–	–
40′–50′	–	–	–	–	–	–	–	–	–	–	–	–
50′–00′	–	–	–	–	–	1	–	–	–	–	1	–
73° 00′–15′	–	1	1	2	5	2	4	–	–	–	1	1
15′–25′	6	8	31	18	25	21	19	–	19	16	10	6
25′–35′	–	1	2	1	–	1	–	–	–	2	1	1
35′–45′	–	–	2	–	–	1	–	–	–	–	–	–
Total recoveries	28	22	72	32	36	35	21	–	31	24	26	22
Releases	67	63	132	69	72	63	45	–	68	55	55	57
% Recovery	42	35	55	46	50	56	47	–	46	44	47	39

TABLE II. TOTAL NUMBER OF RECOVERIES FROM AREAS SPECIFIED, MINIMUM RECOVERY TIME IN DAYS IN EACH GROUP, AND THE MEDIAN TIME IN GROUPS CONSISTING OF THREE OR MORE BOTTLES.

	Total No. Recoveries	Median Time	Minimum Time
Long Island shore:			
East of 72°20′	1	–	43
20′–30′	10	8	6
30′–40′	5	13	5
40′–50′	6	8	3
50′–00′	14	6	3
73°00′–10′	36	7	2
10′–20′	23	5	2
20′–30′	30	7	1
30′–40′	5	11	4
40′–50′	2	–	8
50′+	1	–	4
New York-Connecticut shore:			
72°30′–40′	2	–	11
40′–50′	–	–	–
50′–00′	2	–	7
73°00′–15′	17	7	2
15′–25′	179	2	1
25′–35′	9	8	2
35′–45′	3	72	7

but this probably means only that there are fewer people on the beaches in winter and more breakage due to winter storms. Many of the recoveries were made by children, and the slightness of seasonal variation suggests that they frequented the beaches in considerable numbers at all seasons. This impression is strengthened by Table II, in which the minimum and median arrival times seem relatively short, even in areas such as the eastern Long Island shore, where most of the bottles were found in winter.

DISCUSSION

Certain aspects of drift bottle distribution were clearly in accord with present data on residual transport. One would expect few bottles in the western part of the Sound, where Fig. 1 indicates a net transport eastward. The movement of water southeastward from the Connecticut and Thames Rivers could be expected to fend off landings on the eastern Connecticut shore. The seasonal distribution of recoveries on eastern Long Island is also credible, although supporting evidence is anecdotal. Available current measurements in the central part of the Sound, mostly taken in summer, show little consistency in current patterns; but in winter and spring, during periods of maximum drainage, grass has commonly been observed floating southeastward from the Housatonic River well toward the Long Island shore. This movement of river water logically could lead to an eastward current along Long Island, which would carry drift bottles farther than they would be likely to go in seasons of minimum drainage.

Residual drift, however, cannot entirely explain the results. Recorded rates of drift of the bottles commonly were of the order of 10–20 cm/sec, which exceeded most of the residual tidal movements calculated. Yet it is obvious that drift bottles give minimal estimates of current speed, since they make no allowance for the time the bottles may have lain on the beach before discovery or for the possibility that they may have taken a devious route from the point of release to the point of recovery.

An alternative possibility is that winds significantly affect the drift. Examination of individual records shows that several bottles liberated on the same or succeeding days were likely to be recovered in close proximity, and that the direction of movement appeared to be correlated with the wind. As a preliminary analysis, all cases of two or more nearby landings were examined with respect to the apparent direction of movement (a straight line between points of release and capture) and the vectorial average of wind speed and direction during the time afloat. Fig. 2 is a graph of 82 sets of landings plotted against average wind direction. The correlation is obvious, and the coefficient of .81 is highly significant ($P = <.001$).

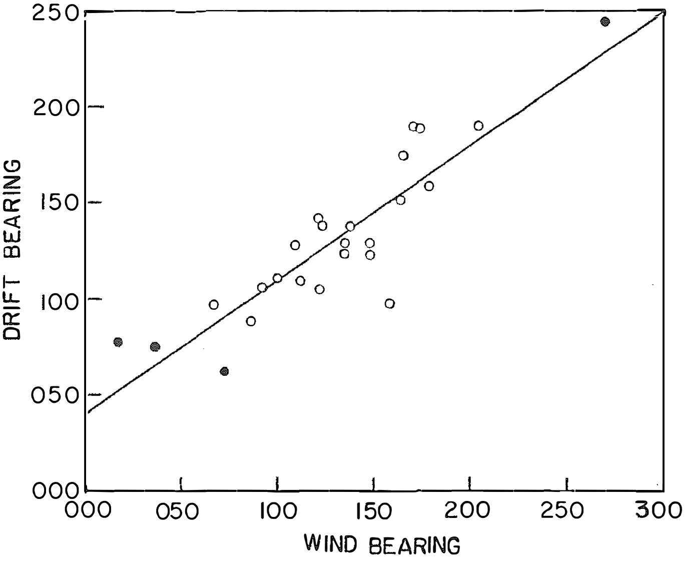

Figure 2. Mean direction of drift bottle movement in relation to wind direction plotted as the direction in which the wind is moving. Circles are recoveries from the south shore; dots, north shore. Each point is a mean of 2–8 observations, as explained in text.

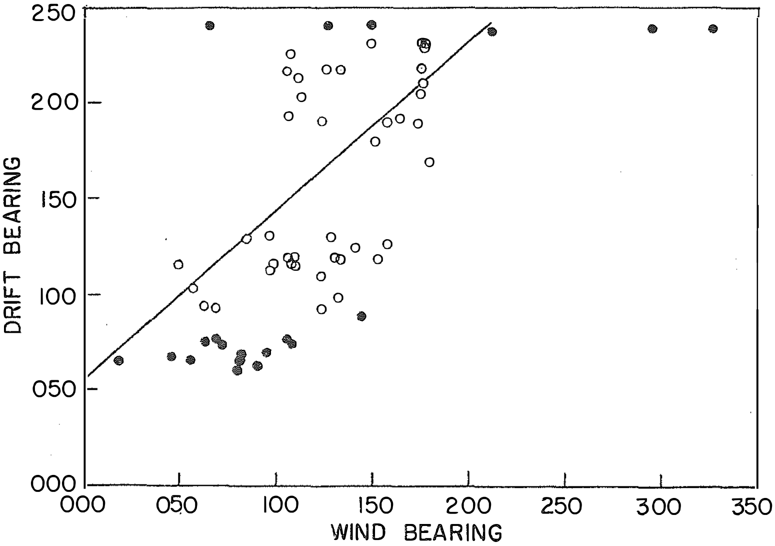

Figure 3. Further studies of bottle drift vs. wind direction. Circles are recoveries from the south shore; dots, north shore. These are single observations rather than combinations of two or more concordant results as shown in Figure 2.

Subsequently all other observations were analyzed (totaling 41 for drift toward the south shore), with results that are shown in Fig. 3. The correlation here is only .56, but this is still significant ($P = <.001$).

Landings along the north shore are included in the figures but not in the correlations. The Connecticut shore line in this area is oriented roughly northeast and southwest, and the apparent drift of bottles found here necessarily conformed to the trend of the shore line. Hence a precise analysis of wind and drift directions would be spurious and would be quite a different situation from the study of bottles which had been exposed to a long fetch in their journey from northern to southern shores. Qualitatively, however, northeast movement along the north shore was associated with west winds, and with a few exceptions, southwest movement occurred during periods when the prevailing wind was from the east.

Hypothetically, three factors are involved in the correlation of wind and bottle movements: (a) wind drift of the surface layer, which theoretically will be to the right of the wind because of Coriolis force but will be subject to modification due to the geometry of a relatively enclosed system, (b) downwind wave transport, (c) downwind leeway produced by wind stress on exposed parts of the bottle. These three components cannot be accurately separated, (b) and (c) in particular being virtually indistinguishable. It is pertinent first to inquire whether the movement was significantly to the right of the wind, because this would demonstrate the importance of wind drift and at the same time

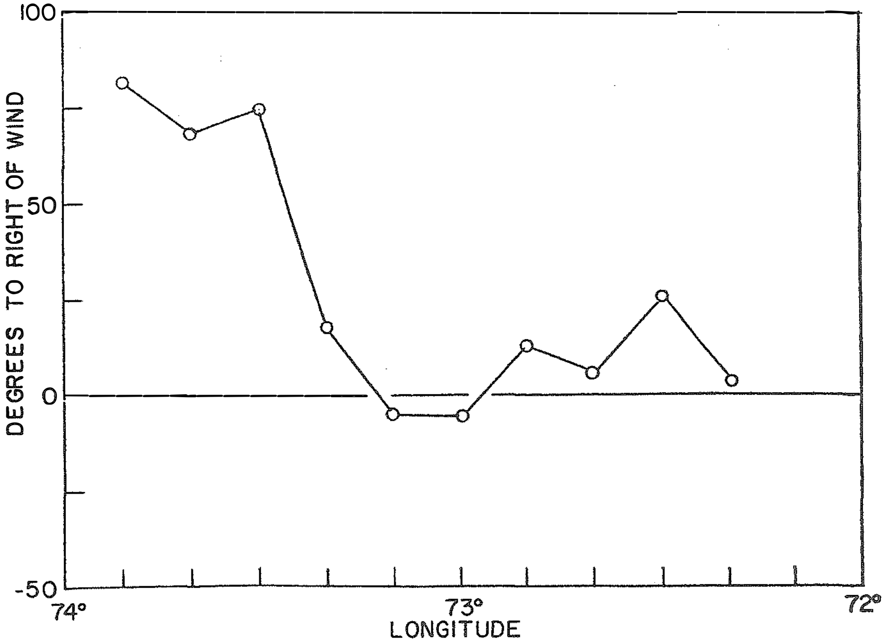

Figure 4. Bearing of bottle drift minus wind bearing (deviation to right of wind), averaged by 10′ segments of longitude along the Long Island shore.

would suggest that leeway was not important enough to invalidate the use of drift bottles in describing water movements. However, the answer to this question is not altogether simple. Fig. 4 shows the deviation of south shore landings averaged by longitude. Bottles that went west had a larger deviation than those drifting east, and there was a reversal in the middle section. This prevents precise analysis but is not unexpected. North and northeast winds would tend to drive water across the Sound and set up a westward moving current along the barrier introduced by the Long Island shore, provided the wind drift were sufficient to overcome a tendency toward eastward residual drift in this area. Westward moving currents here would increase the apparent deviation to the right of the wind of any bottles that were carried an appreciable distance in such a current. Conversely, west winds would produce an eastward current along the shore that would reduce the apparent deviation. Between Long. 73°00′ and 73°10′ W, where the reversal occurs, the effect of wind-driven currents is augmented by a residual tidal drift which averages about 12 cm/sec to the east (Riley, 1956).

These considerations lead to the conclusion that the drift bottles conform to the expected pattern of wind-driven currents and that leeway, although possibly introducing a significant error, is not important enough to mask this pattern.

The question of whether leeway significantly affects the speed of drift can be examined in another way. For this purpose, only the bottles previously illustrated in Fig. 2 were considered, because their case histories indicated that they had traveled by reasonably direct routes and had not lain for a long time on the beach. Mean rates of drift were calculated from the elapsed time and the distance in a straight line between points of release and recovery. Results are plotted in Fig. 5 against the mean vectorial wind speed during the same period. The effect of wind on drift currents, as derived from estimates in the U. S. Coast and Geodetic Survey Tidal Current Tables, is drawn as a smooth curve. Although the points are scattered widely, they fall in approximately equal numbers on each side of the curve and give no impression of systematic differences that could be ascribed to excessive leeway.

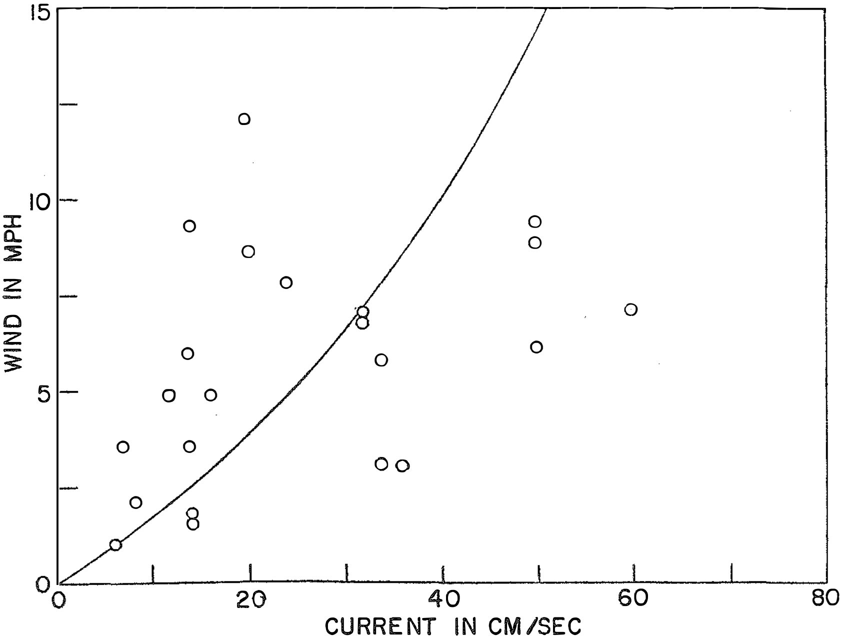

Figure 5. Mean speed of bottle drift in relation to mean vectorial wind speed. Smooth curve represents average relation between wind and surface current as given in U. S. Coast and Geodetic Survey Current Tables.

Finally, with regard to observed seasonal variations, the transport of bottles to the eastern end of Long Island in winter and spring is believed to be caused both by the predominance of strong west winds during this period and by a change in the transport pattern that is associated with increased drainage. In summer, when south and southwest winds predominate, a majority of the landings were on the Connecticut shore. In short, wind appears to be the most important factor in determining surface water movements in Long Island Sound, although residual tidal drift also exerts an influence.

REFERENCES

LELACHEUR, E. A. and J. C. SAMMONS

1932. Tides and currents in Long Island and Block Island Sounds. Spec. Publ. U. S. Coast Geod. Surv., *174*: 1–184.

PRYTHERCH, H.F.

1929. Investigation of the physical conditions controlling spawning of oysters and the occurrence, distribution, and setting of oyster larvae in Milford Harbor, Connecticut. Bull. U. S. Bur. Fish., *44*: 429–503.

RILEY, G. A.

1952. Hydrography of the Long Island and Block Island Sounds. Bull. Bingham oceanogr. Coll., *13* (3): 5–39.

1956. Oceanography of Long Island Sound, 1952–1954. II. Physical oceanography. Bull. Bingham oceanogr. Coll., *15*: 15–46.

Mathematical Model of Nutrient Conditions in Coastal Waters

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ABSTRACT

A mathematical model is developed to illustrate the distribution of nitrate and phosphate in coastal waters. The model depends on the existence of a deep water source of nutrients at the edge of the continental shelf and determines nutrient distribution in relation to horizontal and vertical mixing and biological rates of regeneration and utilization. It is shown to be applicable to the coastal region off southern New England with respect to nutrient concentrations, N:P ratios, and productivity levels. General conclusions are that the usual pattern of exchange betweeen inshore and offshore waters tends to enrich the coastal zone irrespective of enrichment by freshwater drainage, and that nitrate is more likely to be a limiting factor than phosphate, because of its inherently slower rate of regeneration.

INTRODUCTION

Coastal waters generally are more productive than the open sea. Two factors are believed to be responsible, in varying degrees according to local circumstances. The first is shoreward transport, from the edge of the continental shelf, of deep and nutrient rich water, which then becomes available to surface phytoplankton populations in the inshore waters as a result of tidal vertical mixing. The other is enrichment by freshwater drainage.

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Ketchum and Keen (1955) have analyzed salt balance in the coastal waters from Cape Cod to Chesapeake Bay. The annual river flow into this area is less than 1 % of the volume of sea water within the area considered. This drainage obviously must be mixed with a much larger volume of offshore water in order to produce the observed salinity of the coastal region. Analyses that are available (for example, Riley, 1959) indicate that the nutrient content of river water is not markedly higher and at times is much lower than that of deep, offshore water. Freshwater drainage, therefore, is believed to be a minor and almost insignificant source of enrichment in this region except in local and semi-enclosed areas such as Narragansett Bay and Long Island Sound. In the Sound, despite its limited exchange with outside waters and abundant freshwater supply, enrichment from oceanic waters appears to be about equal to that derived from drainage (Harris, 1959).

Ryther and Yentsch (1958) have shown that the New England coastal waters of 25 to 50m depth have an annual phytoplankton production of about 160 g C/m^2. Production declines in a seaward direction, the average estimates being 135 g C/m^2 in the depth range of 50 to 1,000m and 100g between 1,000 and 2,000m. Although these differences are slight, they support a concept to be developed here, namely that inshore waters can support a moderately high level of productivity even though enrichment by drainage is relatively insignificant.

The deep water at the edge of the continental shelf commonly contains 15 to 24 μg-at NO_3-N/l and 1.0 to 1.5 μg-at P/l, with an N:P ratio of about 15:1. In much of the coastal area the ratio is lower than this. As an extreme example it is about 8:1 in Long Island Sound at the time of the midwinter nutrient maximum (Riley and Conover, 1956), and in summer it is likely to be as little as 2:1, even when nitrate, nitrite, and ammonia are all included in the ratio (Harris, 1959). Maximum phosphate levels inshore are equal to or greater than those in deep water offshore; the alteration in the ratio is due to a decrease in nitrogen. In Long Island Sound and probably most of the coastal area, nitrogen is a more limiting factor than phosphate, as might be expected when the N:P ratio in the water is so much lower than that of normal phytoplankton.

Riley (1959) found that the phosphate content of river drainage generally was equal to or less than that of Sound waters, whereas nitrate usually was higher. Thus the anomaly in the N:P ratio is not associated with drainage but must be inherent in the oceanic system. Anomalously low N:P ratios have been noted in certain other situations. Harvey (1945) and Riley (1951) have postulated that the nitrogen cycle operates more slowly than that of the phosphate, requiring a longer time for nitrogen to be returned to the water in soluble form after utilization by phytoplankton. In the present case this would mean that as nutrients move shoreward and are recycled enroute, more nitrogen than phosphorus will remain behind in a bound condition. The situation in

Long Island Sound would then be merely an exaggerated expression of a phenomenon that is common to the whole coastal region, and the latter should be treated as a unit in any quantitative analysis of nutrient problems.

The present paper will examine these hypotheses from a theoretical point of view. A simple mathematical model of coastal circulation will be postulated, and this will be used to examine the nutrient situation and to determine whether simple hypotheses stated in quantitative terms will lead to a realistic distribution of nutrients.

THE PHYSICAL MODEL

Imagine a hypothetical series of stations at 25 km intervals, crossing the shelf at right angles to the coast. Station 1 is in shallow water near shore, and Station 6, 125 km distant, is at the edge of the shelf. These stations are reference points which will be used to compute nutrient concentrations along a transcoastal profile by means of equations written in finite difference form.

The profile will be simplified to a two-layered system of surface and bottom water in which mixing between layers is limited, but mixing within layers is rapid enough to maintain a vertically uniform concentration of nutrients within each layer. The amount of mixing between layers is postulated to decrease in a seaward direction, amounting to 10% interchange of water per day between the two layers at Station 1, 5% at Station 2, 2% at Station 3, and 1% at the remainder. This conforms qualitatively to the concept of increased tidal mixing near shore and is of the right order of magnitude as indicated by computed eddy coefficients.

Probably there is a net seaward advection in the surface layer and a corresponding movement toward shore in the bottom layer. There is also an exchange by horizontal diffusion. Ketchum and Keen (1955) simplified the problem in their treatment of coastal salinity balance by calculating the flushing rate in terms of diffusion alone. Their method will be continued here. Computed values for the coefficient of horizontal eddy diffusivity ranged from 0.58 to $4.96 \times 10^6 \text{cm}^2/\text{sec}$. In round numbers, a 2% horizontal interchange per day between successive stations will be equivalent to an eddy coefficient of $2.9 \times 10^6 \text{cm}^2/\text{sec}$, which is near the mean of computed values.

The general equation for this type of distribution can be written

$$\frac{\delta N}{\delta t} = R + \frac{\delta}{\delta x} \cdot \frac{A_x}{\varrho} \cdot \frac{\delta N}{\delta x} + \frac{\delta}{\delta z} \cdot \frac{A_z}{\varrho} \cdot \frac{\delta N}{\delta z}, \tag{1}$$

in which the local time rate of change of a nutrient N is determined by a biological rate of change R and exchanges by eddy diffusion along the x (horizontal) and z (vertical) axes of the profile. Simple methods of analyzing this type of problem have been described by Steele (1958). Under the conditions stipulated above, the equation for the surface layer at Station 2, for example, can be written

$$\frac{\delta N}{\delta t} = R + .02\,N_1 + .02\,N_3 + .05\,N_2' - .09\,N_2, \tag{2}$$

where N_1, N_2, N_3 are nutrient concentrations in the surface layer at Stations 1, 2 or 3, and N_2' is the concentration in the lower layer at Station 2.

Further assumptions are that the whole system exists in a steady state and that the rate of production of the phytoplankton is controlled by the nutrient concentration. During the spring and summer, when the coastal water is in a quasi-steady state, the quantity of nutrients present in the surface layer at any one time is commonly sufficient for three or four days growth. There is, however, a certain amount of regeneration in the surface layer by zooplankton and bacterial activity, so that the net daily utilization is likely to be of the order of 10% of the concentration of a limiting nutrient. In the present example $R = -.10N_2$, and under these conditions equation (2) reduces to

$$.02\,N_1 + .02\,N_3 + .05\,N_2' - .19\,N_2 = 0. \tag{3}$$

If the biological system is in perfect balance, the net production of the surface layer will be removed to the lower layer, and its nutrient content will be regenerated in the lower part of the water column or on the bottom as rapidly as it is utilized in the surface layer. Hence an equation can be written for the lower layer at Station 2 that is analogous to equation (3) but includes the effect of regeneration. It is

$$.02\,N_1' + .02\,N_3' + .15\,N_2 - .09\,N_2' = 0, \tag{4}$$

where N_1', N_2', N_3' are nutrient concentrations in the lower layer at Stations 1, 2, and 3.

Similar equations may be written for Stations 3 to 5. Station 1 requires the boundary condition that there is no further horizontal exchange in the landward direction. At Station 6 the bottom layer is arbitrarily assigned a nutrient value typical of deep water at the edge of the shelf. A sufficient boundary condition for the surface layer at this station is to assume that the nutrient concentration is constant in a seaward direction. A simultaneous solution then may be obtained with the series of inter-related equations for all of the designated points on the profile, using an appropriate method such as that given by Southwell (1946).

CALCULATED RESULTS

Results are shown in the uppermost of the families of curves in Fig. 1 *A* and and 1 *B*, which are labeled 100 to signify a true biological balance in which regeneration is 100 % of utilization. The deepwater nutrient concentration at the edge of the shelf is designated arbitrarily as 100 %, and the remainder of the curves illustrates relative values in other parts of the profile. The gradient in the bottom water insures movement of nutrients, by diffusion, from the edge of the shelf toward shore. Despite the decrease in nutrients in the lower layer near shore, the concentration in the surface layer is maintained at a fairly high level because of increased vertical exchange. Biological productivity is therefore maintained at a higher level. This kind of distribution is often seen in coastal waters, and suggests that the distribution is due wholly or in part

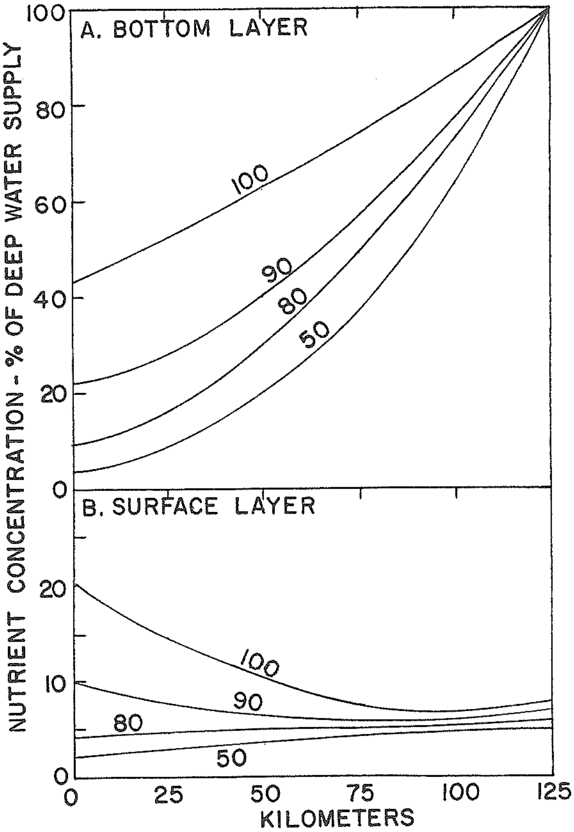

Figure 1. Nutrient gradients along a coastal water profile, arbitrarily rated on a percentage scale relative to the deepwater concentration at the edge of the continental shelf. Calculations are based on equations (3) and (4). The families of curves show gradients that result when regeneration in the bottom layer is variously rated from 50 to 100 % of nutrient utilization in the surface layer. Abscissas represent distance from shore in kilometers.

to enrichment by drainage, but the model shows that an offshore nutrient source plus increased vertical mixing near shore will provide a satisfactory explanation.

It is doubtful whether conditions in nature ever entirely conform to the perfect biological balance postulated above. During the quasi-steady state of the spring and summer season, the total concentration of nutrient elements in the water column, inorganic and combined, is less than that observed at the time of the midwinter maximum, suggesting that some portion of the nutrients which are sedimented on the bottom in combined, particulate form are unavailable for further utilization until after the end of the spring-summer growing season, or that there is a lag between utilization and regeneration which keeps a fraction of the nutrient stock out of circulation at all times.

This situation is readily presented in a model by postulating that regeneration in the bottom layer is some stipulated fraction of utilization in the surface layer, and by altering the coefficient of N_2 in equation (4) accordingly. The curves in Fig. 1 show nutrient concentrations that result when regeneration in bottom waters is varied between 50 and 100% of surface utilization. It is apparent now that biological cycling of nutrients during their transport into the coastal zone will affect the form of the curves and the overall level of productivity. If any considerable part of the nutrients is removed from circulation, there will be that much less available for enrichment of the inshore waters.

Nitrogen concentrations commonly are low and relatively uniform in the New England coastal zone in summer, corresponding to a regeneration rate of about 80% of utilization as pictured in Fig. 1 *B*. Phosphate tends to be higher near shore. This implies a higher regeneration rate for phosphate, which is in accord with the earlier hypothesis that phosphorus is cycled more rapidly than nitrogen.

A final model will investigate N:P relations in somewhat more detail. First it will be assumed that the nitrogen regeneration rate is 80% of utilization and that the source of supply at the edge of the shelf has a concentration of 15 μg-at N/l. The concentration at all stations then can be determined immediately from the relative curves in Fig. 1. It is further postulated (a) that the deepwater phosphate concentration is 1 μg-at P/l, (b) that it is utilized by phytoplankton in a ratio of 1 atom of P to 15 atoms of N, and (c) that its regeneration rate is 100% of utilization. Intuitively it is recognized that the phosphate concentration will be relatively high compared with nitrogen. Hence postulate (b) has the effect of setting nitrogen as the limiting factor, and the coefficient of phosphate utilization will be $0.10N/15$, where N is the concentration of nitrogen in the surface water at any given station. Main features of the results, shown in Fig. 2, are a shoreward increase in surface phosphate and an accompanying decrease in the N:P ratio to a minimum value of 2.2:1. Also the vertical gradient in phosphate is relatively slight, so that the surface concentration at Station 1 is 87 % of the bottom concentration, as compared with 61 % in the case of nitrogen. All of these characteristics are commonly observed in coastal waters in summer.

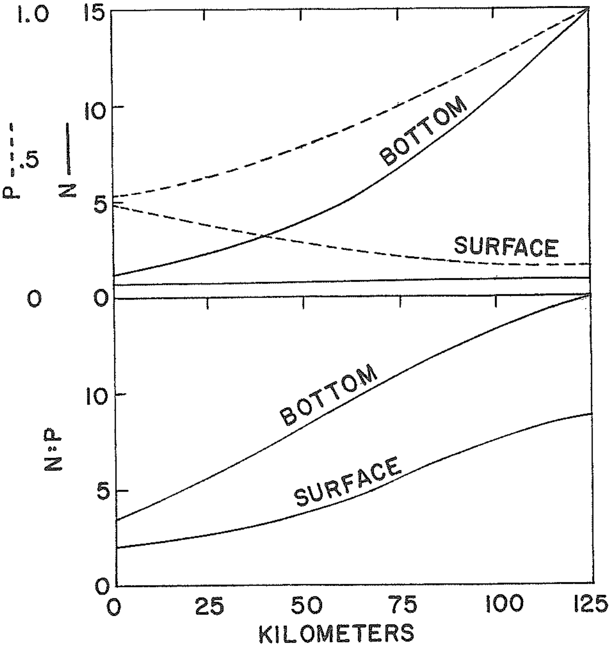

Figure 2. Relationship between soluble nitrogen and phosphorus in a coastal water profile in which nitrogen, with a regeneration rate set at 80% of utilization, is a limiting factor, and phosphate regeneration is postulated to equal utilization. Abscissas represent distance from shore in kilometers.

DISCUSSION

In the particular model that has been postulated, there is little difference in productivity between inshore and offshore waters. A slightly higher rate of nitrogen regeneration would be sufficient to establish a clear-cut gradient. Observations by Ryther and Yentsch (1958), however, show no indication of a pronounced gradient in either nitrate or productivity during the summer season, and the situation that has been postulated seems realistic as far as present knowledge goes.

The slightly higher annual productivity of the inshore waters observed by these authors was mainly the result of higher production levels during the period from December to April. A steady state model is inapplicable to this period, but the summer model has a bearing on autumn and winter nutrient conditions that should be discussed briefly.

The model illustrated in Fig. 2 requires, at the station nearest the coast, a daily removal of 0.14 μg-at N/l from the surface layer in excess of the amount regenerated. This would total 25 μg-at/l during a six-month growing season. Post season return of some or all of this nitrogen to the water column in soluble form would lead to a high concentration in the inshore waters in winter. This is indeed a typical situation in the New England coastal area, where the nitrate concentration reaches a high level, and the N:P ratio increases in winter.

Some of the nitrate undoubtedly is lost from the coastal zone by horizontal eddy diffusion in winter when the concentration exceeds that offshore. This is a slow process, however, as indicated by the work of Ketchum and Keen (1955) on diffusion of freshwater drainage. Thus a large quantity of nutrients remains inshore at the time of the diatom flowering in late winter or spring, leading to a higher level of production than that found in offshore waters.

The model allows for no post-season phosphate regeneration and in this respect is an oversimplification. Observations show an increase in phosphate in summer, as might be expected from the model, and a further increase in autumn which indicates that phosphate regeneration is not 100% as postulated. But the autumn increase in phosphate progresses more slowly than the increase in nitrate so that the N:P ratio gradually rises.

The aim here has been a limited one, namely, to achieve a realistic although admittedly simplified model of nutrient conditions in New England coastal waters. Similar models could be developed to fit other situations, the main variables being the width of the continental shelf, the magnitude of diffusion processes, and the relative importance of freshwater drainage. These variations would be expected to have considerable effect on details of areal distribution and seasonal change, but they probably would not alter the general features that have been described. Most coastal waters are richer than the open sea, and most of them show evidence that nitrogen is the most important limiting factor. The model provides a simple explanation of these features.

The basic hypothesis that nitrogen is cycled more slowly than phosphorus finds some support in experimental work on rates of bacterial decomposition, although the subject has not been documented as thoroughly as might be desired. The main evidence is of an indirect nature; no other way can be found to explain the observed distribution of these elements, and the model bolsters the hypothesis by showing that a quantitative formulation of the hypothesis leads to realistic results.

REFERENCES

HARRIS, EUGENE

1959. The nitrogen cycle in Long Island Sound. Bull. Bingham oceanogr. Coll., *17* (1): 31–65.

HARVEY, H. W.

1945. Recent advances in the chemistry and biology of sea water. Cambridge Univ. Press, 164 pp.

KETCHUM, B. H. and D. J. KEEN
1955. The accumulation of river water over the continental shelf between Cape Cod and Chesapeake Bay. Deep-Sea Res., *3* (suppl.): 346–357.

RILEY, G. A.
1951. Oxygen, phosphate, and nitrate in the Atlantic Ocean. Bull. Bingham oceanogr. Coll., *13* (1): 1–126.
1959. Oceanography of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *17* (1): 9–30.

RILEY, G. A. and S. M. CONOVER
1956. Oceanography of Long Island Sound, 1952–1954. III. Chemical oceanography. Bull. Bingham oceanogr. Coll., *15*: 47–61.

RYTHER, J. H. and C. S. YENTSCH
1958. Primary production of continental shelf waters off New York. Limnol. & Oceanogr., *3*: 327–335.

SOUTHWELL, R. V.
1946. Relaxation methods in theoretical physics. Oxford Univ. Press, 248 pp.

STEELE, J. H.
1958. Plant production in the northern North Sea. Mar. Res. [Scotland] *1958* (7): 36 pp.

Microbiological Studies in Long Island Sound[1]

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ABSTRACT

Seasonal studies of the number of bacteria in Long Island Sound surface waters by plate count methods varied from 1300 to 15,300/ml with a mean of 8370. This exceeded by an order of magnitude the number of phytoplankton cells and organic aggregates present, so that most of the bacteria must have been either free-living or attached to silt and other small particles that were not enumerated. Minimum quantities were found in autumn and early winter. The number increased during the spring, and the peak population was found in August.

Most of the bacteria were non-motile, gram-negative rods. Usual methods were used to isolate and culture individual colonies for tentative generic identification and to measure enzymatic potentialities. *Flavobacterium* was the most common form; it is capable of utilizing a wide variety of substrates.

INTRODUCTION

A descriptive analysis of the bacteria of Long Island Sound was undertaken from June 1962 to July 1963. The project included enumeration by plate counts and isolation of individual colonies for growth on various kinds of media. A tentative classification of the forms present was prepared, although,

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in the present status of marine microbiology, no method of classification is unequivocally accepted by all workers. Aside from any descriptive value that this work may have, investigations of phytoplankton (Riley and Conover, this volume) and non-living particulate matter (Riley, 1963) warranted a microbiological study in order to broaden the general scope of knowledge of the pelagic assemblage in these waters.

In the early stages of this work Dr. John Sieburth of the Narragansett Marine Laboratory, University of Rhode Island, provided much needed advice on culture methods and taxonomic problems. Grateful acknowledgment is expressed for his help.

METHODS

Samples were obtained each month. These included 13 surface samples, two bottom mud samples, and three samples of particulate matter obtained by straining surface water through a sieve of bolting silk. Surface samples were obtained by lowering a sterile glass bottle over the side of the boat with a weight attached so that it could be submerged a little below the surface film while it was filling. Serial dilutions were made with sterile sea water. The concentrations of the original sea water in these dilutions were 10^{-1}, 5×10^{-2}, 10^{-2}, 5×10^{-3}, and 10^{-3}. Samples of 0.1 ml of each dilution were spread on agar plates and incubated in duplicate at temperatures of 27°, 18°, and 9°C.

Bottom mud was collected in a small bottom corer, and a 1 ml sample was removed from the central part of the core with sterile instruments. It was mixed thoroughly with sterile sea water in a Waring blender to break up particles as completely as possible and was plated in dilutions ranging from 10^{-1} to 10^{-10}. Samples of particulate matter were washed from the bolting silk (previously autoclaved) with sterile water. A portion of the catch was collected on a Millipore filter disk for microscopic examination. The remainder was mixed with a Waring blender and plated in dilutions ranging from 10^{-1} to 10^{-4}. They were incubated in the same way as the surface samples.

Initially dilutions and plating were carried out on shipboard, and the petri dishes were stored in a container at 10°C for several hours until they could be brought to the laboratory for incubation. From December 1962 through the remainder of the survey, samples were stored on shipboard after collection and returned to the laboratory for the remainder of the work, which was completed in the afternoon of the day of collection.

Plates were counted daily under a dissecting microscope with final numbers being taken after 8–15 days incubation at 27°, 8–16 days at 18°, and 12–21 days at 9°. Colonies for classification were picked after counting was completed. One plate containing 25–30 discrete colonies was chosen from each temperature group, and additional samples were taken from other plates that had interesting or unusual colonies. They were put into broth media and incubated at the same temperature as that of the original plate. After 2 or 3 days they were tested for morphological characters and inoculated into the various media listed below. All bacteria were tested with gram stain and most of them with capsule and flagella stains.

The following formulas were used for culture media: the original agar plates contained 0.1% trypticase, 0.1% yeast extract, 0.005% $FePO_4$, and 1.5% agar in aged sea water; the broth was the same without the agar. Proteose peptone agar slants contained 0.1% proteose peptone instead of trypticase, and other constituents were the same as previously listed. Distilled water agar slants were made according to the plating formula except that distilled water was used instead of aged sea water.

Several enzyme testing plates were used. In addition to the above listed components of the standard seawater agar, these contained one of the following substrates: for lipase, 1% Tween 80; caseinase, 5% casein; amylase, 0.2% starch; and gelatinase, 0.4% gelatin.

Three antibiotic tests were performed with Penicillin, Terramycin (oxytetracyline, OTC), and 2:4-Diamino-6:7-Di-isopropyl Pteridine (0/129).

RESULTS

Fig. 1 shows maximum plate counts obtained at the three dilutions ranging between 10^{-1} and 10^{-2}. For reasons that will be discussed later, these are believed to be most nearly representative of actual bacterial populations in the surface waters. This graph represents all surface water samples except the first two, taken at the beginning of the program in July 1962, in which counts of 15–1350 cells/ml were obtained. These were so much lower than values obtained in the summer of 1963 that deficiencies in method were suspected.

The three incubation temperatures led to quite different results. At 27° there was a sharp peak in midsummer and lower, somewhat variable values the remainder of the year. At 18° the peak occurred at the same time, but there was a broader period of moderately high concentrations extending from late winter to autumn. The 9° plates had their peak in spring, when the temperature in Sound waters was about at that level, and there was a severe inhibition of growth in summer and early autumn.

The uppermost line in Fig. 1 is the maximum count obtained, irrespective of incubation temperature. Since the maximum number of colonies develops when the incubation temperature more or less corresponds with the temperature of the Sound, this upper curve probably is indicative of the number of bacteria that are capable of active growth in the Sound. The mean number through the year is 8370 colonies/ml, with a total range of 1300 to 15,300 and a standard deviation of ± 2640.

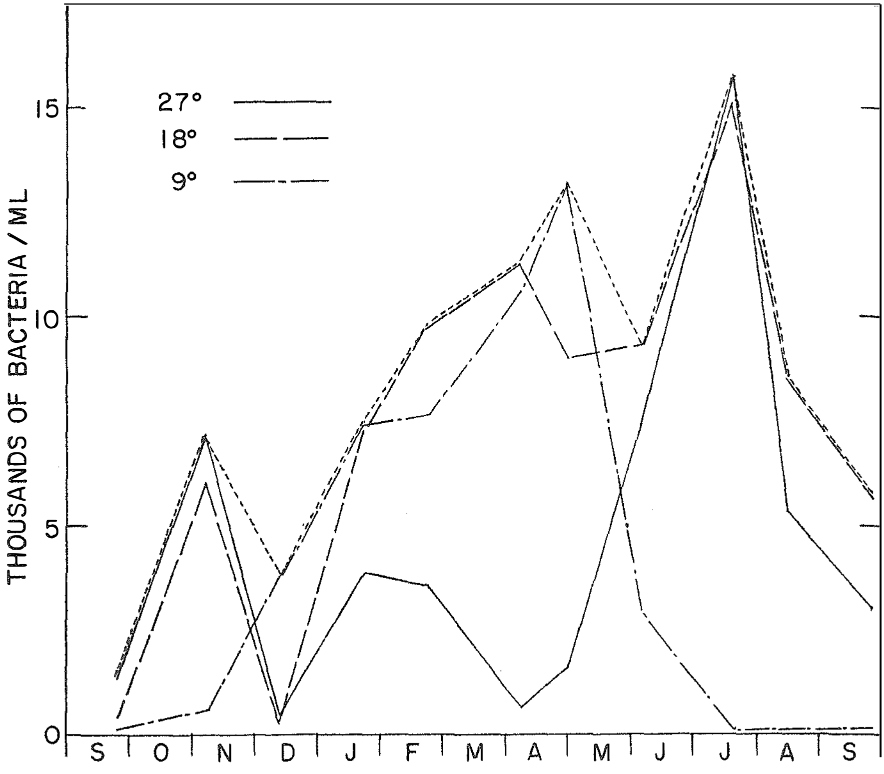

Figure 1. Numbers of bacteria obtained by plating Long Island Sound surface water and incubating at three temperatures. The uppermost curve (dotted line) is a hypothetical seasonal cycle that represents the largest plate counts obtained on each collection date, irrespective of incubation temperature.

Bacteria were classified by genera according to a tentative scheme proposed by Shewan, Hobbs, and Hodgkiss (1960). Altogether, 876 cultures were isolated: 309 at 27°, 321 at 18°, and 246 at 9°. The majority were non-motile, gram-negative, rod-shaped bacteria. Only the *Pseudomonas*, *Vibrio*, *Spirillum*, and one unidentified form were motile. Non-motile forms included *Bacillus*, coryneform bacteria, *Micrococcus*, *Sarcina* (all gram positive), *Flavobacterium*, *Cytophaga*, *Achromobacter*, and *Alcaligenes* (gram negative). The last two were not separated in the classification scheme that was used, and they will be treated together in further discussion. In addition, there were 247 unidentified cultures: 168 did not grow in the original isolation, 6 were discarded as mixed cultures not warranting further examination, 23 were incomplete analyses made in early stages of the project before test procedures became fully established, and 50 were unidentifiable with the tests used.

The distilled water medium was used to test euryhaline tendencies. There were 72 such cultures, including all samples taken and all incubation temperatures. The largest numbers fell into the categories of *Alcaligenes–Achromobacter*, *Pseudomonas*, *Sarcina*, *Flavobacterium*, and unidentified cultures. Numbers were never high, but the largest quantities were found in November–December 1962 and in April 1963, and particularly in cultures grown at 27°. No obvious ecological meaning could be found in these results. Long Island Sound is, of course, subject to continual infusions of freshwater and soil bacteria, and freshwater drainage is near its maximum in April. Drainage is not particularly heavy in early winter, however, and in neither case is the growth at 27° indicative of significance in nature.

Isolation from the plates yielded relative numbers of each genus. The numbers developing at the three incubation temperatures were not ordinarily consistent. This was hardly to be expected, but it introduces complexities in the evaluation of the natural population. In some cases maximum numbers were developed at temperatures quite different from those prevailing in the Sound at the time of collection, and although development is indicative of the existence of a viable population, there is some question as to whether the bacteria were physiologically important at natural temperatures. Problems like these could not be evaluated without much more investigation. Therefore, the description of the relative importance of individual genera must be qualified by saying that it is based upon general evaluation of the array of data obtained in the various isolations, and that its ecological significance is problematical.

With these qualifications, the following is a brief account of the seasonal distribution of the principal genera:

Flavobacterium was in general the most abundant form. It had strong peaks in late winter and spring, was moderately abundant in summer, and declined to minimum numbers in late autumn and early winter.

Achromobacter–Alcaligenes were the most abundant summer forms. They were moderately important at other seasons and showed some development at all incubation temperatures most of the year. However, certain peaks in November 1962 and January 1963 were obtained only at high incubation temperatures, and these probably have little ecological meaning.

Pseudomonas, *Spirillum*, and *Vibrio* contributed significantly to summer peaks and were of very little importance at any other time. The unidentified group also fell mainly in this category.

Coryneforms showed a moderate degree of development at all incubation temperatures in April and otherwise were relatively insignificant.

Four forms showed little seasonal variation except for occasional small and inconsistent peaks at particular incubation temperatures. These were *Bacillus*, *Micrococcus*, *Sarcina*, and *Cytophaga*. *Bacillus* was the most important and contributed significantly to the total population at times when seasonally limited forms were not abundant.

DISCUSSION

Evaluation of bacterial populations by means of plate counts presents problems that are well known. A colony developing on a plate may represent one bacterium or a group of bacteria adhering to a single particle such as a phytoplankton cell, or the spot on the plate may result from the fusion of two or more growing colonies, if the plate is seeded too thickly. Moreover, the composition of the medium or the temperature of incubation may be unsuitable for the growth of some of the naturally occurring bacteria. Direct counts present a different array of problems. If they are done carefully, they commonly yield larger numbers than plate counts, sometimes by an order of magnitude. The chief disadvantage, aside from the technical difficulty of counting, is the fact that they are deficient in information as to systematics and physiological capabilities of the individuals.

The present work has been limited to plate counts and is subject to the qualifications and reservations that have just been expressed. Evaluation is based on the reasoning that the largest plate counts are most nearly representative of actual populations, except in cases of occasional large values obtained with extreme dilutions, which tend to magnify sampling errors. In a majority of cases the largest figures were obtained with a dilution of 10^{-2}, and the general range of 10^{-1}–10^{-2} was chosen (Fig. 1) as being most suitable for the purpose.

In examining the general range of results at different incubation temperatures, the largest counts are commonly found at temperatures approximating those in Long Island Sound at the time of collection. While this is hardly a surprising result, the reasons for it cannot be given precisely. Qualitative examination of the kinds of bacteria does not reveal pronounced seasonal changes, although the possibility exists of a seasonal succession of species that is not detectable by the methods used. Seasonal temperature adaptation of various species is also a possibility.

This study overlapped with a series of analyses of phytoplankton and organic aggregates carried out during a two-year period beginning in June 1961 and described by Riley (1963). During this period the mean number of phytoplankton cells was 450/ml and aggregates were 58/ml, and the total number of other particles counted was less than one-tenth of the mean plate counts.

Any bacteria attached to these particles presumably would show up in plate counts as a single colony, although it is possible that the aggregates would be somewhat broken up by the stirring and agitation involved in dilution and plating. The large majority of bacteria that appear not to be associated with any of the particles enumerated might be free in the water or might be attached to smaller particles not counted. These smaller particles would include silt, small fragments of organic detritus, and possibly naked flagellates and other delicate organisms not readily preserved on filters.

The seasonal cycle of bacteria bears only slight resemblance to cycles of phytoplankton and aggregates. The latter increased irregularly from a low point in August 1962 to a peak in February 1963, and the phytoplankton also reached the peak of its winter flowering in February. Figure 1 shows a similar increase in bacteria during the same period, but the quantity continued to rise during the spring months when phytoplankton and aggregates dropped off to a low level.

The general rise in bacterial numbers during the spring and summer to a peak in late summer is accompanied by chemical evidences of bacterial action such as the development of an oxygen deficit and an increase in phosphate concentration (Riley and Conover, 1956). Riley (1956) concluded that plankton production exceeded utilization of organic matter during the winter flowering and much of the spring period. Hence organic substrates were available, and the increase in bacteria, with associated chemical changes in the water, reflects the gradual utilization of this material. The temperature increase during this season may be important. In general, the bacterial picture involves the total biological situation rather than a direct and immediate relationship with phytoplankton and aggregates.

An earlier section described methods for collecting organic aggregates by filtration through bolting silk, followed by disintegration of particles and study of their bacterial content. The methods used have little value quantitatively. They do not indicate how many bacteria are actually associated with organic aggregates in the sea, because only the largest aggregates were taken by this method. Nevertheless, there was some interest in determining from a qualitative point of view whether the kinds of bacteria associated with aggregates were a selected population or were essentially the same as that obtained by plating whole water samples. In general they proved to be about the same. At one time the possibility was considered that aggregates and bacterial slimes in general might derive much of their substance from encapsulating forms. There is little evidence in present work to support this concept. Present indications are that the aggregates are colonized by random attachment of whatever bacteria happen to be in the water at the time.

Two samples of bottom mud were plated. At moderate dilutions the maximum counts were of the order of 1–2.4 million/ml of mud. Here, as in other similar situations that have been examined, bacterial populations are much more abundant on the bottom than in the water column. Considering the ecological system as a whole, however, the benthic bacteria are not so clearly dominant, as may be indicated by a simple calculation. With an average depth of water of 20m, containing a mean population of 8,000/ml, the total population in the vertical column would be $1.6 \times 10^7/\text{cm}^2$. On the basis of figures just given, a similar total population might be expected to exist in the upper 4–16cm of bottom mud. There are indications in other work that has been done (unpublished data) that bottom stirring by tides and movements of burrowing animals is effective to a depth of 8–10cm, at least to the extent of producing measurable seasonal changes in organic nitrogen content. Thus the quantity of bacteria in bottom muds that can reasonably be expected to affect regeneration rates and other immediate events in the water column is of the same order of magnitude as the bacteria in the water itself.

REFERENCES

RILEY, G. A.

1956. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. Bull. Bingham oceanogr. Coll., *15*: 324–344.

1963. Organic aggregates in seawater and the dynamics of their formation and utilization. Limnol. & Oceanogr., *8*: 372–381.

RILEY, G. A. and S. M. CONOVER

1956. Oceanography of Long Island Sound, 1952–1954. III. Chemical oceanography. Bull. Bingham oceanogr. Coll., *15*: 47–61.

1967. Phytoplankton of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *19* (2): 5–34.

SHEWAN, J. M., G. HOBBS, and W. HODGKISS

1960. A determinative scheme for the identification of certain genera of gram-negative bacteria with special reference to the Pseudomonodaceae. J. appl. Bact., *23*: 379–390.

The Benthic Epifauna of Long Island Sound

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ABSTRACT

A modified oyster dredge was used to obtain 48 collections from Station 1 (sand-shell substrate, 9m) and Station 3A (mud, 16–17m) in Long Island Sound during the period between June 1960 and June 1961. The standing crop of benthic invertebrates was determined and their productivity was estimated; the material was examined with

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particular emphasis on the species that were not only important fish food, but also had not been collected adequately by gear of the type used in previous surveys. The greater diversity of environment at St. 1 resulted in a greater diversity of species there, particularly epifauna, than at St. 3A. Of the total of 144 species, 127 occurred at St. 1, 76 at St. 3A, and 59 were collected at both localities. Mean numerical standing crop was 77.00/m^2, 76.67/m^2 at St. 1, 77.96/m^2 at St. 3A. Mean biomass was 1.098 g/m^2, 1.345 g/m^2 at St. 1 and 0.376 g/m^2 at St. 3A. The epifauna standing crop from St. 1 was 10 times by number and 7 times by weight that from St. 3A, while the numerical abundance of infauna from St. 1 was one half, and its biomass was 1/14th that from St. 3A. At St. 1 the dominant species were *Crangon septemspinosa*, *Asterias forbesi*, hydroids, *Pagurus longicarpus*, *Neomysis americana*, *Ampelisca vadorum*, and *Ampharete acutifrons*. Others of importance were *Nassarius trivittatus*, *Cancer irroratus*, *Neopanope texana sayi*, *Corophium* sp., and the caprellids. The *Nepthys incisa-Yoldia limatula-Nucula proxima* community at St. 3A included *Asterias forbesi*, *Neomysis americana*, *Crangon septemspinosa*, *Retusa canaliculata*, *Nassarius trivittatus*, *Cistenides gouldii*, and *Gemma gemma*, listed in order of their importance in analyses of the biological associations. Standing crops from previous surveys made with an anchor dredge were several orders of magnitude greater than those with the oyster dredge. The discrepancies resulted chiefly from the operations of the two types of gear. The anchor dredge dug deep and also took a large percentage of organisms of small size, while the oyster dredge made a shallow cut, and also caught a greater percentage of organisms of large size. In addition, the catching efficiency of an oyster dredge is low. Correction for a mean efficiency of only 10 % resulted in standing crops that approximated the minimum of those made with the anchor dredge. Nevertheless, more accurate estimates of the abundance of dominant epifauna, such as *Neomysis americana*, *Crangon septemspinosa*, and *Asterias forbesi*, resulted from the oyster dredge collections than from those from the anchor dredge. Dominant species have been discussed in varying detail. Seasonal fluctuations in abundance and breeding, size, age, growth, weight-linear size relationships, mortality rates, productivity estimates, turnover rates, and feeding habits have been analysed. *Ampharete acutifrons*, *Neomysis americana*, *Crangon septemspinosa*, and *Asterias forbesi* showed high turnover rates. Based on the combined data from both Stations 1 and 3A, production of organic matter by *Asterias forbesi* was 87 %, *Crangon septemspinosa* 7 %, and *Neomysis americana* less than 1 % of that of the total epifauna. The production of five principal prey species of juvenile demersal fish totaled 1/10th of that of *Asterias forbesi* and 7 % of the production of the total epifauna. Only a small percentage of available organic material was utilized by the principal fish prey, and Long Island Sound can only support a small fish population compared with the populations of other areas. Serious competition for food within this population is partially prevented by the enormous abundance of copepods, *Neomysis americana*, amphipods, and *Crangon septemspinosa*, and by the preference of the dominant predator, the winter flounder (*Pseudopleuronectes americanus*), for a diet different from that of other members of the fish population.

INTRODUCTION

Previous investigations of animal communities in Long Island Sound indicated that the benthic epifauna is abundant (Burkenroad, 1946; Sanders, 1956; Carey, 1962) and useful as fish food (Richards, 1963b, c). Further information concerning standing crop and species composition is necessary, however, in order to determine the productivity and over-all importance of this group. Such an analysis is attempted in this paper, emphasizing those species whose numerical abundance or biomass, or both, are large. These were necessarily neglected by Sanders (1956) and Carey (1962) because their sampling gear was not adequate for collecting these forms quantitatively. Furthermore, the data presented here permit partial comparison of species abundance in the catches of the anchor dredge, utilized by Sanders and Carey, with those obtained in this survey with a modified oyster dredge.

The term *epifauna* is defined herein as a group of invertebrate animals that lives on or just above the bottom, either attached or motile. (All fish that were caught are included under this heading). *Infauna* consist of both suspension and deposit-feeding species that live freely in the substrate or in buried tubes.

MATERIALS AND METHODS

From June 1960 through June 1961, 48 collections of benthic organisms were made from two localities: Station 1, with a hard bottom at a depth of 9m, 1 mile SE of Charles Island, Connecticut (41.11° N, 73.02° W), and St. 3 A, with a soft bottom, depth 16–17m, 3 miles SSE of Charles Island (41.09° N, 73.01° W). Sediment analyses are given in Table 1. Bottom temperatures ranged from 0.6° to 21.4°C throughout the year, and salinity varied between 25 and 28.5 ‰. For analyses of the oceanographic features of the area see Riley (1956, 1959).

A modified oyster dredge (Fig. 1), 76.2 cm wide with an opening of 62.6 cm, was rigged with a depressor plate (57.2 × 66.0 cm) for rapid diving and with a 3.8-cm cutting bar that scraped the hard bottom to a depth of 1 to 2 cm. On the soft bottom the bar cut deeper. The dredge was rigged with a 25.4-cm wheel mounted on a frame that pivoted on a piece of pipe that, in turn, was attached to the frame of the dredge. A digital counter recorded the revolutions of the wheel, and the geometry of the situation was such that 0.2 revolution equaled one square meter of bottom surface dragged. The dredge was rigged with two different nets attached to a rope tied to all four sides of the frame. One net, 178 cm long, was of 6.3-mm mesh throughout; the other, 162.5 cm long, of stramin mesh (1.5 mm), could be attached inside the first one.

TABLE I. SEDIMENT ANALYSIS OF STATIONS 1, 3, AND 3 A IN LONG ISLAND SOUND.

	Percentage of total particles by weight		
	Stations 1 and 3 (adapted from Sanders, 1956)		Station 3 A (Carey)
Particle Size			
Shell	10.15	0.00	0.00
Soil Grades			
Gravel – greater than 2.0 mm	25.72	0.00	0.00
Sand – less than 2.0 mm – 60 μ	69.85	29.80	35.00
Silt – 50 μ – 2 μ	2.36	35.35	46.00
Clay – less than 2 μ	2.08	34.85	19.00

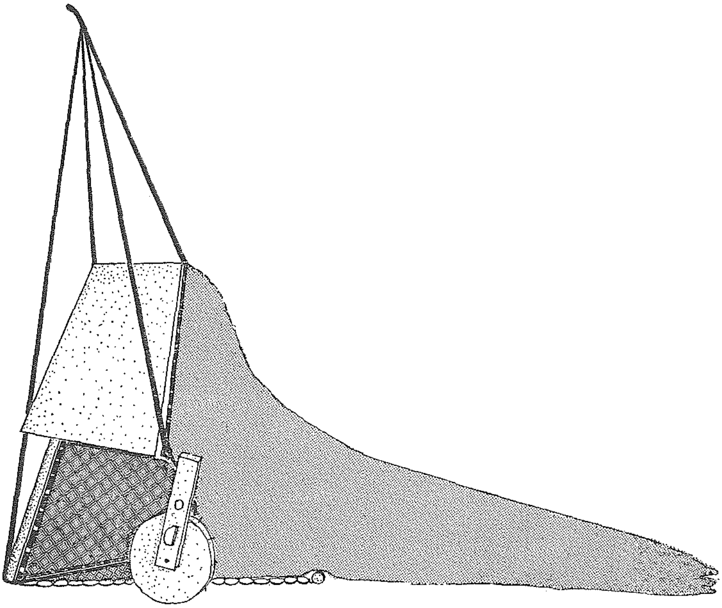

Figure 1. The modified oyster dredge used in this survey of the epifauna of Long Island Sound. See text page 91 for the dimensions.

The dredge was lowered to the bottom. Then an amount of cable was paid out equaling three times the depth of water, after which the dredge was dragged at 2 knots for 30 seconds. The boat was stopped and the dredge was hauled aboard. The calculated area sampled for one 30-second drag with this dredge was 17.1 m^2. The coverage as calculated from counter readings was 2–7 times this area (particularly on the hard bottom), indicating that the dredge continued to move over the bottom during the hauling-in process.

A total of 48 tows was made. Two tows were taken on the same day monthly at each station, one with each net. The sampling period was long enough to reveal seasonal changes, if any, but the total number of samples probably was insufficient for a complete species list, and the main emphasis was placed upon analysis of common and abundant species.

Between 30,000 and 45,000 cm^3 of material were collected in each sample. At times the larger samples were sub-sampled and only 5,100 to 20,400 cm^3 were processed. The large animals were picked out on deck during the process of washing the whole sample through a series of sieves: the largest being a No. 10 (4.8-mm mesh), the smallest a No. 50 (0.3-mm mesh). The material retained on the No. 50 sieve was preserved for further sorting in the laboratory.

For comparative purposes we note that Sanders' anchor dredge dug to a depth of 7.6 cm and took approximately 15,000 cm^3 of sediment. He put 13,000 cm^3 through a No. 10 sieve and 1,500 cm^3 through a No. 50 sieve.

Thus, the lower size limit of the small animals was qualitatively similar in both studies.

In the laboratory our accumulations of large animals and the fine material were re-sorted, and all animals were identified, counted, measured, and weighed. The methods of linear measurements for each major species are given as each is discussed.

Wet and dry weights were determined for all animals. Decalcification of coral, large crustaceans, molluscs, and echinoderms in 1.0 N HCl preceded oven drying, while small crustaceans and species of other groups were placed in aluminum foil dishes and dried immediately. Drying took place between 85 and 95°C for a period of 12 to 336 hours depending upon the length of time necessary for the animal to come to constant weight. Although dry weights were measured to the nearest 0.1 mg, they were considered accurate only to 1 mg, because there was an average change of 0.3 mg in the weights of the aluminum dishes, which contained the animals.

Although considerable variation existed between tows with the 6.3-mm mesh and those with the stramin net, the results were combined, in order to reduce variability due to the size of the organisms. Species of small size were more numerous in the stramin net samples.

Ash weights (with $CaCO_3$ removed in large animals) were determined by burning specimens in a muffle furnace at 650 to 700°C for two hours.

RESULTS

The results are presented in four sections: number of species, standing crops, biological associations, and comparisons of standing crops with the figures of Sanders (1956) and Carey (1962).

Number of Species

A total of 144 species (Appendix Table 1) was collected in our survey: 127 from St. 1, 76 from St. 3A, and 59 from both areas.

With the exception of coelenterates, the majority of the species occurred at St. 1. Among polychaetes and molluscs all epifaunal species were represented at St. 1, whereas one half or less of these were caught at St. 3A. Among the crustacea, species constituting both epifauna and infauna were more evenly divided between stations.

The majority of the species that occurred at both localities was infaunal and consisted principally of polychaetes, amphipods, and molluscs. Some exhibited a lack of strong association with a particular type of sediment, i.e. *Corophium* sp., *Lyonsia hyalina*, and *Cerastoderma pinnulatum*. Others actually turned out to be two different species of the same genus, one at each station, i.e. *Ampelisca vadorum* and *Ampelisca abdita* (Mills, 1963a). Some species collected

TABLE II. STANDING CROPS IN NUMBERS (PER m²) AND IN BIOMASS (g DRY WEIGHT PER m²) OF ORGANISMS AT STATIONS 1 AND 3 A, LONG ISLAND SOUND, TAKEN BY MODIFIED OYSTER DREDGE BETWEEN JUNE 24, 1960 AND JUNE 6, 1961. THE TOTALS (T) ARE LISTED, THEN DIVIDED INTO EPIFAUNA AND INFAUNA. (THE FIRST NUMBERED TOW WAS MADE WITH 6.3-mm MESH NET AT ST. 1, THE SECOND LISTED TOW WAS MADE WITH THE 1.5-mm MESH NET. AT ST. 3 A THESE WERE REVERSED).

		All Organisms						Epifauna						Infauna					
		N		Biomass		Total 1+3 A†		N		Biomass		Totals		N		Biomass		Totals	
Date	Tows	1	3 A	1	3 A	N	Biomass	1	3 A	1	3 A	N	Biomass	1	3 A	1	3 A	N	Biomass
VI-24-60	2+3	13.11	–	0.264	–	–	–	11.55	–	0262	–	–	–	1.66	–	0.001	–	–	–
VII-20-60	4+5 6+7	33.30	116.19	0.185	0.429	65.04	0.278	14.42	1.87	.181	0.148	9.56	0.167	21.19	114.32	0.006	0.280	58.24	0.111
VIII-31-60	8+9* 10+11	156.06	118.23	1.004	1.042	152.21	1.008	82.24	10.00	.946	0.502	33.09	0.901	120.38	108.23	0.202	0.540	119.12	0.107
X- 4-60	12+13 14+16	29.23	32.01	0.262	0.314	29.77	0.272	5.90	0.69	.254	0.110	4.89	0.227	23.32	31.31	0.007	0.204	24.87	0.045
X-31-60	17*+18 19+20	40.70	25.83	1.286	0.204	35.68	1.067	20.30	1.52	.266	0.103	13.97	1.012	20.40	38.80	0.020	0.101	21.72	0.048
XII- 5-60	21+22 23+24	59.96	24.72	0.758	0.607	48.62	0.709	45.95	4.1	.748	0.431	32.48	0.651	14.01	20.61	0.002	0.175	16.14	0.058
I-19-61	25+26 27*+28	44.93	383.12	0.775	0.528	163.83	0.688	28.17	16.4	0694	0.228	24.06	0.546	16.75	366.65	0.018	0.300	139.78	0.117
II-14-61	29+30	46.62	–	0.468	–	–	–	41.15	–	0464	–	–	–	5.47	–	0.004	–	–	–
III-15-61	33+34 35*+36	77.67	48.70	0.845	0.530	67.88	0.739	37.83	3.1	0833	0.104	26.10	0.587	39.83	45.43	0.012	0.426	41.72	0.152
IV-17-61	37+38 39+40	131.21	15.82	1.991	0.133	98.45	1.542	75.64	1.7	1978	0.065	57.78	1.516	55.57	14.10	0.013	0.067	45.55	0.026
VI- 6-61	41*+42 43+44	124.12	45.40	3.888	0.257	95.81	2.582	65.35	3.0	3878	0.199	42.94	2.555	53.71	42.37	0.010	0.058	49.63	0.027
Mean	All	76.67	77.96	1.345	0.376	77.00	1.098	40.66	4.1	1332	0.181	31.29	1.037	35.20	73.77	0.013	0.188	45.10	0.058
σ^2		2230.43	12037.98	1.526	0.076	2315.04	0.513	688.10	26.9	1153	0.024	280.06	0.551	1136.91	12283.45	0.003	0.028	1884.60	0.002

* Sub-sampled. † $\frac{\text{TSt1}}{\text{m}^2} + \frac{\text{TSt3A}}{\text{m}^2}$.

at both stations occurred in large numbers at only one station, i.e. *Nepthys incisa* and *Nucula proxima* at St. 3A, and *Ampharete acutifrons* at St. 1. Movement of common animals such as *Asterias forbesi*, *Crangon septemspinosa*, and *Neomysis americana* accounted for much of the overlap of species between these different stations.

STANDING CROPS

The mean number of all organisms from all tows of both stations combined was 77.00/m², with a mean dry weight of 1.098 g/m² (Table II). The numbers ranged from 29.77 to 163.83/m² (standard deviation (σ) = 48.12) and the biomass was 0.272–2.582 g/m² (σ = 0.716). Sub-sampling slightly overemphasized the standing crops at both stations. Although efforts were made to take aliquot portions, some aggregation of animals obviously resulted from this process (Table II).

The total standing crops showed similar and large variations in frequency distributions throughout the year. The mean number of organisms at St. 1 was 76.67/m² and the mean biomass was 1.345 g/m². At St. 3A the mean number, 77.96/m², was similar to that of St. 1, but the mean biomass was only 0.376 g/m². Variations in number at St. 1 ranged from 13.11 to 156.06/m² (σ = 47.23), and the dry weights from 0.185 to 3.888 g/m² (σ = 1.24). At St. 3A the numbers ranged from 15.82 to 383.12/m² (σ = 109.71) and the biomass from 0.133 to 1.042 g/m² (σ = 0.275). Aggregation in the frequency distribution of the numbers at St. 3A was more noticeable, because fewer samples were taken and the organisms were usually of smaller size than at St. 1.

In Table II the number and biomass pers quare meter on the various sampling dates are given with their infaunal and epifaunal components. The total standing crop for each date was calculated from the combined catches of all tows from both stations. Subtotals were calculated from catches of both tows for each station and sampling date.

The mean total number of epifaunal animals for the combined stations was similar to the mean total number of infaunal species, yet the biomass of the former was 18 times that of the infauna, since the body sizes of the individual organisms constituting the epifauna were larger than those of the infauna. The large variations in standing crops apparently had no seasonal significance, but were probably due to variations in sampling efficiency. The numbers of epifauna (both stations combined) ranged from 4.89–57.78/m^2 and the biomass varied between 0.167 and 2.555 g/m^2. The numbers of infauna ranged from 16.14 to 139.78/m^2, the biomass 0.026–0.152 g/m^2.

Standing crops of these two groups at each station showed expected differences based on the conclusions of Sanders (1956, 1958) concerning animal-sediment relationships. The mean number of epifauna from the sand-shell area was 10 times that taken from the mud locality, and the mean biomass was seven times. On the other hand, the mean number of infauna from St. 1

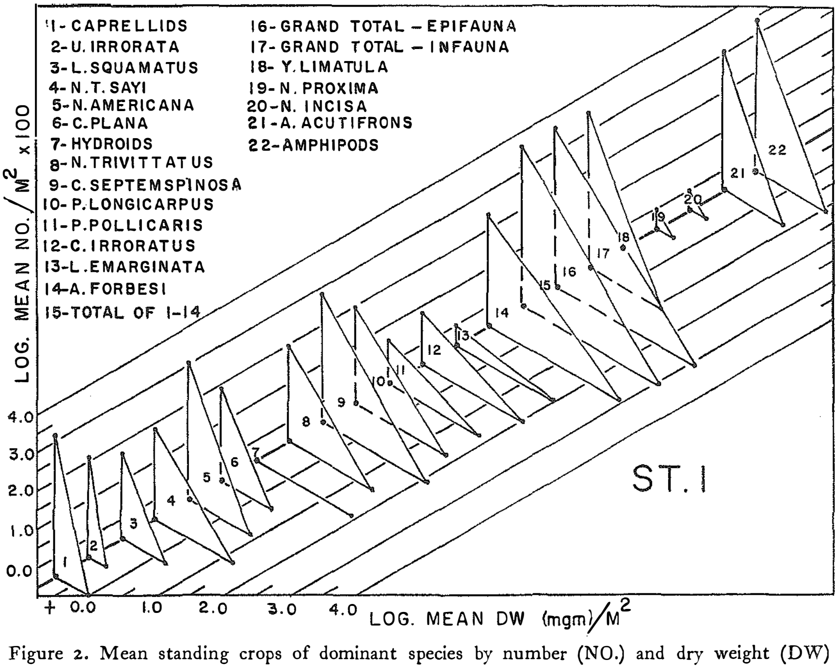

Figure 2. Mean standing crops of dominant species by number (NO.) and dry weight (DW) at Station 1. Plus sign in abcissa denotes dry weight less than one milligram. No collections were made in September or May (see text page 97).

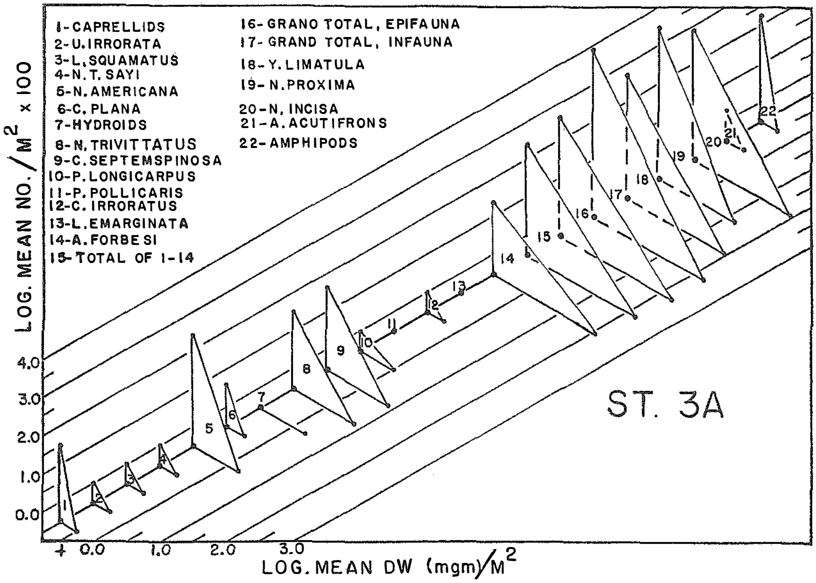

Figure 3. Mean standing crops of dominant species by number (NO.) and dry weight (DW) at Station 3A. Plus sign in abcissa denotes dry weight less than one milligram. No collections were made in June 1960, September, February, or May (see text page 97).

was only one half, and the mean biomass one-fourteenth of that collected at the mud station.

Fourteen species of epifauna (see Appendix Table II) were dominants in the community and many were important fish prey. At St. 1 they ranged in abundance from 0.172 to 3.842 g/m^2 and in number from 1.83 to 51.14/m^2, and constituted on the average 97% by weight and 50% by number of all the epifauna. At St. 3A, they ranged in abundance from 0.063 to 0.501 g/m^2 and in number from 0.62 to 15.6/m^2, and averaged 78% by weight and 95% by number. Comparison of the two areas revealed large differences in the relative abundance of these species (Figs. 2 and 3). A few common species were not collected by the dredge. These included *Squilla empusa* (?), *Limulus polyphemus*, and *Loligo* sp., which were taken during the earlier fish trawling program in 1955–57. *S. empusa* lives in burrows and was perhaps passed over, and *Loligo* is pelagic and agile, thus escaping the dredge. The fact that no horseshoe crabs were taken remains unexplained. All three species are of large size, and would add considerably to the standing crop.

Both the numbers and biomass of the organisms were considered. The logarithms of the mean standing crops are illustrated in Figures 2 and 3. Isometric projections are used to indicate the number and biomass simultaneously, and each interval represents an order of magnitude in the standing crops. In this way the importance of an organism in the community at a particular time is more fully represented than by either number or weight alone. Moreover, the choice of measurement of any standing crop depends somewhat upon the interest of the investigator and also the reader. Estimates of productivity and energy transfer require measurements of biomass, while the ecology of single species is primarily concerned with numbers. These graphs also illustrate the basic differences in total numbers and total weights of epifauna and infauna, as previously discussed.

BIOLOGICAL ASSOCIATIONS

Analyses of the biological associations of both stations were adapted from the method of Fager (1957). The results shown in Tables III A and III B were obtained from 11 samples from St. 1 and nine samples from St. 3A. The frequency of the rank of each species, as one of the ten most abundant species, is given for its number and its biomass. The species are listed in order of the product score of their biological indices, the calculation of which is based on a sum of weighted frequencies. For example, *Crangon septemspinosa* ranked highest in number in no samples, second highest in six samples, third in one, fifth in two, and sixth in two. To obtain the biological index for number (N), each frequency was multiplied by its weighting factor (Score) and the products totaled as follows:

$$\begin{aligned} 6\times 9 &= 54 \\ 1\times 8 &= 8 \\ 2\times 6 &= 12 \\ 2\times 5 &= \underline{10} \\ & 84 \end{aligned}$$

In this manner both numbers and biomass are given equal importance, thus preventing overestimates of the importance of species of large size. The highest score obtainable for a species at St. 1 is 12,100 (110 × 110) and for a species at St. 3A is 8,100 (90 × 90). To attain this maximum score a species would have to rank first in abundance, with regard to both number and weight, in all samples at each station. No species would be expected to attain the maximum, since species of little weight are usually numerically more abundant than heavy ones. However, there are species with high product scores and these are considered more important in the community. The frequency with which each species is included among the ten most abundant species, and the frequency of its occurrence in all of the samples are also listed.

According to the system outlined above, *Crangon septemspinosa* was clearly the dominant species at St. 1 followed by *Asterias forbesi*, the hydroids, *Pagurus longicarpus*, *Neomysis americana*, *Ampelisca vadorum*, and *Ampharete acutifrons*. *Nassarius trivittatus*, *Neopanope texana sayi*, *Corophium* sp., and the caprellids were consistently members of the community.

Dominance at St. 3A was shared by *Nepthys incisa*, *Yoldia limatula*, and *Nucula proxima*. *Asterias forbesi*, consistently present, was also important. *Neomysis americana*, *Crangon septemspinosa*, *Retusa canaliculatum*, *Nassarius trivittatus*, *Cistenides gouldii*, and *Gemma gemma* were other important species in the community.

Station 1 had greater number of species among the first ten than St. 3A. The four most dominant species at St. 3A scored greater than 20% of the possible maximum, and three of these belong to the infauna. At St. 1 only one species scored as high, and it was a member of the epifauna. The three infaunal dominants of St. 3A, *Nepthys incisa*, *Yoldia limatula*, and *Nucula proxima*, did not occur among the top ten of St. 1, while *Crangon septemspinosa* did so at both stations. Three species, *Asterias forbesi*, *Nassarius trivittatus*, and *Neomysis americana*, showed similar positions in the dominance hierarchy at both stations. These are all epifaunal organisms, which usually are less restricted by the type of sediment than are the infauna. The remaining components varied, but their frequencies created a pattern of decreasing dominance that was similar in both areas.

Nineteen species (66%) at St. 1 were present in 80% or more of all samples, and 13 (69%) of these were members of the ten most abundant species in more that seven samples by either number or weight. At St. 3A, of the 12 species (46%) present in 80% of the samples, 11 of these (92%) were among the ten most abundant by number or biomass in more than six samples. The greater diversity at St. 1, including a greater variety of epifauna, perhaps explains why the fish from the sand-shell substrate consistently contained more food and a greater diversity of food in their stomachs than the fish from the silt-clay substrate (Richards, 1963c).

COMPARISON OF STANDING CROPS ESTIMATED FROM CATCHES OF THE ANCHOR DREDGE WITH THOSE FROM CATCHES OF THE MODIFIED OYSTER DREDGE

Differences of several orders of magnitude existed between the standing crops of benthic fauna estimated by Sanders (1956) and those given above, (Table IV). At St. 1 the mean number of all organisms estimated by Sanders (7,957) is 100 times that estimated from the catches of the oyster dredge (77). Sanders' estimated biomass of these organisms is 13.5 times higher than that estimated from oyster dredge hauls. If only those organisms greater than 0.2 g are considered, the discrepancies in the mean numbers become much less. Only 5.5 times as many organisms were taken by Sanders' dredge as by the oyster dredge. The difference in the estimated biomass of the larger organisms was about the same as that for the total fauna. Similar discrepancies occurred between the estimates of the fauna from the mud substrate (Table IV), except that the discrepancy was not so great in the comparison of relative biomasses of organisms greater than 0.2 g.

TABLE III A. FAUNAL FREQUENCY EVALUATION BY NUMBER (N) AND BY DRY WEIGHT (DW) OF 11 SAMPLES FROM STATION 1. SPECIES ARE LISTED ACCORDING TO THE PRODUCT OF THEIR BIOLOGICAL INDICES.

	Rank of Abundance																						Frequency (Number of Samples)		
	1		2		3		4		5		6		7		8		9		10		Bio-logical Index*		Product Score	Among First Ten		Present
	Score																									
	10		9		8		7		6		5		4		3		2		1							
	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N×DW	N	DW	
Crangon septemspinosa	0	1	6	5	1	2	0	3	2	0	2	0	0	0	0	0	0	0	0	0	84	92	7728	11	11	11
Asterias forbesi	0	6	0	1	0	4	1	0	2	0	0	0	0	0	0	0	2	0	0	0	23	101	2323	5	11	11
Hydroids†	–	1	–	1	–	3	–	0	–	2	–	2	–	1	–	1	–	0	–	0	–	72	–	–	11	11
Pagurus longicarpus	0	0	0	1	0	1	0	1	1	2	2	3	0	2	3	1	1	0	2	0	29	62	1798	9	11	11
Neomysis americana	4	0	0	0	1	0	1	1	0	0	0	0	1	2	1	1	0	1	0	1	62	21	1302	8	6	10
Ampelisca vadorum	2	0	1	0	3	0	0	0	3	0	0	0	1	0	0	2	0	4	0	1	75	15	1125	10	7	11
Ampharete acutifrons	2	0	1	0	3	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	58	18	1044	7	3	11
Nassarius trivittatus	0	0	0	0	0	0	0	3	0	3	0	1	2	1	1	0	0	2	3	0	14	52	728	6	10	11
Neopanope t. sayi	0	0	0	0	0	0	0	0	0	0	1	2	0	3	0	2	3	1	1	3	12	33	396	3	5	11
Corophium sp.	1	0	3	0	2	0	2	0	1	0	0	0	0	0	0	0	0	1	0	0	73	2	146	9	1	11
Lepidonotus squamatus	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	2	19	5	95	4	3	11
Caprellids	2	0	0	0	0	0	3	0	2	0	0	0	1	0	1	0	1	0	0	0	62	0	62	10	0	11
Cancer irroratus	0	2	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	50	50	0	6	8
Pagurus pollicaris	0	0	0	1	0	0	0	3	0	0	0	0	0	1	0	1	0	1	0	0	0	39	39	0	7	9
Crepidula plana	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	2	2	16	2	32	5	2	8
Erichthonius brasil'sis	0	0	0	0	0	0	1	0	0	0	2	0	1	0	1	0	1	0	0	0	26	0	26	6	0	9
Unciola irrorata	0	0	0	0	0	0	1	0	0	0	1	0	2	0	1	0	0	0	2	0	25	0	25	7	0	11
Libinia emarginata	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	15	15	0	2	3
Nemerteans	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	10	0	10	3	0	9
Exogone dispar	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	7	1	0	8
Astrangiae danae†	–	0	–	0	–	0	–	0	–	1	–	0	–	0	–	0	–	0	–	0	–	6	6	–	1	1
Ensis directus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	6	6	0	2	3
Alcyonidium polyoum†	–	0	–	0	–	0	–	0	–	0	–	1	–	0	–	0	–	0	–	0	–	5	5	–	1	4
Cephalothrix linearis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	5	0	5	2	0	9
Stenothoe cypris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	3	1	0	9
Polinices duplicatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	3	0	1	3
Ovalipes o. ocellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	3	0	1	1
Neanthes succinea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	2	0	1	10
Polydora ciliata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	2	1	0	3

* If the biological index is zero, it is considered to be one for the purpose of calculating the product score.

† These cannot be counted.

TABLE III B. FAUNAL FREQUENCY EVALUATION BY NUMBER (N) AND BY DRY WEIGHT (DW) OF 9 SAMPLES FROM STATION 3 A. SPECIES ARE LISTED ACCORDING TO THE PRODUCT OF THEIR BIOLOGICAL INDICES.

	Rank of Abundance																									Frequency (Number of Samples)
	1		2		3		4		5		6		7		8		9		10		Bio-logical Index*		Product Score	Among First Ten		Present
	Score																									
	10		9		8		7		6		5		4		3		2		1							
	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW	N×DW	N	DW	
Nepthys incisa	2	1	2	6	2	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	74	80	5920	9	9	9
Yoldia limatula	1	1	2	2	3	5	2	1	0	0	0	0	0	0	1	0	0	0	0	0	69	75	5175	8	9	9
Nucula proxima	4	0	2	0	1	1	2	2	0	1	0	1	0	0	0	2	0	1	0	0	80	41	3280	9	8	9
Asterias forbesi	0	6	0	2	0	1	0	0	2	0	1	0	0	0	0	0	1	0	2	0	21	86	1806	6	9	9
Neomysis americana	0	0	0	0	2	0	1	0	1	0	2	3	0	1	0	1	0	1	0	1	39	25	975	6	7	8
Crangon septemspinosa	0	0	0	0	0	0	1	0	1	3	0	1	2	3	0	0	1	0	0	0	23	35	805	5	7	9
Retusa canaliculata	1	0	1	0	1	0	0	1	2	0	1	0	0	0	0	1	0	1	0	2	44	14	616	6	5	6
Nassarius trivittatus	0	0	0	0	0	0	0	2	0	2	0	2	0	2	2	0	1	0	2	0	10	44	440	5	8	8
Cistenides gouldii	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	3	1	1	1	14	21	294	6	5	8
Gemma gemma	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	2	0	0	13	8	104	3	3	7
Polinices duplicatus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	1	0	1	5	15	75	1	5	7
Ampelisca abdita	0	0	0	0	0	0	0	0	2	0	3	0	1	0	0	0	0	0	0	2	31	2	62	6	2	9
Cerastoderma pinn'tum	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2	0	0	4	12	48	1	4	6
Caprellids	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	2	0	1	0	15	0	15	6	0	8
Ampharete acutifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	4	3	12	2	1	5
Lyonsia hyalina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	4	3	12	2	1	5
Citheridea americana	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	12	0	12	2	0	2
Callinectes sapidus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10	0	1	1
Sarsiella zostericola	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	9	1	0	3
Hydroids†	–	0	–	0	–	0	–	0	–	0	–	1	–	0	–	1	–	0	–	0	–	8	8	–	2	5
Pagurus longicarpus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6	6	0	1	6
Bittium alternatum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0	4	1	0	4
Oxyurostylis smithi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3	1	3	1	1	2
Macoma tenta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	3	0	1	3
Polydora ciliata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	2	1	0	1
Maldanid polychaete	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1

* If the biological index is zero, it is considered to be one for the purpose of calculating the product score.

† These cannot be counted, and perhaps should be ranked higher in the list.

TABLE IV. Comparison of Standing Crops Estimated from Catches of the Anchor Dredge, 1954–55, and the Oyster Dredge, 1960–61.

AVERAGE FROM ALL TOWS

		ANCHOR DREDGE				OYSTER DREDGE			
Locality	Size	N/m^2	Range	DW/m^2	Range	N/m^2	Range	DW/m^2	Range
Station 1	All	7,957	–	24	8–45(158)	77	13–156	1.78	0.2–5.5
	>0.2 g	12.97	–	22	–	2.4	–	1.43	–
Station 3	All	5,844	–	4.9	1–16	–	–	–	–
	>0.2 g	1.1	–	0.8	–	–	–	–	–
Station 3A	All	–	–	–	–	78	12–383	0.42	0.1–1.0
	>0.2 g	–	–	–	–	0.2	–	0.16	–

DATA FROM A SINGLE TOW AT ST. 1:

	IV–19–54 (ANCHOR DREDGE)		IV–17–61 (OYSTER DREDGE)	
	N/m^2	DW/m^2	N/m^2	DW/m^2
Hydroids	+	12.89	+	0.095
Ampharete acutifrons	236	0.22	0.42	0.001
Lepidonotus squamatus	68	0.38	0.14	0.001
Neomysis americana	190	0.13	8.53	0.007
Ampelisca vadorum *Corophium* sp. *Erichthonius brasiliensis*	3321	1.64	54.2	0.008
Unciola irrorata	91	0.31	0.88	0.002
Caprellids	23	0.004	52.1	0.004
Crangon septemspinosa	91	4.98	6.4	0.217
Pagurus longicarpus	84	2.37	1.36	0.051
Pagurus pollicaris	53	124.79	0.03	0.128
Neopanope t. sayi + *Panopeus herbstii*	212	7.55	0.82	0.040
Cancer irroratus	0	0.00	0.11	0.545
Nassarius trivittatus	23	0.28	3.02	0.080
Crepidula plana	334	0.29	0.33	0.100
Asterias forbesi	0	0.00	10.9	4.850
Epifauna only	2058	154.00	75.64	2.84
All Species	6742	157.87	131.0	2.85
Average dry weight per organism in g.		0.023		0.022

That these discrepancies were not the result of lumping many tows from different seasons is shown by the data in Table IV which compare two individual sampling dates. The standing crop of the sample from St. 1 on April 19, 1954, taken by anchor dredge, was 50 times as large as that estimated from the catch of the oyster dredge on April 17, 1961, even though the mean dry weight per organism was similar. Only with respect to the number of epifaunal species was the relative abundance in the sample of the oyster dredge greater than that of the anchor dredge. Factors that contribute to these discrepancies are discussed below.

There was a difference of six years between these two surveys, and there might have been changes in overall abundance. Carey (1962), however, sampled the same general area with an anchor dredge in 1956–57 and obtained quantitative estimates similar to those of Sanders. Variations in relative abundance of dominant species occurred, but the overall standing crops were of the same order of magnitude in both anchor dredge surveys. This indicates a stable population of benthic fauna in these localities during those years.

The number of tows on which the estimates were based was different. While Sanders and Carey based their estimates on 34 and 30 tows, respectively, 48 tows were made with the oyster dredge. This difference is considered unimportant, because all seasons of the year were sampled in all surveys, and because of the large differences between tows with the same gear.

The two dredges were operated differently. The distance covered, the depth of substrate sampled, and the amount of material were all important factors that determined the vulnerability and size of the species collected. The anchor dredge, sampling 0.4 m^2 of substrate to a depth of 7.6 cm, filled its bag immediately. Consequently, a greater percentage of infauna and of organisms of small size would be expected in these samples than in those of the oyster dredge. The latter, which collected twice as much material, covered on the average 100 times the area of the anchor dredge and cut to a depth of 2 cm on the hard bottom (a greater depth was sampled in the mud). It caught a higher percentage of epifauna of large size. Species such as *Cancer irroratus*, *Pagurus pollicaris*, *Libinia emarginata*, and *Asterias forbesi*, were more vulnerable to the oyster dredge. The oyster dredge usually caught a greater number of species of large size, while the anchor dredge caught a greater number of species of small size.

Similar differences in catches were also evident in a comparison of our survey with the one made by Sanders (1960) in Buzzards Bay, Massachusetts. Within Buzzards Bay, Sanders attempted to compare paired samples of a scallop dredge with those of the anchor dredge (personal communication). His results were similar to ours. Not only was there great reduction of numbers in the scallop dredge samples, but qualitative differences were large. In addition, huge fluctuations occurred in the numbers of animals such as *Neomysis americana*.

Apparently, an epifaunal dredge is an inefficient gear that differentially samples the available species. For instance, scallop dredges in the Bay of Fundy, Canada, showed a range of 0.4 to 25 % in efficiencies depending upon mesh size and age of the scallops (*Placopecten magellanicus*) (Dickie, 1955). The efficiency of a dredge, rigged with commercial mesh ($2^5/_8$″), averaged 5 % on rocky inshore bottom and 12.5 % on level offshore ground. The oyster dredge used in Long Island Sound had smaller mesh sizes, but the average size of the available specimens was smaller. Even though the substrate was rockless at the stations sampled in Long Island Sound, its efficiency was perhaps comparable to that of the Canadian scallop dredge, and an estimate of 10% over-all efficiency appears reasonable. The mean standing crops at St. 1, based on this estimate would then be 767/m^2 and 13.45 g/m^2.

PRODUCTIVITY

Estimates of production are based on the method of Sanders (1956; pp. 390–395; see p. 393 for a sample calculation) in which the amount of organic matter produced annually is estimated from growth, mortality, and recruitment. Furthermore, turnover rates, that is, the ratio of production to standing crop, were calculated. These estimates are admittedly complicated by many factors that cannot be well defined, among them the effect of variations in dredge efficiency on length frequencies and on standing crops, the movements of animals away from collecting stations, and the lack of information on reproductive cycles. Constant recruitment, net escapement, and other factors presented problems with certain species and are discussed where pertinent. For all these reasons, only a few dominant species were selected for production estimates, namely, *Asterias forbesi*, *Crangon septempinosa*, and *Neomysis americana*. These were chosen because of their abundance, their availability to the dredge, and the importance of the latter two species as fish food. Although the catch of *Ampharete acutifrons* may have varied depending on the depth of the cut of the dredge, it was chosen because of its importance as food for juvenile *Pseudopleuronectes americanus*, the commonest fish in this area (Richards, 1963a, b). Other infaunal species are not discussed because they have been treated by Sanders (1956), Carey (1962), and Mills (1963a, b).

Ampharete acutifrons. This polychaete was an important member of the community, particularly at St. 1. It occurred there in all samples and ranked numerically among the first ten species 64% of the time (Table III A). Its standing crop, which ranged in number from 0.07 to 99.3/m^2 averaged 16% of the total infauna. Its dry weight, ranging from less than 1 to 63 mg/m^2, averaged 54% of the infauna. Wet weights were 1 to 478 mg/m^2 and varied depending upon the season of the year. *A. acutifrons* was not abundant at St. 3A (Table III B and Fig. 3), ranging in numbers from 0 to 0.21/m^2 and in dry weight from 0 to less than 1 mg/m^2. Since differences in the catches occurred between the stramin and the 6.3-mm mesh nets, the data were combined. The stramin net retained nearly twice the number that were caught in the coarser net, and the specimens were frequently of smaller size.

A. acutifrons lives in leathery tubes which are covered on the exterior by sand grains of rather uniform size. These tubes lie in a vertical position near the surface of the substrate so that the tentacles of the worm are exposed during feeding. The worm is a selective deposit feeder, ingesting a great deal of mud and sand. Examination of the gut contents showed that both diatoms and dinoflagellates were included. The amount of ingested material varied considerably. Dragoli (1961) showed that *Melinna palmata* (a related genus) in the Black Sea, feeding irregularly through the day, ingested enough mud to nearly equal one half of its own weight. In Long Island Sound in August, *Ampharete acutifrons* contained so much mud and sand that the ash weight, measured as a percentage of dry weight, was 8% higher than in October, when the animals were not feeding so heavily. Variations in feeding caused the individual dry weights to vary so much that most of the analyses of growth and abundance were based on wet weights, which varied less.

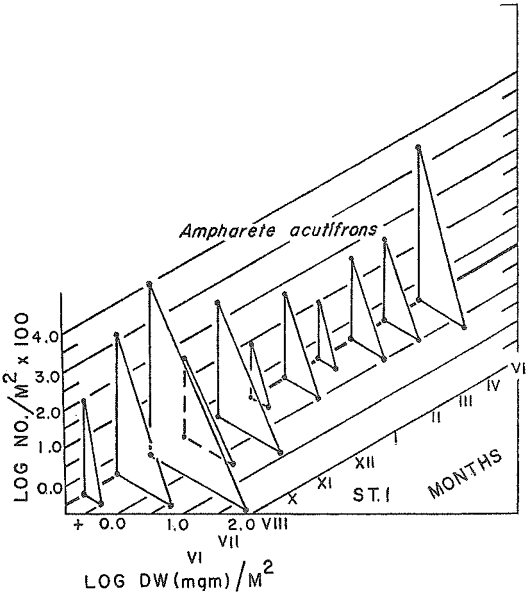

Figure 4. Standing crop of *Ampharete acutifrons* by number (NO.) and dry weight (DW) for each collection date at Station 1. No collections in September or May. Plus sign in abcissa denotes dry weight less than one milligram.

A. acutifrons, occurred throughout the year at St. 1 and was most abundant from June through October (Fig. 4). It suddenly declined in density in December, and few were taken through the winter. Its abundance suddenly increased again in June. During August to November it was also present at St. 3A.

The population was usually divided into two size groups: those from 2 to approximately 14 mm and those from 15 to 22 mm. The first group was further divided into those which were 2 to 6 mm and those from 7 to 14 mm. The smallest specimens were new recruits, which appeared from June through

November. They were apparently the products of two spawning periods, the principal one in the spring and another in the fall. Specimens in the medium size group were the most common in nearly all samples. These apparently ranged in age from two to ten months. During October, when the majority were probably five to six months old, a few spawned; eggs were noted at that time in two individuals, each 10 mm long. The group of specimens of large size, approximately one year old, bred in spring and summer and then disappeared. Eggs were noted in those between 13 and 22 mm, but no further attempt was made to sex these specimens.

An analysis of growth was complicated by three factors: 1) the almost constant addition of new recruits, 2) the overlap in size between those only six months old and the one-year-olds, and 3) the appearance of a group of ampharetids of small size during winter, which may not have been *Ampharete acutifrons*. The presence of *Amage auricula*, an ampharetid of smaller size than *Ampharete acutifrons*, in the spring collections, confirmed the suspicion that the winter group was perhaps a different species. These individuals were removed prior to calculating the growth of the zero-year class. Following attempts to account for these factors, the average increase in length was computed and is shown in Table V. The greatest increase occurred in summer shortly after settling and again during early spring prior to spawning. At these times the weight increase was also most rapid, as evidenced by the seasonal variation in the regression of the wet weight on the total length (Table V). The more rapid rate of weight increase in summer was partially due to breeding and to the fast growth and heavy feeding of the zero-year class. For the computation of productivity, however, the average constants were suitable.

An apparent high post-spawning mortality of the one-year class occurred (Fig. 5).

An estimate of productivity, computed according to Sanders' method (1956, p. 393), appeared at first glance to be high. A total annual production of

TABLE V. GROWTH OF *Ampharete acutifrons* AT STATION 1, MEASURED BY THE AVERAGE LENGTH OF THE 1960 YEAR-CLASS THROUGHOUT THE YEAR, WITH THE REGRESSIONS OF WET WEIGHT (WW) ON TOTAL LENGTH.

	LENGTH		REGRESSION
MONTH	AVERAGE	INCREMENT	LOG WW–LOG L RELATIONSHIP
April	0.0		—
June	4.7	4.7	Log WW = 2.46 Log L − 1.59
July–August	10.6	5.9	Log WW = 2.63 Log L − 2.00
October–November	12.9	2.3	Log WW = 2.40 Log L − 1.66
December–March	13.7	0.8	—
April	18.3	5.6	—
			AVERAGE
			Log WW = 2.55 Log L − 1.87

0.719 g/m² wet weight with a mean standing crop of 0.157 g/m² wet weight resulted in a ratio of 4.58. Two factors should be considered: 1) for the purpose of computation the zero-year class in all four seasons included both new recruits and those six months old, 2) mortality included change in abundance.

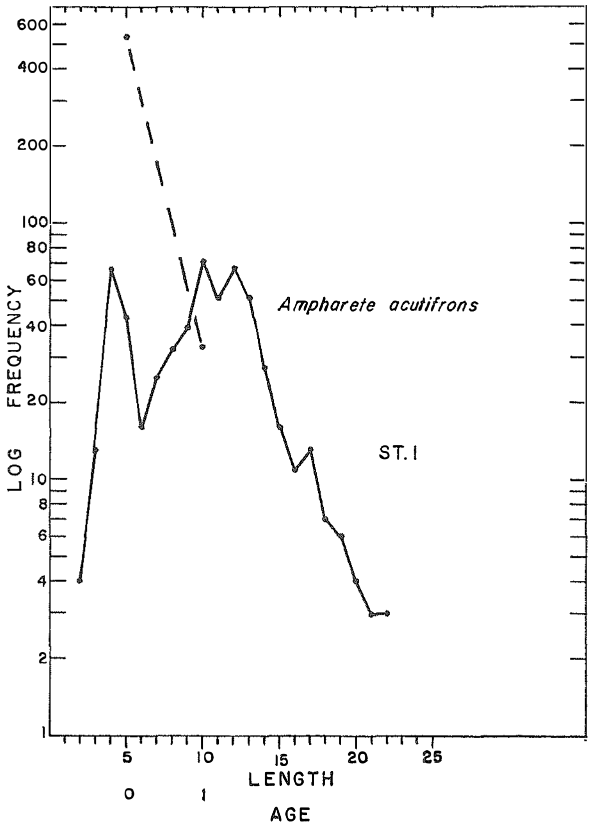

Figure 5. Catch curves for *Ampharete acutifrons* from Station 1 in one-mm length intervals (solid line) and for two age groups, the zero- and one-year-olds (dashed line).

The second point is important, because there was a sudden increase in density in spring of individuals that were six months to one year old. These may have come from an adjoining area, and their effect would be to increase the figure for total production. On the other hand, *A. acutifrons* is a short-lived organism that sometimes spawns twice a year. Under these circumstances, a turnover rate close to 5.0 was expected (Sanders, 1956). Consequently, a ratio of 4.58 may not be far off.

Only three species of juvenile fishes preyed on *A. acutifrons*. Two of these, *Stenotomus chrysops* and *Etropus microstomus*, are migrants which ate this species spasmodically (Richards, 1963b). The other, *Pseudopleuronectes americanus*, the most common resident fish, concentrated heavily on this prey and therefore had a highly productive source of food almost free from the competitive efforts of other predators.

Neomysis americana. Probably the most numerous of all benthic epifauna in Long Island Sound, mysids occurred in nearly every sample from both stations. The measure of their abundance depended on the type of net used with the dredge. Because of their small size, they escaped through the meshes of the 6.3-mm net, so that the combined data tend to underestimate mysid density. For this reason, although combined data are used to measure relative abundance, discussions of seasonal fluctuations and productivity will be based on data from the stramin net only.

N. americana constituted 13°/₀ by number and 0.2°/₀ by weight of all epifauna from St. 1. The mean standing crop (based on combined catches) by number was $10.31/m^2$ and by weight was $0.006\ g/m^2$. At St. 3A, *N. americana* constituted 62°/₀ by number and 1°/₀ by weight of all epifauna. Numerically the mean standing crop was $2.57/m^2$, and the mean biomass was $0.002\ g/m^2$. Based on stramin net catches only, the mean standing crops at St. 1 by number were $21.62/m^2$ and by weight $0.012\ g/m^2$, and at St. 3A, $4.34/m^2$ and $0.004\ g/m^2$.

Considering their small size, it was amazing how frequently mysids were among the 10 most common species in terms of biomass, and this attests to their enormous numbers. At both stations mysids were fifth in rank (Tables III A, B). Their enormous importance as fish food (Richards, 1963b, c) probably resulted from such obvious availability.

Seasonal fluctuations in density occurred, particularly at St. 1. In general, mysids were exceedingly abundant during the period from late fall through spring and were nearly absent during summer and early fall (Fig. 6). During winter, fluctuations in their density were random, while in summer their disappearance was dramatic and their return gradual. At St. 3A, seasonal changes in abundance were less obvious than at St. 1, but followed the same general trend. At both localities, the fluctuations were attributed to various intrinsic factors including size, breeding, and vertical migration.

The pattern of diurnal vertical migration, which is a common feature of mysid behavior (Hulbert, 1957), varied depending upon the stage in the breeding cycle and the size of the organisms (Herman, 1963). During the breeding season, adults undertook extensive migrations; during the rest of the year, they remained somewhat stationary near the bottom. On the other hand, the juveniles continued their diurnal vertical migrations throughout the year. In Long Island Sound the adults were most abundant near the bottom during the cold half of the year, the time of least light and breeding activity. Their own behavior, as well as the lack of light by which to see, increased their vul-

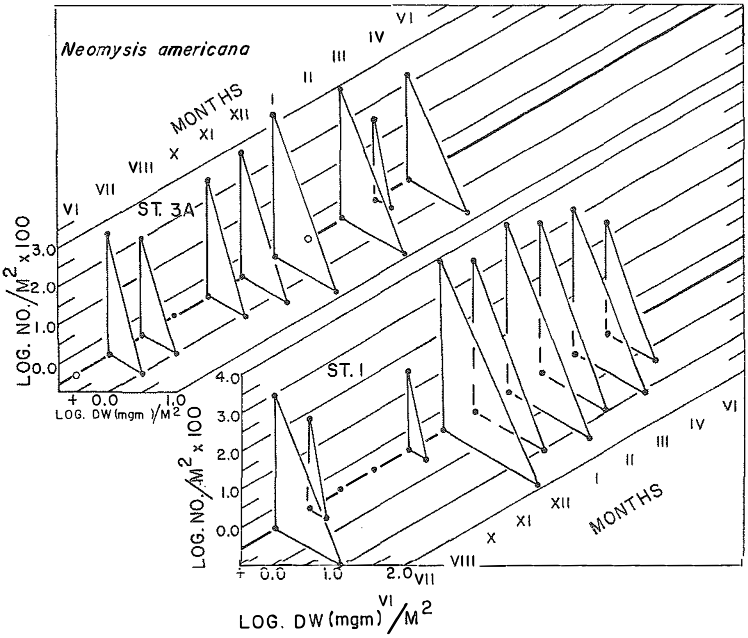

Figure 6. Standing crops of *Neomysis americana* by number (NO.) and dry weight (DW) for each collection date at Stations 1 and 3A with the 1.5-mm mesh net only. No collections from St. 1 in September or May; no collections from St. 3A in June 1960, September, February, or May. Plus signs in abcissas denote dry weights less than one milligram.

nerability, not only to the dredge but also to fish predators. In the warm half of the year, the increased spawning activity of mysids decreased their abundance near the bottom. Dredge samples and fish stomachs contained fewer mysids during this time of year than during the winter and spring (Richards, 1963b).

Size is usually measured from the anterior edge of the eye socket or of the tip of the rostrum to the posterior tip of the telson. Because the posterior end of the telson was frequently broken off, linear measurements were made from the anterior tip of the rostrum to the base of the telson. This "standard" length is convertible to total length by the following formula: Total length = 1.10 × "standard" length + 0.65. The discussion of size groups is based on "standard" lengths, but total lengths are given in parentheses for comparative purposes.

The length of *N. americana* ranged from 3.0 to 12.7 mm (4.0–14.6) (Fig. 7), and this compared favorably with the range of the mysids taken from fish stomachs (Richards, 1963b). Throughout the year both the range in length and the mean length increased progressively. They ranged from 4.0 to 8.9 with a mean of 6.5 mm (5.1–10.4, $\overline{7.8}$) in the spring, and increased to 3.5–10.4 with a mean of 7.0 mm (3.9–12.1, $\overline{8.4}$) in the fall, and to 3.5–12.7 with a mean of 8.5 mm (3.9–14.6, $\overline{10.0}$) in winter and early spring.

N. americana could be divided into two distinct groups on the basis of size: less than 6.0 mm (T.L. = 7.3), and 6.5 mm (7.8) and above. This break also appeared in the cumulative percentages of the length frequencies plotted on probability paper by the method of Harding (1949). Apparently, these groups represented two stages of maturity, juveniles and adults, and not two separate year-classes.

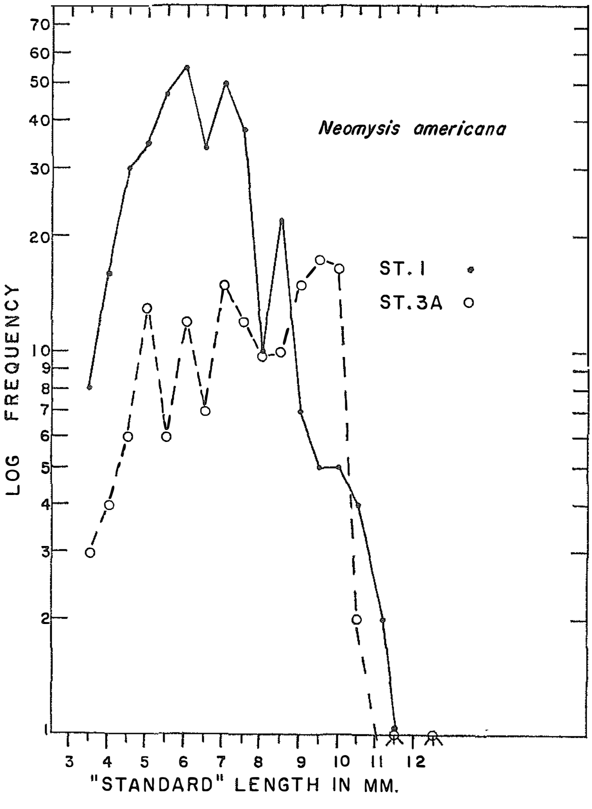

Figure 7. Catch curves for *Neomysis americana* from Stations 1 and 3A.

Within the first group, the juveniles, the appearance of any significant differences in mean length at each season was prevented by the constant influx of new individuals (Table VI). Recently hatched mysids were not taken in the dredge, but they occurred pelagically in all months with the exception of July and August (Deevey, 1956). Small juveniles, 3.0–3.5 mm (T.L. 4.0–4.5) were found in the dredge hauls between November and March and again in June. Those between 3.0 and 6.0 mm (5.0–7.5) occurred in greatest quantity from December to March. The mean lengths of the adults, on the

TABLE VI. MEAN "STANDARD" LENGTHS (mm) OF EACH SIZE GROUP OF *Neomysis americana* BASED ON THE COMBINED DATA FROM STATIONS 1 AND 3 A. MEAN TOTAL LENGTHS IN PARENTHESES.

GROUPS	SEASONS			
	Summer	Fall	Winter	Spring
Juveniles (<6.0)	5.6 (6.8)	5.4 (6.6)	5.3 (6.5)	5.7 (6.9)
Adults (>6.5)	7.2 (8.6)	7.9 (9.3)	8.0 (9.5)	8.5 (10.0)

other hand, increased progressively from summer through the following spring, the season in which the largest individuals occurred (Table VI).

Growth estimates were difficult, because of the paucity of larvae and the overlap in sizes of adults at various ages, calculated on a monthly basis. Estimates were further complicated by the breeding cycle.

N. americana breeds throughout the year with peaks of activity occurring at various times. In Narragansett Bay, Rhode Island, the two major spawning peaks were in May–June and in October (Herman, 1963). In Long Island Sound, ovigerous females were caught in April and in June. Under such circumstances, it was difficult to state whether a mysid hatched in spring grew to 10 mm by fall and spawned then, or whether it grew to 10 mm by the following spring and spawned.

Individuals from various length categories were weighed separately in June and in January. The wet weights ranged from 1.7 to 7.1 mg and the dry weights (not decalcified) from 0.3 to 1.4 mg. There were significant differences in weights of mysids taken in June from those taken in January. Mysids were heavier in June than in January, yet the slopes of the rate of weight increase were similar. Within the June group, slightly heavier ovigerous females produced a curvilinear increase in weight with size, which was more obvious in dry weight than wet weight. Since weight varied significantly with the season, two formulas expressing the weight-length relationship were calculated, and both were utilized in the estimates of productivity. Weights of those between April and September were calculated from:

$$\text{Log DW} + 1 = 0.742 \text{ Log L} - 0.353,$$

and weights of those from October through March were calculated from:

$$\text{Log DW} + 1 = 0.975 \text{ Log L} - 0.598.$$

Log L refers to the logarithm of the "standard" length, and may partially account for the obvious lack of isometry in the rate of increase of weight. The differences between these slopes and the expected one of 3.0 was so great, however, that some other factor must be involved.

Productivity estimates of the combined data from both stations were based on the catch in all four seasons of two size groups constituting juveniles and the adults. A total annual production of 36.2 mg/m^2 (dry weight) gave a ratio with the mean standing crop (9.9 mg/m^2) of 3.66, which falls between those for long-lived and short-lived species (Sanders, 1956). Constant recruitment, breeding migrations, and sampling error affected the estimates both of productivity and standing crop. Considering these factors, as well as the possibility that individuals may breed twice, the calculated turnover rate of 3.66 appeared to be a little low.

Total mortality, roughly approximated from the catch curve (Fig. 7), varied with size. A decline in frequency occurred at 8.5 mm at St. 1 and at 10.4 mm (T.L. 12.1) at St. 3A. Considering only the latter, the rate of decrease was approximately 99%, most of which was probably caused by fish predation. More than 75% of the species of juvenile demersal fishes and 25% of the individuals ate this organism in Long Island Sound. It should also be noted that heavy predation by *Crangon septemspinosa* was found in Narragansett Bay by Herman (1963).

Neomysis americana is primarily a filter feeder (Hopkins, 1958), and gut contents of those from Long Island Sound consisted primarily of green food remains. Its greatest abundance coincided with the late winter plankton bloom (Conover, 1956), which occurred a few weeks prior to the beginning of the mysid breeding season.

Crangon septemspinosa. Sand shrimp, which are undoubtedly one of the most common invertebrates in southern New England waters, were almost always among the ten most abundant species in our samples both numerically and by weight (Tables III A, B). Their mean standing crop at St. 1 by number was 6.62/m^2, 9% of all epifauna, and their mean biomass was 0.135 g/m^2, 10% of all epifauna. At St. 3A the mean number was 0.44/m^2, 11% of all epifauna, and the mean biomass was 0.006 g/m^2, 3% of the total epifauna. At St. 1 fluctuations about these averages were less than at St. 3A. The greater stability of the population at St. 1 resulted in a more accurate estimate of the annual production there than at St. 3A.

Patchiness and aggregation, indicated by the numerical data from both stations (Appendix Table II), obscured seasonal changes in shrimp abundance. Although fluctuations were slight, increased standing crops were noted at both stations during late summer, the season of maximum water temperatures, and during late winter, the time of minimum temperatures (Fig. 8). Perhaps the increased abundance, at least in winter, was the result of offshore movement. Shrimp are common in the estuaries during most of the year except the winter, a time when they apparently disperse into deeper water, perhaps to prevent the type of osmoregulatory difficulties indicated by Flugel (1960), who found that the efficiency of osmoregulation decreased so much in brackish water of low temperature (less than 5°C) that *Crangon crangon* would be unable to live in such an environment in the winter. Under conditions of high temperatures osmoregulatory efficiency was also affected.

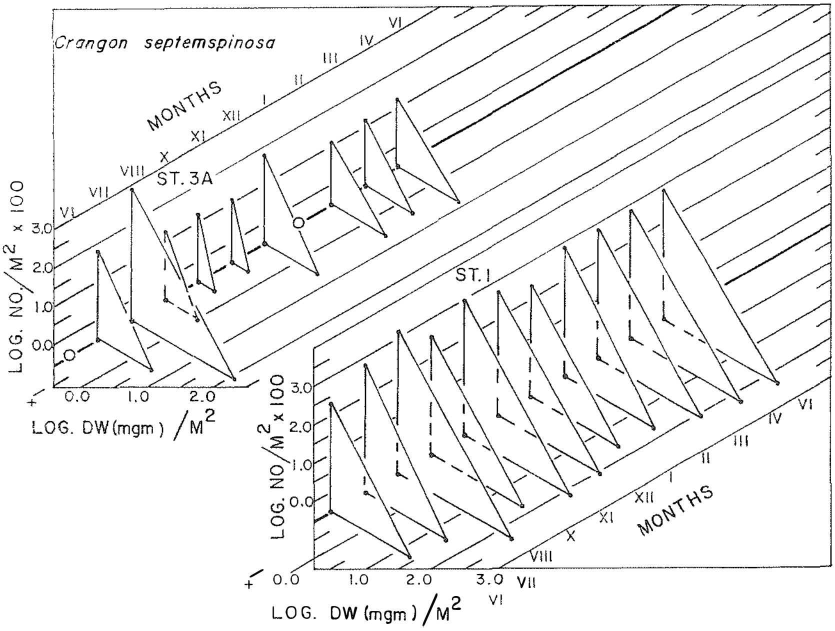

Figure 8. Standing crops of *Crangon septemspinosa* by number (NO.) and dry weight (DW) for each collection date at Stations 1 and 3A. No collections from St. 1 in September or May; no collections from St. 3A in June 1960, September, February, or May. Plus signs in abcissas denote dry weights less than one milligram.

While the Long Island Sound survey was in progress, Price (1962) investigated certain aspects of the life history of *Crangon septemspinosa* from Delaware Bay. Our data are similar to his, and many of his conclusions, as well as those of Allen (1960) concerning *Crangon allmani* in British waters, are pertinent to the Long Island Sound shrimp population.

There were differences, however, in the methods of measuring length. Price (1962) measured "total" length from the anterior tip of the spine on the antennal scale to the posterior tip of the telson; we measured "standard" length from the anterior tip of the rostrum to the base of the telson. A regression analysis of "total" length (T.L.) on "standard" length (S.L.) resulted in a straight line relationship expressed as,

$$\text{T.L.} = 1.48\ \text{S.L.} - 0.06.$$

In the sections of this paper that contain comparisons with Price's data, total lengths converted from "standard" lengths are included in parentheses. Weight-length relationships, age analyses, mortality estimates, etc. of the Long Island Sound population are based on "standard" lengths. The sex of specimens less than 16 mm (23.1 T.L.) was not determined. Fol-

TABLE VII. Range and Mean "Standard" Lengths of *Crangon septemspinosa* Collected with a 6.3-mm Mesh and a 1.5-mm Mesh Net at Stations 1 and 3 A in Long Island Sound. Percentage of Ovigerous Females is Included.

	STATION 1				STATION 3 A			
	6.3 mm		1.5 mm		6.3 mm		1.5 mm	
Month*	Range	Mean	Range	Mean	Range	Mean	Range	Mean
VI	8–29	19.3	3–27	8.7	–	–	–	–
VII	8–30	13.9	4–22	8.3	–	–	5–18	11.4
VIII	12–27	19.4	6–28	18.4	7–25	16.9	3–20	8.2
X	13–24	19.3	5–27	16.7	–	–	–	–
XI	8–29	18.4	4–29	16.8	6–4	–	4–16	8.8
XII	10–37	20.5	10–31	19.6	–	–	–	–
I	9–34	17.9	9–32	18.3	–	–	–	–
II	11–26	16.2	7–27	12.9	–	–	–	–
III	13–38	24.4	7–25	13.8	–	–	–	–
IV	11–39	25.8	13–34	25.5	9–29	20.0	8–11	9.5
VI	16–34	25.1	15–23	–	15–31	23.5	16–23	19.8

6.3 and 1.5-mm mesh net tows combined.

	STATION 1		STATION 3 A		PERCENTAGE OVIGEROUS FEMALES	
	Range	Mean	Range	Mean	Station 1	Station 3 A
VI	3–29	11.8	–	–	15	–
VII	4–30	10.2	5–18	11.4	3	7
VIII	6–28	19.2	3–25	15.3	49	17
X	5–27	18.1	9–22	–	13	0
XI	4–29	17.3	5–18	8.8	0	0
XII	10–37	20.0	8–10	8.7	2	0
I	9–34	18.2	7–15	11.1	0	0
II	7–27	14.5	–	–	1	–
III	7–38	16.9	9–32	19.7	3	0
IV	11–39	25.6	8–29	16.9	12	14
VI	16–34	25.1	15–31	22.5	36	17

* No collections were made at either station in September or May, and at Station 3A in June 1960 or in February 1961.

lowing the procedure of Price (1962), all such specimens are listed as immature.

The range in length of sand shrimp from Long Island Sound depended upon the mesh size of the net (Table VII). The stramin net caught a greater number of shrimp of small size, while the 6.3-mm mesh net took a greater number of large size. The mean length of those taken with the 6.3-mm mesh usually averaged between 2 and 11 mm longer than those taken in the stramin net. Therefore, the data from both tows were combined. In addition, a difference existed between shrimp from the two localities in both range of length and in mean length. Shrimp from St. 1 averaged 3 to 11 mm longer than those from offshore, particularly during fall and spring (Table VII). The cause of this difference is unknown, but it may be a result of the distribution of pelagic larval stages.

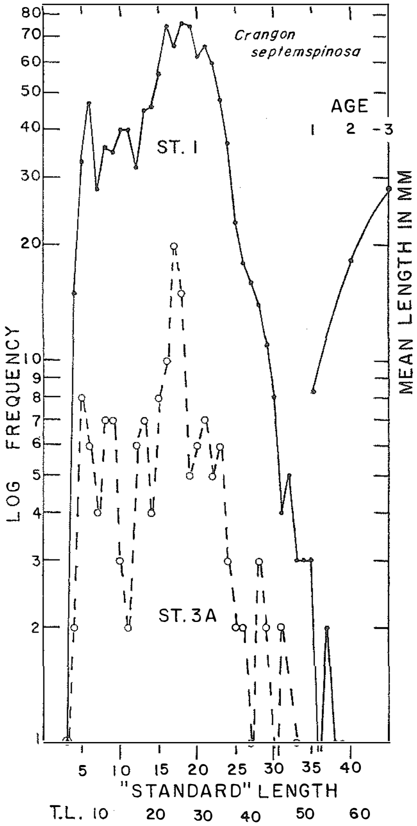

Figure 9. Catch curves of *Crangon septemspinosa* from Stations 1 and 3A. Linear growth curve from St. 1 only.

Catch curves and length frequencies were analysed for each station separately (Fig. 9). Delaware Bay female shrimp ranged from 5.9 to 70 mm (T.L.), the males only to 47 mm (T.L.) (Price, 1962). Females in a sample from Frenchman's Bay, Maine (taken by Richards) were as long as 78 mm (T.L.). Female shrimp from Long Island Sound ranged from 3 (4.4) to 39 mm (57.1), and males only to 34 mm (49.7). The majority of all shrimp were between 14 and 25 mm (21–37). Shrimp from St. 3A only, ranged from 3 to 31 mm (4.4–45.3), the majority between 20 and 23 mm (30–34).

Seasonal variations in length frequencies resulted principally from the influx of recruits, growth, and the time of breeding. At all times, at least two peaks occurred in the frequencies and usually there were three. Seasonal changes in the positions of these peaks indicated the fluctuations in abundance and in size of the age groups constituting the population. A large number of newly hatched specimens first joined the population in June; recruits continued to appear through November. During June–July, two other groups were present, one varying in length from 8 to 19 mm and containing no ovigerous females, the other, longer than 20 mm and containing ovigerous females. Egg-bearing females of the 8-to-19-mm group appeared from August through October. From December through March, a stable population occurred, consisting of three groups none of which showed any increase in length. These groups ranged in length from 7 to 13 mm and 14 to 24 mm, and greater than 25 mm. Growth occurred in the spring, and the recruits of the preceding summer constituted the non-breeding group in the 8-to-19-mm category. The only other group present in early spring was made up of the large specimens, 23 to 39 mm, belonging to the older year-classes in which ovigerous females between 27 and 39 mm were common. Evidence from change in the position of the peaks in length frequencies, combined with the results of a probability plot of cumulative percentages of length frequencies (Harding, 1949), indicated that Long Island Sound shrimp averaged 12 mm (17.7 T.L.) at the end of their first year, and 24 mm (35.2) at the end of their second year. No estimates were made of the size at the end of the third year, because specimens as old as that were rare in the area.

These results differ somewhat from those of Price (1962). Specimens from Delaware Bay were 16 mm (23) at the end of their first year, and 29 mm (42) at the end of their second year. Price (1962) calculated a growth rate of 1.6 mm per month, which showed no seasonal variations. Our data indicate that growth either stopped or slowed down during the winter. The differences in mean sizes at the end of each year were approximately equal to the total amount of growth for three months based on an increase of 1.6 mm per month. Apparently, winter growth in Delaware Bay accounted for the differences in ultimate mean size of each year-class between the two regions.

The breeding season in Long Island Sound was similar to that in Delaware Bay. Ovigerous females occurred in all months except November and January (Table VII). One-year-olds spawned from August through October, the older groups spawned throughout the rest of the year. The greatest percentage of two-year-old ovigerous females occurred in June.

Mortality in the second and third years, estimated from the right limb of the catch curve (Fig. 9), varied between 84 and 87%. No estimates of mortality were made during the first year.

Analyses of weight-length relationships of *C. septemspinosa* from Long Island Sound were extensive and involved non-decalcified wet and dry weights and calcium-free wet and dry weights for shrimp of different size categories at different seasons of the year. Calcium-free dry weight was found to be the most accurate, because its rate of increase varied little between seasons, except in winter, or between size groups. The regression formula, based on all collections, is,

$$\text{Log DW} = 2.869 \text{ Log L} - 2.303,$$

with a standard error of 0.157 and a 99%-fiducial limit of 0.194. Dry weights ranged from 2 to 79 mg. Weight estimates were combined with the length-frequency data in order to calculate annual productivity.

Shrimp production at St. 1 was estimated separately from that of St. 3A, because of the differences in sizes and densities between the two areas. Random movement of shrimp in and out of these areas was automatically included and perhaps produced significant errors that would be more pronounced at St. 3A than at St. 1.

The estimated production at St. 1 was 0.519 g/m^2 in a year, resulting in a ratio of 3.82 with the standing crop (0.135 g/m^2). This ratio appeared to be reasonable; it was not as high as those amphipods with two generations per year, nor as low as those for long-lived polychaetes and molluscs (Sanders, 1956). At St. 3A a gross production of 0.071 g/m^2 in a year resulted in a ratio of 11.88 to the standing crop, which was much too high.

The importance of shrimp production to the total community is obvious. Not only did *Crangon septemspinosa* constitute 10% of the entire epifauna, but it constituted a major portion of the food of many species of demersal fish in both Delaware Bay (Fitz and Daiber, 1963) and Long Island Sound (Richards, 1963b, c). Moreover, shrimp are both scavengers and carnivores (Price, 1962; Herman, 1963). The presence of sand in the gastric mills of Long Island Sound shrimp along with *N. americana* and unidentified polychaetes showed that these shrimp were benthic carnivores at least part of the time, exploiting the same food resources as the juvenile demersal fish.

Asterias forbesi. Because of their destruction of commercially valuable shellfish in southern New England, starfish have been investigated extensively (e.g., Mead, 1901; Galtsoff and Loosanoff, 1939; Burkenroad, 1946; Loosanoff, 1961). Data from our survey concerning their general abundance, size, food, etc., were similar to those of previous investigators. Starfish densities were of the same order of magnitude in 1960–61 as in 1935–36. Burkenroad (1946) estimated a standing crop of 13.7 g/m^2 (wet weight) in water less than 40 feet deep, and 5.6 g/m^2 for Long Island Sound as a whole. In 1960–61 the mean biomass at St. 1 was 10.91 g/m^2 (wet weight), at St. 3A, it was 1.72 g/m^2.

In terms of weight, *A. forbesi* was among the ten commonest species in every tow (Table III A, B). Numerically, it occurred less frequently in this group. At St. 1, the mean biomass of 0.770 g/m^2 (dry weight) constituted 57% of all epifauna, but the mean number, 2.25/m^2, constituted only 3%. At St. 3A,

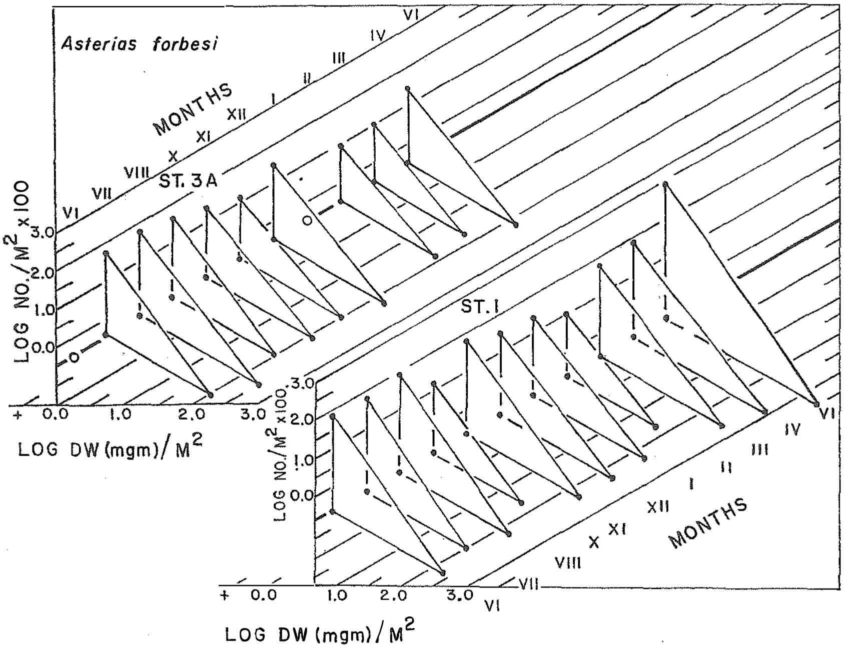

Figure 10. Standing crops of *Asterias forbesi* by number (NO.) and dry weight (DW) from Stations 1 and 3A. No collections from St. 1 in September or May; no collections from St. 3A in June 1960, September, February, or May. Plus signs in abcissas denote dry weights less than one milligram.

the mean biomass of 0.124 g/m² constituted 69% of all epifauna, while the mean number, 0.24/m², was 6%.

No extensive seasonal movements or migrations were expected (Galtsoff and Loosanoff, 1939). Nevertheless, a slight decrease in abundance occurred during the fall and winter and an increase during the spring (Fig. 10). The general decrease in October at St. 1 coincided with a huge increase in numbers further inshore (Herman R. Glas, personal communication). No correlations were made at other seasons. Fluctuations in abundance between Stations 1 and 3A were independent. That these two groups remained somewhat separate was further indicated by differences in their age structures based on length frequencies and experimental data (Galtsoff and Loosanoff, 1939).

Starfish were measured according to the method of Galtsoff and Loosanoff (1939), which is illustrated in Fig. 11. Both wet and calcium-free dry weights were recorded. The general range in size of 571 starfish was from less than 1 mm to 155 mm; the majority were between 60 and 90 mm (Fig. 11). Metamorphosing larvae, which were 3 mm or less, were not weighed. Wet weights of the larger animals ranged from 0.086 to 59.63 g. Dry weights ranged from 0.035 to 1.344 g. At St. 1 the range in length was from less than 1 mm to

150 mm, and the mean was 73 mm. Included were metamorphosing larvae and small starfish from 14.8 mm to less than 1 mm. At St. 3A, on the other hand, no larvae occurred; the size range was 40 to 155 mm, and the mean was 79 mm. Seasonal fluctuations in the size of starfish were noticeable at both stations. The influx of the new year-classes during summer and fall decreased the mean sizes of the populations. At St. 1, excluding larvae, the mean size was 79 mm in spring and decreased to 61 mm in the summer, while at St. 3A, a spring mean of 82 mm was followed by a decrease in summer to 76 mm.

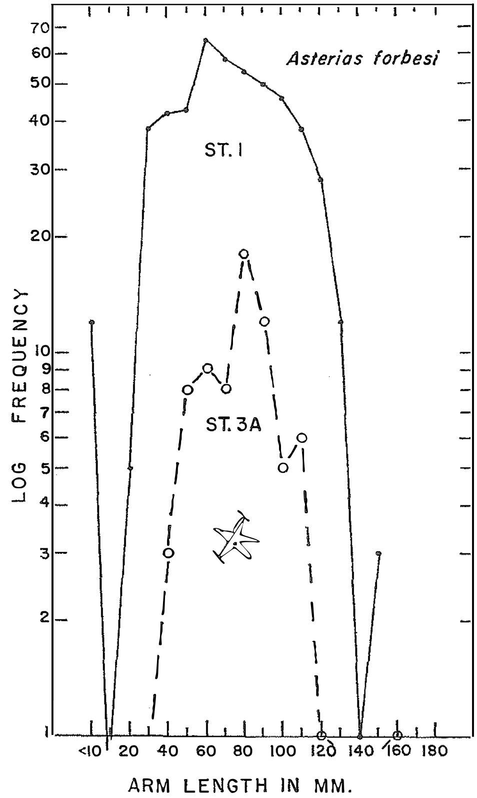

Figure 11. Catch curves of *Asterias forbesi* from Stations 1 and 3A.

During the late 1950's, a peak in starfish density apparently occurred (Richards, 1963a), and this resulted in a decrease in growth rate. Our epifauna survey occurred toward the end of this period and we caught a larger percentage of smaller specimens than did Galtsoff and Loosanoff (1939). Experimentally, these authors estimated the maximum length of a zero-year starfish to be

TABLE VIII. MEAN SIZE (mm) OF EACH YEAR CLASS OF *Asterias forbesi* FROM STATIONS 1 AND 3 A DURING THE SEASONS OF THE YEAR.

STATION	SEASON			
	Summer	Fall	Winter	Spring
		0-year		
1	28	45	44	47
3 A	48	55	50	51
		1-year		
1	74	90	115	94
3 A	86	95	73	86
		2-year		
1	–	–	140	134
3 A	–	155	–	–
		Total Number Measured		
1	43	73	87	297
3 A	15	24	8	24

approximately 80 mm. Our data indicate a maximum of approximately 65 mm. The first year-class ranged between 66 and 125 mm, and those of greater size were combined as the second year-class. The mean size of the zero-year group was slightly greater at St. 3 A than at St. 1 (Table VIII), because no specimens less than 40 mm occurred on the mud substrate. Dispersal of the larger members of this year-class from the hard bottom was indicated.

Weight-length relationships varied depending on whether wet or dry weights were measured. Variations in dry weights were caused by incomplete decalcification of the internal lattice-work and by disintegration of body material. The large fiducial limits of the regression of dry weights on lengths (Table IX), compared with those of wet weights, precluded the use of dry weights in the estimates of productivity.

TABLE IX. REGRESSION ANALYSES OF WET WEIGHT AND CALCIUM-FREE DRY WEIGHT ON LENGTH OF *Asterias forbesi* FROM STATIONS 1 AND 3 A, LONG ISLAND SOUND.

	STATIONS			
	1		3 A	
	Wet	Dry	Wet	Dry
Degrees of freedom	108	41	39	22
$b_1 = Sy(x-\bar{x})/s(x-\bar{x})^2$*	2.922	3.096	2.265	2.511
$b_0 = (\bar{y} - b_1 \bar{x})$	−2.677	−4.110	−2.576	−3.050
δ	0.017	0.128	0.122	0.255
99% Fiducial limits of β_1	0.017	0.240	0.306	0.959
Fiducial limits as a percentage of b_1	< 1%	7.8%	13.5%	38.1%

* Williams (1959).

Starfish from St. 1 increased in weight more rapidly than those from St. 3 A (Table IX). Not only were large specimens nearly always fatter at St. 1 than those of the same size at St. 3 A, but less variation occurred in their weight. The locality of St. 1 was a more favorable environment for starfish than the muddy area farther offshore.

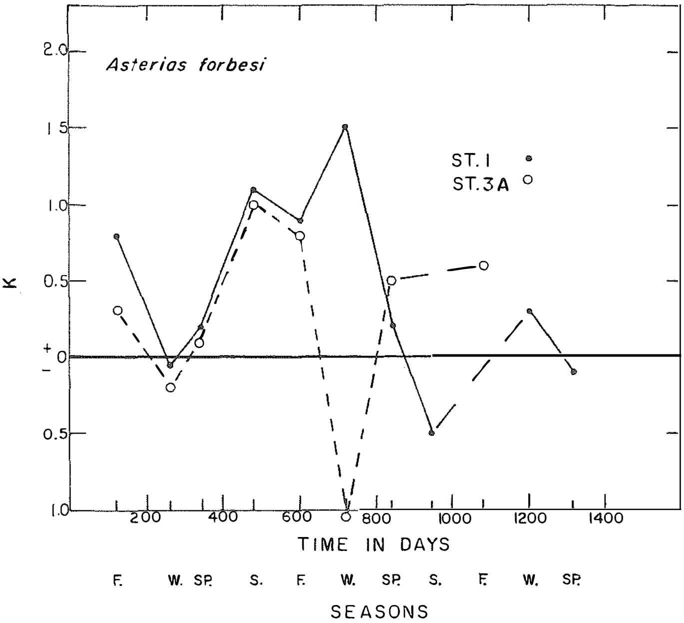

Figure 12. Change in instantaneous growth rates (k) of *Asterias forbesi* with time in days or with seasons. Data from Stations 1 and 3 A.

Instantaneous growth rates of starfish from each station were compared by plotting k (Brody, 1945) against time in days (Fig. 12). Growth rates at St. 1 were consistently greater than at St. 3 A. A large discrepancy occurred among the 1 $^1/_2$ year-olds. Those from St. 1 gained weight throughout the fall, whereas those from St. 3 A stopped growing. At both stations, k was negative during the winter, a period of no growth or actual decrease in weight resulting from poor feeding (Galtsoff and Loosanoff, 1939).

Production estimates demonstrated similar effects of the differences in the environments. Gross annual production at St. 1 was 104.16 g/m^2 and that for St. 3 A was 4.52 g/m^2. The standing crops were 10.91 g/m^2 and 1.72 g/m^2, respectively; the resulting ratios of productivity to standing crop were 9.54 at St. 1 and 2.64 at St. 3 A. All data combined produced a ratio of 8.61.

The large turnover rate at St. 1 was not entirely due to production. A large increase in numerical abundance of all year-classes occurred in the spring,

TABLE X. STOMACH CONTENTS OF *Asterias forbesi* FROM LONG ISLAND SOUND, 1960–1962.

	STATION 1			STATION 3 A		
		No.	%		No.	%
		Empty			Empty	
Total Number	362	317	88	118	80	68
Season:						
Summer	37	22	59	15	7	47
Fall	90	79	87	47	26	55
Winter	83	79	96	32	29	91
Spring	152	137	90	24	18	75
		With Food			With Food	
Total Number		45	12		38	32

Prey:	No. with:	%	Prey Size*	No. with:	%	Prey Size*
Hydroid	2	4	–	0	0	–
Nepthys sp. setae	0	0	–	1	3	–
Cistenides gouldii	0	0	–	2	5	22.4
Sand tube	0	0	–	1	3	–
Citheridea americana	1	2	–	0	0	–
Sarsiella zostericola	0	0	–	2	5	1.3
Neomysis americana	5	11	7.4–8.9	1	3	–
Leptocheirus pinguis	3	7	–	0	0	–
Unciola irrorata	1	2	–	0	0	–
Caprella linearis	2	4	4.8	0	0	–
Crangon septemspinosa	1	2	7.2†	0	0	–
Pagurus longicarpus	1	2	–	0	0	–
Neopanope t. sayi	1	2	–	1	3	–
Shell bits	6	13	–	2	5	–
Nucula proxima	0	0	–	12	32	1.0–4.3
Yoldia limatula	0	0	–	2	5	7.5
Lyonsia hyalina	1	2	–	0	0	–
Gemma gemma	0	0	–	1	3	–
Macoma tenta	2	4	7.2	0	0	–
Ensis directus	7	16	–	0	0	–
Mulinia lateralis	0	0	–	4	10	1.2–3.6
Clam-Unidentified	1	2	1.0–1.6	0	0	–
Crepidula sp.	3	7	–	0	0	–
Bittium alternatum	0	0	–	5	13	1.3–2.2
Nassarius trivittatus	2	4	3.0	0	0	–
Retusa canaliculata	0	0	–	13	34	1.4–3.7
Asterias forbesi	2	4	larva	0	0	–
Tautogolabrus adspersus	1	2	–	0	0	–
Sand and mud	27	–	–	12	–	–

* Length in mm.

† Carapace length only.

perhaps as a result of movement from shallower water. Thus, the mortality and growth estimates in spring included the effects of this movement. A turnover rate somewhere between that for St. 1 and that for St. 3A was perhaps correct.

The significance of such a great production of starfish is important, not only to the shellfish specialist, but also to the fish ecologist. In Long Island Sound, the juvenile demersal fish population is small compared to that of other areas (Richards, 1963b), while the phytoplankton and the infauna populations are large (Riley, 1955). Since nearly 50% of the epifauna consisted of *A. forbesi*, approximately one-half of it was unavailable as fish food. Burkenroad (1946) understandably felt that great changes would result in the animal populations in Long Island Sound if the numbers of *A. forbesi* were depleted.

Direct competition for food between starfish and demersal fish was suggested by Hatanaka and Kosaka (1959). In Sendai Bay, Japan, they found *Asterias amurensis* feeding on the same food utilized by the flounder, *Limanda yokohamae*. At both stations in Long Island Sound, a few crustaceans, such as *Neomysis americana*, some amphipods, and *Crangon septemspinosa*, were eaten occasionally by starfish. Since these prey were favorites of the fish, competition may have occurred. But the majority of the food found in starfish stomachs consisted of molluscs (Table X), which are not heavily preyed upon by fish, with the exception of *Stenotomus chrysops* and *Sphaeroides maculatus* (Richards, 1963b). *Ensis directus*, *Macoma tenta*, *Nassarius trivittatus*, and *Crepidula* sp. were eaten by starfish at St. 1, while *Nucula proxima*, *Mulinia lateralis*, *Bittium alternatum*, and *Retusa canaliculata* were eaten at St. 3A. The high percentage of empty stomachs (Table X) was misleading, particularly among the starfish at St. 1, where they probably preyed upon large lamellibranchs. Starfish from St. 3A, however, were more dependent upon burrowing molluscs, most of which were of smaller size than the lamellibranchs on the hard substrate. Empty stomachs in winter (Table X) were expected, because starfish seldom eat during that time of year (Loosanoff, 1961). It would seem that direct competition for food between *Asterias forbesi* and fish was not important in Long Island Sound. There was indirect competition in that the starfish were able to utilize a large percentage of the organic material available. The direct competition for the large stock of planktonic food was at a lower level in the food chain, however, and the kinds of animals that developed were, for reasons by no means well understood, the sort that were suitable for supporting starfish and much less effective as food for fin fish.

DISCUSSION

Since delineation of the role of the benthic epifauna in the community structure partially depended upon an analysis of their importance as fish food, their production in terms of organic content was important. To put the data into these terms, samples taken at all seasons of the year were ashed in a muffle furnace in order to determine the relation between dry weight and organic content in the various species concerned. The percentages obtained were applied to information already available on the dry weight of the standing crop and the turnover rate. Estimates of organic content of each important constituent are listed in Table XI, and in the remainder of the discussion the terms standing crop and production will specifically refer to organic matter.

The estimates in Table XI include only those species discussed. Under "others" are ten species or species-groups whose standing crops have not been discussed, but are listed in Appendix Table II. No annual production figures are given, but a reasonable estimate, derived in a similar fashion to the figures for the species discussed, is 306 mg/m^2. This is made up chiefly of amphipods, *Pagurus* spp., *Cancer irroratus*, and *Nassarius trivittatus*. For purposes of comparison, estimates of the production of infauna (Sanders, 1956) and juvenile fish (Richards, 1963a, b) are included.

TABLE XI. STANDING CROPS AND ANNUAL PRODUCTION OF ORGANIC MATTER OF BENTHIC SPECIES IMPORTANT AS JUVENILE FISH FOOD. DATA FROM STATIONS 1 AND 3 A ARE COMBINED AND EXPRESSED IN MILLIGRAMS.

	Mean St. Crop in Dry Weight/m^2	Mean St. Crop in Organic Weight/m^2	Turnover Rate	Annual Production In organic Weight/m^2
From this Survey:				
Ampharete acutifrons ...	5.5	4.3	4.58	19.7
Neomysis americana	5.0	4.9	3.66	17.9
Crangon septemspinosa ...	102.6	99.5	3.82	380.1
Asterias forbesi	603.9	585.8	8.61	5043.7
Others	299.1	284.1	–	306.0*
TOTAL...	1016.1	1262.7		5767.4
From Sanders (1956):				
Nepthys incisa	1915.3	1551.3	2.16	3350.8
Amphipods	1445.1	1300.6	5.00	6503.0
Others	3360.4	–	–	–
TOTAL...	8624.0	7761.6	2.58	20024.9
Demersal Fish				
Juveniles	15.2	14.7†	2.10**	30.9

* Summed data for eight groups: *Lepidonotus squamatus*, amphipods, *Unciola irrorata*, caprellids, *Pagurus* spp., *Cancer irroratus*, *Nassarius trivittatus*.

† Dry weight and ash content percentages determined from Vinogradov (1953).

** Turnover rate estimated from Richards (1963 b). Note that the turnover rate estimated from Pearcy (1962 a) is 2.55 for *Pseudopleuronectes americanus* in the Mystic River, Connecticut, a suitable environment for juveniles.

Asterias forbesi constituted 46% of the standing crop of epifauna, but as much as 87% of the production. No other epifaunal species produced as much material as the starfish. The next most abundant species, *Crangon septemspinosa*, produced 6.5% of the total production of organic material.

Of the infauna, *Nepthys incisa* and amphipods, constituting 36% of the standing crop, made up 17% and 32% of the production respectively.

The species that formed important demersal fish food were divided into two groups: adult fish food and juvenile fish prey. The former included *Nepthys incisa* and other polychaetes, *Neomysis americana*, amphipods, *Crangon septemspinosa*, and crabs (e.g., Smith, 1950; Richards et al., 1963; Fitz and Daiber, 1963). According to Sanders (1956), the infaunal component of this group of prey constituted 50% of the total infaunal production, excluding meiofauna and bacteria. Organic matter production based on catches by the oyster dredge of the crabs and semi-pelagic crustaceans approximated 13% of that of starfish and only 11% of that of the total epifauna. An estimate of the organic matter produced by adult fish prey (11,500 mg/m^2), calculated from the combined catches of the two types of gear (Table XI), amounted to 45% of that of all benthic invertebrates.

Aside from zooplankton, prey of juvenile fish consisted of many of the same species, with the exception of the crabs. Production of the infaunal component of this group was similar to that mentioned above. Production of the group as a whole, based on oyster dredge collections, constituted 8% of that of the total epifauna. Further breakdown of this group included only principal prey: *Ampharete acutifrons*, *Neomysis americana*, and *Crangon septemspinosa*. Their combined annual production was less than 1/10th that of the starfish and amounted to 7% of the total epifauna.

In attempting to compare productivity of fish with their prey, the problems are more difficult. The diet of fish tends to change with age, making an overall estimate more complicated. The standing crop of adult fish was perhaps underestimated in the collections of the small fish trawl, and movements of the fish made assessment of the stock uncertain. Moreover, the heavier elements in the infauna became more important as prey with increasing age of the fish. This was particularly true of *Nepthys incisa*. This species and others of like habit were not sampled adequately by the oyster dredge. Although the above estimates are approximations, they indicated that large amounts of organic matter flowed in directions not directly useful to the fish; that is, to bacteria, nematodes, and starfish.

As indicated in earlier papers, the majority of the species of juvenile demersal fishes consumed the same species of prey, namely copepods, *Neomysis americana*, and *Crangon septemspinosa*. Copepods (chiefly *Temora longicornis*), being abundant and small, were particularly suitable as food for fish larvae and fry and were an excellent source of supplementary food for large juveniles, especially during winter and spring.

Neomysis americana was an important food for juvenile fish of all sizes, because of its numerical abundance and its vertical migratory pattern. Both factors would tend to permit extensive feeding without over-depletion of the stock of prey, thus preventing extensive interspecific competition among the juvenile fish. In addition, adult mysids tended to be entirely benthic during the winter and this increased their availability as food at a time when the variety of crustacean predators increased. Competition for the ubiquitous *C. septemspinosa* also was a possibility, not only within the demersal fish community, but also between these species and pelagic fish predators. Nevertheless, the fact that the sand shrimp is probably the favorite food of fish along the Atlantic coast attests to its abundance and to factors preventing serious competition. In Long Island Sound, not only did sand shrimp occur in all localities, both inshore and offshore, but its production was one of the highest of all fish prey.

The winter flounder, *Pseudopleuronectes americanus*, which is undoubtedly the most abundant demersal fish in these waters, usually inhabits estuaries and inshore waters during its larval and much of its early juvenile life. Hence it is removed from direct competition with most of the other juvenile fish under consideration, despite similarities in diet (Pearcy, 1962b). Juveniles caught at Stations 1 and 3A specialized on prey less utilized by other species. Of these, one of the most important was *Ampharete acutifrons*, whose turnover rate was almost that of the amphipods, the second favorite group of prey of the flounder. These polychaetes and amphipods, which are short-lived and produce two generations per year, not only occurred in the open waters of the Sound, but also inhabited the estuaries, where zero- and first-year *Pseudopleuronectes americanus* abounded. The adult flounder in this area most likely fed upon the most abundant polychaete in the infauna, *Nepthys incisa*, as well as on productive amphipods. Adults of other predator species, while still concentrating on semi-pelagic crustaceans and on amphipods, added crabs to their diets.

Apparently, enough food of sufficient variety existed in Long Island Sound to support the meager fish population dominated by *Pseudopleuronectes americanus*. Nevertheless, increased abundance or diversity of the fish population can not be expected. The muddy nature of the substrate over much of the Sound, the inefficiency of zooplankton feeding (Riley, 1955), the abundance of the indigenous meiofauna, as well as the huge production of *Asterias forbesi* in the open waters, precludes the possibility of a vigorous fish population of large individuals in this area.

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REFERENCES

ALLEN, J. A.
1960. On the biology of *Crangon allmani* Kinahan in Northumberland waters. J. Mar. biol. Ass. U. K., n.s. *39*: 481–508.

BRODY, S.
1945. Bioenergetics and growth. Reinhold, New York, 1,023 pp.

BURKENROAD, M. D.
1946. General discussion of problems involved in starfish utilization. Bull. Bingham oceanogr. Coll., 9 (3): 44–58.

CAREY, A. G., JR.
1962. An ecological study of two benthic animal populations in Long Island Sound. Ph. D. dissertation, Yale University: 61 pp., appendices.

CONOVER, S. A. M.
1956. Oceanography of Long Island Sound, 1952–1954. IV. Phytoplankton. Bull. Bingham oceanogr. Coll., *15*: 62–112.

DEEVEY, G. B.
1956. Oceanography of Long Island Sound, 1952–1954. V. Zooplankton. Bull. Bingham oceanogr. Coll., *15*: 113–155.

DICKIE, L. M.
1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. J. Fish. Res. Bd. Can., *12*: 797–857.

DRAGOLI, A. L.
1961. Peculiar feeding habits in the Black Sea polychaete *Melinna palmata* Grube. Dokl. Akad. Nauk SSSR (Eng. Transl. biol. Sci. Sec.), *138*: 970–973.

FAGER, E. W.
1957. Determination and analysis of recurrent groups. Ecology, *38*: 586–595.

FITZ, E. S., JR. and F. C. DAIBER
1963. An introduction to the biology of *Raja eglanteria* Bosc 1802 and *Raja erinacea* Mitchill 1825 as they occur in Delaware Bay. Bull. Bingham oceanogr. Coll., *18* (3): 69–97.

FLUGEL, HANSJURGEN
1960. Über den Einfluss der Tempertur auf die osmotische Resistenz und die Osmoregulation der decapoden Garnele *Crangon crangon* L. Kieler Meeresforsch., *16*: 186–200.

GALTSOFF, P. S. and V. L. LOOSANOFF

1939. Natural history and method of controlling the starfish (*Asterias forbesi* Desor). Bull. U. S. Bur. Fish., *49*: 75–132.

HARDING, J. P.

1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. biol. Ass. U. K., n.s. *28*: 141–153.

HATANAKA, M. and M. KOSAKA

1959. Biological studies on the population of the starfish, *Asterias amurensis*, in Sendai Bay. Tohoku J. agric. Res., *9*: 159–178.

HERMAN, S. S.

1963. Vertical migration of the oppossum shrimp, *Neomysis americana* Smith. Limnol. & Oceanogr., *8*: 228–238.

HOPKINS, T. L.

1958. Mysid shrimp important fish food. Estuar. Bull., (Summer): 4–6.

HULBURT, E. M.

1957. The distribution of *Neomysis americana* in the estuary of the Delaware River. Limnol. & Oceanogr., *2*: 1–11.

LOOSANOFF, V. L.

1961. Biology and methods of controlling the starfish, *Asterias forbesi* (Desor). Fish. Leafl., Wash., No. 520: 11 pp.

MEAD, A. D.

1901. The natural history of the star-fish. Bull. U. S. Fish Comm. (1899), *19*: 203–224.

MILLS, E. L.

1963 a. A new species of Ampelisca (Crustacea: Amphipoda) from eastern North America, with notes on other species of the genus. Canad. J. Zool., *41*: 971–989.

1963 b. The biology of an ampeliscid amphipod crustacean sibling species pair. Ph. D. dissertation, Yale University: 160 pp.

PEARCY, W. G.

1962 a. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). III. Distribution, abundance, growth, and production of juveniles; survival of larvae and juveniles. Bull. Bingham oceanogr. Coll., *18* (1): 39–64.

1962 b. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). IV. Food habits of larvae and juveniles. Bull. Bingham oceanogr. Coll., *18* (1): 65–78.

PRICE, K. S., JR.

1962. Biology of the sand shrimp, *Crangon septemspinosa*, in the shore zone of the Delaware Bay region. Chesapeake Sci., *3*: 244–255.

RICHARDS, S. W.

1963 a. The demersal fish population of Long Island Sound. I. Species composition and relative abundance in two localities, 1956–57. Bull. Bingham oceanogr. Coll., *18* (2): 5–31.

1963 b. The demersal fish population of Long Island Sound. II. Food of the juveniles from a sand-shell locality (Station 1). Bull. Bingham oceanogr. Coll., *18* (2): 32–72.

1963 c. The demersal fish population of Long Island Sound. III. Food of the juveniles from a mud locality (Station 3A). Bull. Bingham oceanogr. Coll., *18* (2): 73–101.

RICHARDS, S. W., D. MERRIMAN, and L. H. CALHOUN
1963. Studies on the marine resources of southern New England. IX. The biology of the little skate, *Raja erinacea* Mitchill. Bull. Bingham oceanogr. Coll., *18* (3): 5–67.

RILEY, G. A.
1955. Review of the oceanography of Long Island Sound. Deep-Sea Res., 3 (suppl.): 224–238.
1956. Oceanography of Long Island Sound, 1952–1954. II. Physical oceanography. Bull. Bingham oceanogr. Coll., *15*: 15–46.
1959. Oceanography of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *17* (1): 9–30.

SANDERS, H. L.
1956. Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. Bull. Bingham oceanogr. Coll., *15*: 345–414.
1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. & Oceanogr., *3*: 245–258.
1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. & Oceanogr., *5*: 138–153.
Personal Communication, dated October 24, 1963.

SMITH, F. E.
1950. The benthos of Block Island Sound. Ph. D. dissertation, Yale University: 213 pp., appendices.

VINOGRADOV, A. P.
1953. The elementary chemical composition of marine organisms. Mem. Sears Found. Mar. Res., No. 2: 483–493, 497–503.

WILLIAMS, E. J.
1959. Regression analysis. John Wiley and Sons, New York, 214 pp.

APPENDIX TABLE I. List of Benthic Invertebrates and Fishes Taken in the Catches of the Modified Oyster Dredge from Stations 1 (×) and 3 A (+), Long Island Sound.

Protozoa:		
Foraminifera, unidentified		+
Porifera:		
Cliona sp.	×	
Microciona prolifera	×	
Bryozoa:		
Alcyonidium polyoum	×	
Bowerbankia gracilis	×	
Membranopora sp.	×	
Coelenterata:		
Thuiaria argentea	×	
Hydrallmania falcata	×	
Halecium halicinum	×	+
Obelia gelatinosa	×	+
Lafoea sp.	×	+
Cerianthus sp.		+
Astrangia danae		+
Turbellaria:		
Stylochus zebra	×	
Nemertina:		
Cephalothrix linearis	×	+
Cerebratulus luridus	×	
Amphiporus sp.	×	+
Unidentified (2)	×	+
Polychaeta:		
Lepidonotus squamatus	×	
Polynoidae, unidentified	×	
Eteone lactea	×	
Eteone longa ?	×	
Phyllodoce fragilis	×	
Phyllodoce groenlandica	×	+
Phyllodoce sp.	×	
Paranaitis speciosa	×	+
Eumida sanguinea	×	
Exogone dispar	×	
Autolytus cornutus		+
Neanthes succinea	×	
Nereis pelagica	×	
Nereis sp.	×	
Nepthys incisa	×	+
Nepthys caeca	×	
Nepthys sp.	×	
Polychaeta:		
Glycera dibranchiata	×	+
Glycera americana	×	
Glycera sp.	×	
Diopatra cuprea	×	
Onuphis nebulosa	×	+
Ninoe nigripes	×	+
Arabella iricolor	×	
Polydora ciliata	×	+
Streblospio benedicti		+
Spionidae, unidentified (2)	×	+
Flabelligera affinis	×	+
Travisia carnea	×	
Capitallidae, unidentified		+
Maldanid	×	
Maldane sp.	×	+
Cistenides gouldii		+
Melinna cristata	×	+
Ampharete acutifrons	×	+
Amage auricula	×	
Amphitrite sp.	×	
Lysilla alba		+
Polycirrus eximus	×	
Potamilla neglecta	×	
Sabella crassicornis	×	
Sabella microphthalma	×	
Eupomatus dianthus	×	
Unidentified	×	+
Crustacea:		
Cytheridea americana	×	+
Sarsiella zostericola		+
Centropages sp.	×	
Temora longicornis	×	
Eurytemora sp.		+
Labidocera aestiva		+
Acartia clausi	×	
Balanus balanoides		+
Neomysis americana	×	+
Heteromysis formosa	×	
Diastylis polita	×	
Oxyurostylis smithi		+
Edotea montosa	×	+
Bopyrid isopod	×	
Anonyx n. sp.	×	
Orchomenella minuta	×	+
*Ampelisca vadorum**	×	
*Ampelisca abdita**		+

(Continued)

(Appendix Table I continued)

Crustacea:		
Stenothoe cypris	×	
Calliopius laeviusculus	×	
Carinogammarus mucronatus	×	
Gammarus annulatus	×	+
Melita nitida	×	
Leptocheirus pinguis	×	+
Podoceropsis nitida	×	
Erichthonius brasiliensis	×	+
Unciola irrorata	×	+
Corophium sp.	×	+
Caprella linearis	×	+
Paracaprella tenuis	×	+
Deutella incerta	×	+
Caprellid	×	+
Crangon septemspinosa	×	+
Shrimp, unidentified		+
Pagurus longicarpus	×	+
Pagurus pollicaris	×	+
Pinnixia sayana		+
Ovalipes o. ocellatus	×	+
Callinectes sapidus		+
Cancer irroratus	×	+
Panopeus herbstii	×	
Neopanope texana sayi	×	+
Pelia mutica	×	
Libinia emarginata	×	
Mollusca:		
Nucula proxima	×	+
Yoldia limatula		+
Anadora transversa	×	
Anomia simplex	×	
Pandora gouldiana	×	+
Lyonsia hyalina	×	+
Cerastoderma pinnulatum	×	+
Mollusca:		
Gemma gemma		+
Macoma tenta	×	+
Ensis directus	×	
Mulinia lateralis	×	+
Saxicava arctica	×	
Polinices duplicatus	×	+
Crepidula fornicata	×	
Crepidula plana	×	+
Limpet, unidentified	×	
Cerithiopsis subulata	×	+
Siela adamsii	×	
Bittium alternatum	×	+
Eupleura caudata	×	
Mitrella lunata	×	+
Nassarius trivittatus	×	+
Retusa canaliculata	×	+
Cylichna alba		+
Aeolidia papillosa	×	+
Snail, unidentified		+
Chaetognatha:		
Sagitta sp.	×	
Echinodermata:		
Asterias forbesi	×	+
Pisces:		
Anchoa mitchilli	×	+
Anguilla rostrata	×	
Syngnathus fuscus	×	
Ammodytes hexapterus	×	
Prionotus carolinus	×	
Myoxocephalus aeneus	×	+
Scopthalmus aquosus	×	+
Pseudopleuronectes americanus	×	

* Described by Eric L. Mills (1963 a).

APPENDIX TABLE II. Abundance by Number per Square Meter (N), Dry Weight in Grams per Square Meter (DW), and Abundance Rank (in Parentheses) of 14 Selected Epifaunal Species, Listed in Order of their Abundance by Weight at Station 1.

	VI-24		VII-20		VIII-31		X-4		X-31		XII-5	
	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW
STATION 1:												
Asterias forbesi	0.93(4)	0.220(1)	0.85(3)	0.100(1)	1.05(7)	0.83 (3)	0.20(6)	0.044(3)	0.86(8)	0.248(3)	0.41(7)	0.245(1)
Crangon septemspinosa	2.01(2)	0.025(2)	6.18(1)	0.028(2)	17.44(1)	0.270(1)	3.28(1)	0.047(2)	9.47(1)	0.150(4)	4.92(2)	0.113(3)
Cancer irroratus	0 –	0 –	0.04(10)	+ (11)	0.04(10)	0.001(10)	0 –	0 –	0.23(10)	0.277(1)	0.08(11)	0.056(4)
Libinia emarginata	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Hydroids	–	0.004(5)	–	0.006(5)	–	0.015(7)	–	0.141(1)	–	0.093(6)	–	0.149(2)
Pagurus longicarpus	0.05(9)	0.003(6)	0.49(4)	0.018(3)	3.63(3)	0.267(2)	0.31(5)	0.007(5)	2.23(2)	0.103(5)	0.78(5)	0.036(6)
Pagurus pollicaris	0 –	0 –	0.02(11)	0.011(4)	0.01(11)	0.020(6)	0 –	0 –	0.12(11)	0.266(2)	0.06(12)	0.073(5)
Nassarius trivittatus	0.21(6)	0.004(4)	0.25(7)	0.003(7)	0.99(8)	0.081(4)	0.18(7)	0.009(4)	0.43(9)	0.016(8)	0.17(10)	0.008(9)
Neopanope texana sayi	0.10(7)	+ (8)	0.16(9)	0.002(8)	1.06(6)	0.035(5)	0.41(4)	0.006(6)	1.12(5)	0.082(7)	0.61(6)	0.019(8)
Neomysis americana	4.44(1)	0.004(3)	0.42(5)	+ (9)	0 –	0 –	0 –	0 –	0.12(12)	+ (12)	32.15(1)	0.027(7)
Crepidula plana	0 –	0 –	0 –	0 –	0.12(9)	+ (11)	0 –	0 –	1.04(6)	0.008(9)	1.26(4)	0.004(10)
Lepidonotus squamatus	1.65(3)	0.002(7)	1.86(2)	0.004(6)	1.84(4)	0.004(8)	0.15(8)	+ (7)	0.50(8)	0.001(10)	0.32(8)	0.002(11)
Caprellids	0.38(5)	+ (9)	0.18(8)	+ (12)	1.12(5)	+ (12)	0.66(2)	+ (9)	1.37(4)	+ (13)	4.44(3)	0.001(12)
Unciola irrorata	0.08(8)	+ (10)	0.40(6)	+ (10)	7.23(2)	0.004(9)	0.43(3)	+ (8)	2.16(3)	0.001(11)	0.32(9)	+ (13)
STATION 3 A:												
Asterias forbesi	–	–	0.43(2)	0.118(1)	0.52(2)	0.374(1)	0.33(1)	0.107(1)	0.22(2)	0.100(1)	0.12(4)	0.077(1)
Crangon septemspinosa	–	–	0.61(1)	0.004(2)	8.23(1)	0.111(2)	0.18(2)	0.001(3)	0.20(3)	+ (3)	0.12(3)	+ (5)
Cancer irroratus	–	–	0 –	0 –	0.11(6)	0.004(4)	0 –	0 –	0 –	0 –	0 –	0 –
Libinia emarginata	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Hydroids	–	–	–	0 –	–	0 –	–	+ (4)	–	0 –	–	+ (3)
Pagurus longicarpus	–	–	0 –	0 –	0 –	0 –	0.04(4)	+ (5)	0.04(5)	0.003(2)	0 –	0 –
Pagurus pollicaris	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Nassarius trivittatus	–	–	0.04(5)	0.001(3)	0.52(3)	0.013(3)	0.11(3)	0.002(2)	0 –	0 –	0.08(2)	0.004(2)
Neopanope texana sayi	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Neomysis americana	–	–	0.25(3)	+ (4)	0.21(5)	+ (5)	0 –	0 –	0.85(1)	+ (4)	3.58(1)	0.002(4)
Crepidula plana	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Lepidonotus squamatus	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Caprellids	–	–	0.14(4)	+ (5)	0.42(4)	+ (6)	0 –	0 –	0.06(4)	+ (5)	0.18(2)	+ (6)
Unciola irrorata	–	–	0 –	0 –	0 –	0 –	0 –	0 –	+ (6)	+ (6)	0.06(5)	+ (7)

(Continued)

(Appendix Table II continued)

	I-19		II-14		III-15		IV-17		VI-6		Mean	
STATION 1:	N	DW	N	DW	N	DW	N	DW	N	DW	N	DW
Asterias forbesi	0.32(6)	0.205(2)	0.12(9)	0.046(3)	0.74(6)	0.437(1)	0.98(6)	0.875(1)	10.90(2)	3.258(1)	2.25(4)	0.770(1)
Crangon septemspinosa	2.64(3)	0.037(4)	7.46(2)	0.039(4)	6.93(3)	0.118(3)	6.42(3)	0.217(3)	6.60(3)	0.261(2)	6.62(3)	0.135(2)
Cancer irroratus	0.12(10)	0.398(1)	0.02(12)	0.020(5)	0.11(10)	0.140(2)	0.11(11)	0.388(2)	0 –	0 –	0.06(11)	0.116(3)
Libinia emarginata	0 –	0 –	0.01(13)	0.254(1)	0 –	0 –	0.01(13)	0.082(6)	0.03(12)	0.174(3)	0.01(13)	0.072(4)
Hydroids	–	0.037(3)	–	0.049(2)	–	0.026(5)	–	0.095(5)	–	0.058(4)	–	0.064(5)
Pagurus longicarpus	0.41(4)	0.011(6)	0.30(7)	0.018(6)	0.60(7)	0.047(4)	1.36(5)	0.051(8)	0.62(8)	0.014(6)	0.93(7)	0.047(6)
Pagurus pollicaris	0.01(12)	0.001(9)	0.02(11)	0.002(10)	0.03(12)	–	0.03(12)	0.128(4)	0.07(12)	0.007(8)	0.04(12)	0.045(7)
Nassarius trivittatus	0.26(8)	0.018(5)	0.09(10)	0.002(9)	0.77(5)	0.023(6)	3.02(4)	0.080(7)	1.91(4)	0.052(5)	0.94(6)	0.031(8)
Neopanope texana sayi	0.31(7)	0.004(8)	0.33(6)	0.007(8)	0.33(9)	0.001(8)	0.082(8)	0.035(9)	0.89(6)	0.011(7)	0.60(8)	0.018(9)
Neomysis americana	18.45(1)	0.007(7)	25.04(1)	0.010(7)	14.20(1)	0.005(7)	8.53(2)	0.007(11)	1.87(5)	0.002(11)	0.31(2)	0.006(10)
Crepidula plana	0.19(9)	0.001(10)	0.90(4)	+ (11)	0.50(8)	0.001(9)	0.33(9)	0.010(10)	0.47(9)	0.002(10)	0.49(9)	0.003(11)
Lepidonotus squamatus	0.05(11)	+ (13)	0.12(8)	+ (14)	0.08(11)	+ (12)	0.14(10)	0.001(13)	0.24(10)	0.003(9)	0.046(10)	0.002(12)
Caprellids	3.17(2)	+ (11)	3.48(3)	+ (12)	11.99(2)	+ (10)	52.14(1)	0.004(12)	31.98(1)	0.002(12)	4.19(1)	0.001(13)
Unciola irrorata	0.34(5)	+ (12)	0.52(5)	+ (13)	0.87(4)	+ (11)	0.88(7)	+ (14)	0.66(7)	+ (13)	1.14(5)	+ (14)
STATION 3 A:												
Asterias forbesi	0.28(5)	0.203(1)	–	–	0.09(6)	0.066(1)	0.10(5)	0.050(1)	0.31(4)	0.170(1)	0.24(5)	0.124(1)
Crangon septemspinosa	0.69(4)	0.004(4)	–	–	0.14(5)	0.004(5)	0.16(3)	0.003(3)	0.22(5)	0.007(2)	0.44(2)	0.006(2)
Cancer irroratus	0 –	0 –	–	–	0 –	0 –	0 –	0 –	0 –	0 –	+ (11)	+ (8)
Libinia emarginata	0 –	0 –	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Hydroids	–	0 –	–	–	–	0.010(2)	–	0 –	–	+ (5)	–	0.002(5)
Pagurus longicarpus	0 –	0 –	–	–	0.02(8)	0.003(6)	0 –	0 –	0.01(6)	+ (5)	0.01(7)	0.001(6)
Pagurus pollicaris	0 –	0 –	–	–	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
Nassarius trivittatus	1.28(2)	0.015(2)	–	–	0.31(3)	0.007(3)	0.18(2)	0.006(2)	0.43(2)	0.005(3)	0.34(3)	0.006(3)
Neopanope texana sayi	0 –	0 –	–	–	0.04(7)	0.001(7)	0 –	0 –	+ (8)	+ (6)	0.01(9)	+ (7)
Neomysis americana	12.50(1)	0.004(3)	–	–	1.71(1)	0.006(4)	1.00(1)	0.002(4)	1.49(1)	0.002(4)	2.57(1)	0.002(4)
Crepidula plana	0 –	0 –	–	–	0.28(4)	+ (8)	0 –	0 –	0 –	0 –	0.04(6)	+ (10)
Lepidonotus squamatus	0 –	0 –	–	–	+ (9)	+ (9)	0 –	0 –	+ (9)	+ (9)	0.01(10)	+ (11)
Caprellids	0.85(3)	+ (5)	–	–	0.38(2)	+ (10)	0.14(4)	+ (5)	0.35(3)	+ (7)	0.29(4)	+ (9)
Unciola irrorata	0 –	0 –	–	–	0 –	0 –	0 –	0 –	0.01(7)	+ (8)	0.01(8)	+ (12)

+ = < 0.001 g/m² and < 0.01 N/m².

Energetics of The Benthos of Long Island Sound

I. *Oxygen Utilization of Sediment*

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TABLE OF CONTENTS

ABSTRACT

The oxygen uptake of sediment cores from central Long Island Sound was measured in the laboratory during a study of the energetics of the benthos. There appears to be a seasonal cycle of oxygen utilization in the sediment with a maximum in late summer. The metabolism of the dominant macro-infauna accounts for only a small part of the O_2 uptake. The smaller organisms and bacteria, therefore, must consume most of the energy on the bottom of Long Island Sound.

INTRODUCTION

It has been demonstrated in recent years that community structure can be studied effectively by investigating the flow of energy through its component parts. Odum and Smalley (1959), Odum (1959), Teale (1957, 1959), Kuenzler (1961), Wieser and Kanwisher (1961), and others have shown that these methods are applicable and valuable in the study of the aquatic and intertidal marine environment. When the energy involved both in metabolism and biological production of a species population is considered, dissimilar species can be directly compared by their energy utilization, while their abundance or biomass or both may be misleading.

This study was an attempt to clarify the role of the dominant macro-invertebrates in shallow, marine, level-bottom animal communities and to increase our understanding of the role played by the bottom in the energetics of the marine ecosystem. The oxygen uptake of sediment cores from the soft bottom community was measured to provide background information for further studies on the relative importance of the macro-infauna to the total energetics of the bottom of Long Island Sound.

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MATERIALS AND METHODS

A station in central Long Island Sound was sampled for benthic infauna from March 1958 through August 1960. The position of this station (Station 3) is 41°06.3′ North Latitude and 73°00.2′ West Longitude. The sediment was soft, sticky mud with an average composition of 17.6% sand, 50.2% silt, and 32.2% clay. Fourteen cores were obtained, mostly in pairs, with a Phleger, or similar corer, without a core-catcher. The mud core was retained in the plastic liner (inside diameter 3.5 cm, area 9.6 cm^2, length about 35.5 cm) after collection and during the experiments. The mud-water interface was relatively undisturbed.

All experiments were run under conditions as natural as possible. The cores were immersed in a running seawater tank in which the temperature closely approximated the bottom temperatures in the field. The dissolved oxygen was generally not allowed to fall below environmental limits. Salinity of the water used in the experiments was close to that *in situ*. A cork in the lower end of the core liner retained the sediment and a layer of paraffin oil three to four centimeters thick overlying the water sealed the tube from contact with the atmosphere (see Figure 1).

Possible oxygen uptake of the water column above the sediment was minimized by using filtered water. The water obtained in the tube at the time of collection was siphoned off without disturbing the sediment. HA-Millepore-filtered seawater without antibiotics was then added to the experimental and control tubes. The filtered water was brought to ambient temperature in the seawater tank by equilibration for one hour after filtration.

Preliminary experiments demonstrated that pronounced and rapid stratification of dissolved oxygen occurred within the tube when the water was not mixed. Hydrographic investigations in the Sound have shown that a current with a velocity up to one knot occurs about a meter above the bottom (Riley, 1956a). Thus, gentle stirring with a reciprocating wire seemed realistic.

An experiment to determine the effect of stirring on the uptake of the sediment was conducted. Three similar cores were treated identically except for the amount of stirring used. "Minimum" was defined for the experiment, as no stirring until just prior to the final sampling, "standard" as a very rough approximation of the current velocities at depth in Long Island Sound, and "maximum" as vigorous stirring just below the velocity that stirred the sediment.

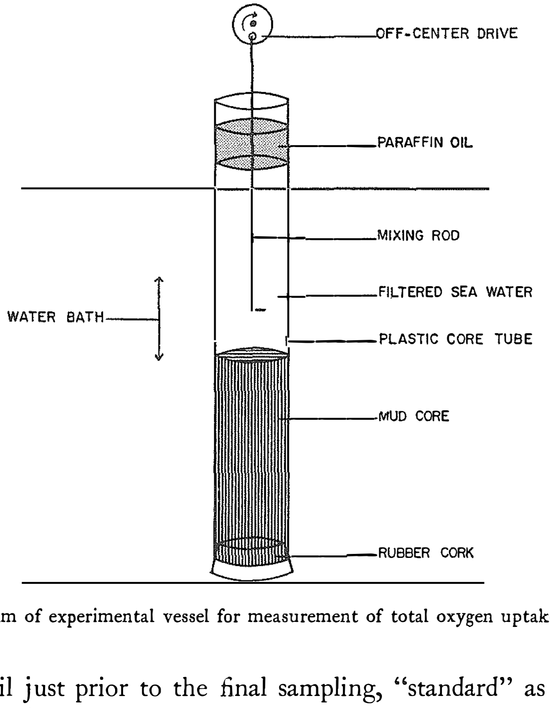

Figure 1. Diagram of experimental vessel for measurement of total oxygen uptake of mud cores.

Water samples (1.3 cc) were taken at the start and finish of the experimental runs from the middle of the water column by pushing a syringe through the paraffin layer. Rates of oxygen uptake were obtained by measuring the concentration of dissolved oxygen in the sample with a Scholander microgasometric analyzer (Scholander, et al., 1955). Corrections were made for the decreasing volume of water, and experiments were run in duplicate whenever possible. The duration of the experiments generally was short (2.0 to 5.6 hours, depending on temperature and season), although a few were run for about 24 hours.

TABLE I. OXYGEN UPTAKE OF LONG ISLAND SOUND SEDIMENT.

Date	Temp (°C)	Initial O_2 Concentration (ml/liter)	Final O_2 Concentration (ml/liter)†	Length of Experiment (hrs.)	Initial Volume of Water (cc)	Total Uptake per Core (μl/hr)	Uptake per Control (μl/hr)	Macrofaunal Uptake per Core (μl/hr)	Uptake per Core Minus Control and Macrofauna (μl/hr)	Av. Corrected Uptake per Core (μl/hr)	Av. Corrected Uptake per m^2 (ml/hr)
1958											
June 17	16.0	4.48	2.63	23.7	78	6.2	3.7	0.0	2.5	3.5	3.6
	16.0	4.34	1.91	23.4	77	8.1	3.7	0.0	4.4	–	–
July 22	19.0	3.03	2.05	2.0	80	41.0	4.0	0.3	36.7	34.6	36.0
	19.0	3.53	2.66	2.0	80	36.5	4.0	0.0	32.5	–	–
1959											
February 12	−0.1	6.73	6.65	6.5	130	2.9	0.0	0.0	2.9	2.9	3.0
May 14	10.0	5.40	5.38	2.0	100	6.5	0.2	0.4	5.9	10.3	10.7
	10.0	5.23	5.00	2.0	100	15.0	0.2	0.2	14.6	–	–
June 18	14.0	5.32	2.57	24.0	60	7.7	2.9	0.0	4.8	4.8	5.0
July 21	21.5	4.32	0.81	5.2	100	67.7	0.0	0.2	67.5	67.5	70.3
Sept. 25	21.0	4.03	2.98	2.0	134	72.3	0.0	0.5	71.8	45.8	47.7
	21.0	3.41	2.31	2.5	43	20.4	0.0	0.6	19.8	–	–
1960											
April 5	a 5.0*	6.18	0.72	2.0	85	26.8	0.0	0.1	26.7	26.7	27.8
	b 5.0	6.45	6.27	2.0	85	8.1	0.0	0.1	8.0	8.0	8.3
	c 5.0	5.66	5.64	2.0	85	1.6	0.0	0.1	1.5	1.5	1.6

* Stirring experiment: a "maximum", b "standard", c "minimum".

† Uncorrected for volume change.

After experimental runs, the sediment was removed and sieved through a screen with a 0.3 mm aperture (US Standard No. 50). The macrofauna, when present, were separated, identified, and measured. In studies to be reported later, measurements of respiration of macrofauna were made on a broad spectrum of animal sizes and environmental temperatures, and a respiration nomogram was constructed (Carey, 1962). Respiration values, corrected for size and temperature, were read from the nomogram and were subtracted from the total uptake of the core. After estimates of the oxygen uptake by the macrofauna of each core had been subtracted, the oxygen uptake of the sediment and smaller organisms per square meter of sediment surface was calculated.

RESULTS

Data from the core experiments described above are listed in Table I. The average corrected oxygen uptake varied from 3.0 to 70.3 ml/m^2/hr. In order to compensate partially for the paucity of winter and fall data, a weighted average was obtained. It was 20.4 ml/m^2/hr.

Oxygen uptake per square meter of sediment surface was averaged for the duplicate experiments, and the resulting values were plotted by month (see Figure 2). A seasonal change with a maximum in July is apparent.

Stirring velocity and consequent amount of circulation in the plastic core tube had a definite effect on the total oxygen uptake of the system. The maximum stirring increased the uptake threefold over that observed after the standard stirring. The minimum stirring reduced uptake to less than 20°/₀ of that obtained with the standard stirring value. The natural water exchange at Station 3 probably lies between these two extremes. The standard stirring rate seems a reasonable approximation of the natural conditions.

DISCUSSION

Although the data are scattered over a period of 23 months, a yearly cycle in oxygen uptake of the sediment at Station 3 seems evident. The cycle may be correlated with nutrient and temperature conditions in Long Island Sound. A maximum of nitrate and phosphate is present in the water column soon after the summer stratification breaks down in the fall (Riley, 1959). The maximum oxygen uptake occurred during the periods, when *in situ* temperatures were highest, and low values occurred during periods when the environmental temperatures were low.

Biological activity is undoubtedly the major process contributing to oxygen uptake in the soft sediments of Long Island Sound. Hayes and MacAulay (1959) found oxygen consumption in lake sediments to be correlated with the

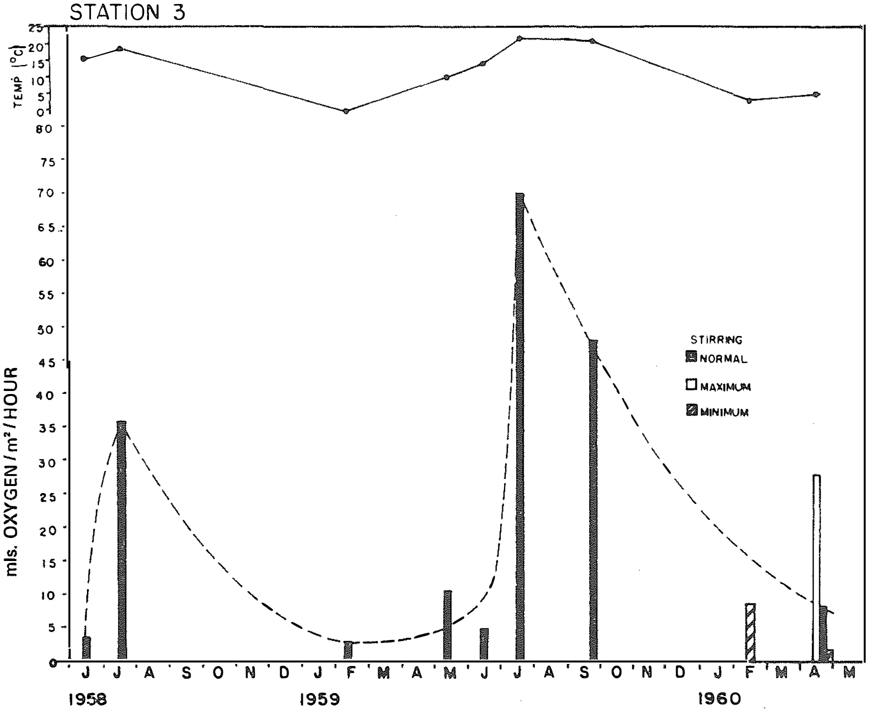

Figure 2. Oxygen uptake of sediment from Station 3, Long Island Sound, corrected for macrofaunal respiration. Upper graph shows ambient temperatures.

bacterial count at the sediment surface. In estuaries and on the continental shelf, chemical uptake of oxygen may be insignificant compared to that of the biota (Hayes, 1964). Reduced conditions in the sedimentary environment of central Long Island Sound probably represent an oxygen debt built up by past biological activity. Though the amount of reduction of the sediments below the interface may be very large (Kato, 1956; Teal and Kanwisher, 1961), the amount of oxygen diffusing through the intact sediment-water interface is likely to be small. The oxygen diffusing through to the reduced zone is considered here as part of the total metabolic activity of the bottom.

The observed seasonal cycle of sedimentary oxygen uptake is probably a result of the effects of higher temperatures and rates of organic input on the respiration and population growth of the bacteria, microfauna, and meiofauna. Of the forms smaller than 0.1 mm, the bacteria are undoubtedly the major energy consumers on the bottom (Wieser and Kanwisher, 1961; and Kanwisher, 1962). Teal (1959) estimated that 56% of the grass on a Georgia salt marsh is metabolized by bacteria. Data from lake sediment studies by Lönnerblad (1930) indicate that the major part of microorganism respiration is bacterial. Using mud from productive lakes, Lönnerblad found that oxygen uptake could be prevented by poisoning the bacteria. Assuming a Q_{10} of respiration of 2, the yearly cycle found in the present study suggests major differences in bacterial population sizes rather than merely increased respiration. After adjustment for the respiration of the resident macrofauna, the average total oxygen uptake of sediment from central Long Island Sound (20.4 ml/m^2/hr) compares well with the uptake of other sediments, both freshwater and marine. Wieser and Kanwisher (1961) found the oxygen uptake of intertidal sandy mud to be 26 to 36 cc/m^2/hr, using similar techniques developed independently of those described for this study. Kanwisher (1962) determined the oxygen uptake of marine sediments near Woods Hole, Massachusetts in 10 to 20 m depth to be 15 cc/m^2/hr in the summer when temperatures were 10 to 15°C. In the winter at temperatures of 0°C, the sediment uptake was 5 to 8 cc/m^2/hr. Hayes and MacAulay (1959) determined the oxygen uptake of a variety of lake sediments and found an average utilization of 11.4 ml/m^2/hr at 11 ± 1.5°C. Riley (1956b) has computed average oxygen uptake rates for the bottom of the central region of Long Island Sound from oceanographic data. During 1952–54, he found a mean value of 12.6 ml/m^2/hr with a range of 4.6 to 36.6 ml/m^2/hr for ten five-week periods. Although the methods of Riley and those of this study contain possible sources of error, these independent methods resulted in similar estimates of oxygen uptake of the bottom of central Long Island Sound.

The two dominant members of the macro-infauna in the soft bottom community of the Sound are *Nephtys incisa* (Malmgren), a polychaete worm, and *Nucula proxima* (Say), a small protobranch lamellibranch. Sanders (1956) found that these two species constituted 58 °/o of the biomass (dry wt.) at Station 3. The average respiration of the two species populations in the Sound was found to be only 3.4 °/o of the total average oxygen uptake of the sediment and smaller organisms (Carey, 1962). At a mud bottom area, shallower and closer to shore than Station 3, Richards (1963) and Richards and Riley (1967) did not find large epifauna to be abundant. These larger organisms are likely to be even less important at Station 3 and would then consume relatively small amounts of oxygen. It seems unlikely that the total macrofaunal respiration would amount to more than five times that of the two species populations studied, or a maximum of about 17 °/o of the total energy that is consumed by the smaller organisms. Such an estimate is close to that derived by Wieser and Kanwisher (1961) for the macrofauna in an intertidal mud community. They estimated the distribution of energy utilization on the bottom as follows: nematodes, 10 to 33 °/o; macrofauna, 10 to 15 °/o; and bacteria and protozoa, over 50 °/o.

A mud-water interface has a bacteria-controlled organic exchange. It is stimulated by plankton fallout, and by oxygen (Hayes, 1964). Long Island Sound is a rich system and produces more phytoplankton than the zooplankton can utilize. Riley (1956b) estimated that the annual production of phytoplankton is about 205 g C/m^2, 31 % of which is used by the benthic flora and fauna. The bottom functions, therefore, as a major component of the energetics of the ecosystem. Although the macrofauna are the most obvious members of the soft bottom benthic community, they appear to play a relatively minor role in the total utilization of energy in Long Island Sound.

SUMMARY AND CONCLUSIONS

1. Evidence of a seasonal cycle in the total oxygen uptake of the sediment in central Long Island Sound with a maximum in the summer was found. Maximum bacterial, microfaunal, and meiofaunal metabolism seems a reasonable explanation for the increase in oxygen uptake.
2. The respiration of the two dominant species populations of macro-infauna in the soft mud bottom of central Long Island Sound was small compared with the total uptake of the sediment. *Nephtys incisa* and *Nucula proxima* play a minor role in the energetics of the total benthic community. The meiofauna, microfauna, and bacteria must utilize the major portion of the energy consumed on the bottom.

REFERENCES

Carey, A. G., Jr.
1962. An ecological study of two benthic animal populations in Long Island Sound. Ph. D. dissertation, Yale University: 61 pp., appendices.

Hayes, F. R.
1964. The mud-water interface. Oceanogr. Mar. Biol., *2*: 121–145.

Hayes, F. R. and M. A. MacAulay
1959. Lake water and sediment V. Oxygen consumed in water over sediment cores. Limnol. & Oceanogr., *3*: 291–298.

Kanwisher, J.
1962. Gas exchange of shallow marine sediments. *In* Symposium on the Environmental Chemistry of Marine Sediments. Occ. Publ. Graduate Sch. Oceanogr., Univ. Rhode Island, *1*: 13–19.

Kato, K.
1956. Chemical investigations on marine humus in bottom sediments. Mem. Fac. Fish. Hokkaido, *4*: 91–209.

Kuenzler, E. G.
1961. Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. & Oceanogr., *6*: 191–204.

Lönnerblad, G.
1930. Über die Sauerstroffabsorption des Bodensubstrats in einigen Seentypen. Bot. Notiser, 1930: 53–60.

Odum, E. P.
1959. Fundamentals of Ecology. W. B. Saunders Co., Philadelphia. 546 pp.

ODUM, E. P. and H. E. SMALLEY

1959. Comparison of population energy flow of a herbivorous and deposit-feeding invertebrate in a salt marsh ecosystem. Proc. nat. Acad. Sci., Wash., *45*: 617–622.

RICHARDS, S. W.

1963. The demersal fish population of Long Island Sound. Bull. Bingham oceanogr. Coll., *18* (2): 1–101.

RICHARDS, S. W. and G. A. RILEY

1967. The benthic epifauna of Long Island Sound. Bull. Bingham oceanogr. Coll., *19* (2): 89–135.

RILEY, G. A.

1956 a. Oceanography of Long Island Sound, 1952–1954. II. Physical Oceanography. Bull. Bingham oceanogr. Coll., *15*: 15–61.

1956 b. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. Bull. Bingham oceanogr. Coll., *15*: 324–344.

1959. Oceanography of Long Island Sound 1954–1955. Bull. Bingham oceanogr. Coll., *17* (1): 9–30.

SANDERS, H. L.

1956. Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. Bull. Bingham oceanogr. Coll., *15*: 345–414.

SCHOLANDER, P. F., L. VANDAM, C. L. CLAFF, and J. W. KANWISHER

1955. Microgasometric determination of dissolved oxygen and nitrogen. Biol. Bull., Woods Hole, *109*: 328–334.

TEAL, J. M.

1957. Community metabolism in a temperate cold spring. Ecol. Monogr., *27*: 283–302.

1959. Energy flow in the salt marsh ecosystem. Proc. Salt Marsh Conf. Univ. Georgia, pp. 101–107.

TEAL, J. M. and J. KANWISHER

1961. Gas exchange in a Georgia salt marsh. Limnol. & Oceanogr., *6*: 388–399.

WIESER, W. and J. KANWISHER

1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. Limnol. & Oceanogr., *6*: 262–270.

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