BULLETIN OF THE BINGHAM OCEANOGRAPHIC COLLECTION

OCEANOGRAPHY OF LONG ISLAND SOUND

AND GUIDE FOR PREPARING FIGURES

BULLETIN

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THE BINGHAM OCEANOGRAPHIC COLLECTION
Peabody Museum of Natural History, Yale University

Oceanography of Long Island Sound[1]

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Issued June 1959 · New Haven, Connecticut, U. S. A.

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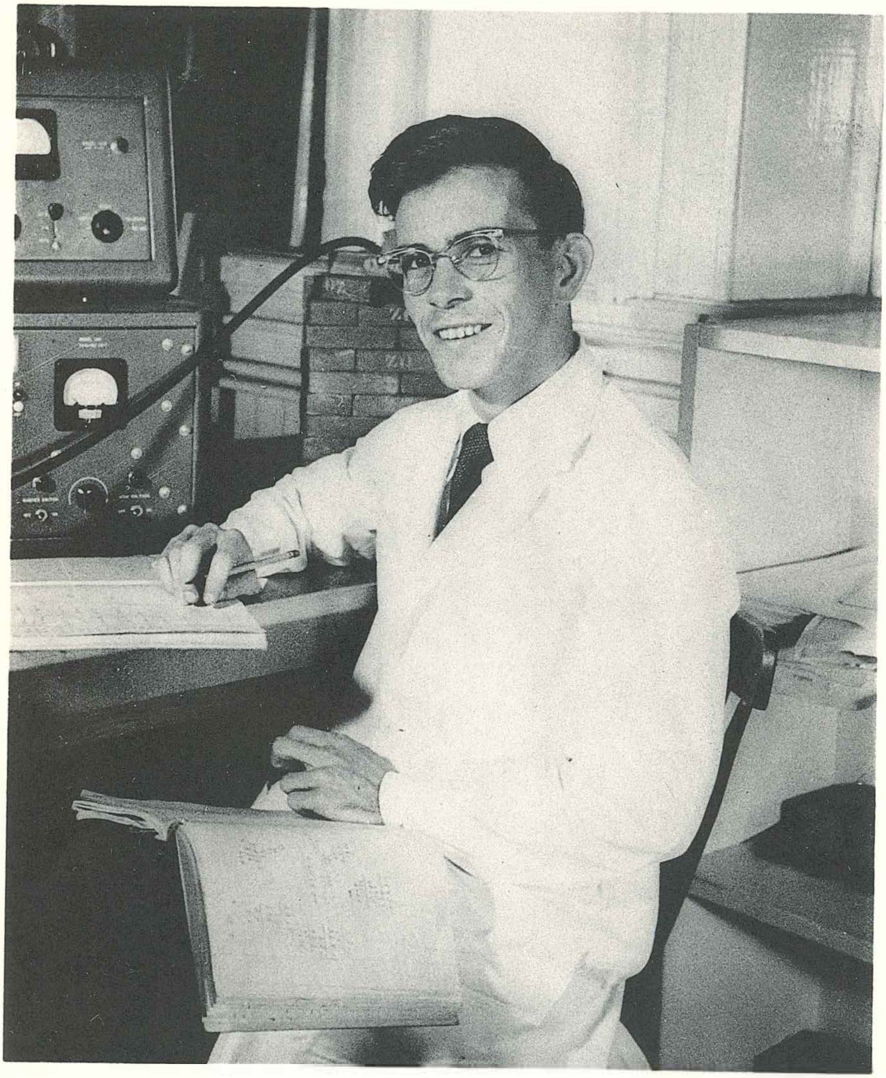

EUGENE HARRIS

1928-1956

A promising young oceanographer was lost when Eugene Harris died on February 4, 1956 in his 28th year and in his fourth year as a graduate student at Yale University. What was to have been his first important contribution to oceanography is recorded in this volume, which is dedicated to his memory.

Eugene was born in Brooklyn, New York on August 18, 1928 to Louise and Redvers Harris. When he was two years old his parents returned to their former home in Gloverstown, Newfoundland, where his brother Ralph was born a few months later.

Eugene's father died in September 1939 and his mother later remarried, leaving the boys in the care of their grandmother and their uncle Leslie Harris.

At the close of his elementary education in the United Church School of Gloverstown in 1945, Eugene was awarded a King George the Fifth Scholarship, of which there were five in the province. This provided two years' education at the Memorial College, now the Memorial University, of Newfoundland. During holidays he worked for the Anglo-Newfoundland Development Company and then spent a year on one of its surveying crews in order to earn money to continue his studies.

He entered Dalhousie University, at Halifax, Nova Scotia in the autumn of 1948 and earned his B.Sc. two years later. It was sometime during this period that he turned from his original intention of entering the medical profession and decided to become a biologist. Accordingly he began work on his master's degree at Dalhousie in 1950 under the direction of Professor F. Ronald Hayes. He continued to earn his way, working now during his holidays with the Fishery Research Board of Canada, particularly on a salmon survey that was in progress on the Miramichi River.

The summer of 1951 was saddened by the death of his brother, who, like their father twelve years before, was stricken with cancer. Nevertheless, Eugene completed his thesis, entitled "Phosphorus metabolism in zooplankton and microorganisms as studied by the use of radiophosphorus", and the M.Sc. degree was duly awarded by Dalhousie.

The autumn of 1952 found Gene departing his homeland and entering the last lap of his professional training at Yale as a graduate student in the Department of Zoology. It was then that I first met him, a little man, but lithe and tough from years in the Canadian Bush. His dark eyes were intent and intelligent. A slight tic of the cheek muscle betrayed a painful shyness.

The shyness wore off with the months although his deeper feelings remained buried under a nearly impenetrable reserve.

At this time I was just getting underway in a study of Long Island Sound, a routine survey of the major ecological variables into which might be fitted the more specialized, short-term projects of graudate students and staff members, so that the whole might eventually be a fairly comprehensive study of the biology of the waters that lap our doorstep. Gene and I in the course of time discussed the place that he might take in this scheme of things. We discussed various possibilities, among them a continuation of his previous work on phosphorus metabolism, or a study of the nitrogen cycle. It was already becoming apparent that nitrogen was the key element in the economy of the Sound. I was rather astonished when he chose to work on the nitrogen cycle, despite my warning as to the difficulty of the task, but subsequent events proved that I had underestimated his tenacity.

Gene reviewed the literature. He was granted a summer fellowship at the Woods Hole Oceanographic Institution where he pursued the evaluation of methods and profited from the advice of Francis Richards, Bostwick Ketchum, and other members of the Woods Hole staff. It turned out that he taught as well as learned, for it was at least partly due to his interest and enthusiasm that they have taken up similar studies in their own waters.

The next year Gene passed his Ph.D. examination. He determined the nitrogen and phosphorus content of some net plankton collections that I had made, and these analyses were combined with my data into a paper which we published together. He continued patiently to study and practice the various nitrogen methods, choosing a few, discarding most of them as inadequate for his purposes. I chafed at the slowness of his progress but abided by his judgment. In October 1954 he pronounced himself ready at last to start a survey. By this time I had been able to offer a research assistantship under a grant from the Office of Naval Research, which relieved him of the teaching duties that had supported him until now.

In our frequent trips to sea in the months that followed, he was an invaluable addition to the crew, a cheerful and tireless worker under the most trying conditions and a good shipmate.

His program went forward rapidly. Then, so gradually that we were not aware at first, this changed. By early summer he was obviously weary and ill. In July there was an emergency operation. Others followed, and we finally realized that there was no hope of recovery.

Gene occupied his last days with books and music, with painting, the compilation of his data, and with friends. Perhaps for the first time he realized that he had friends. This proud and quiet little man had tried to face the world alone. But people were drawn to him despite his apparent diffidence and occasional biting sarcasm, for these mannerisms failed to conceal the fundamental gentleness and warmth of his nature. And in his last days he learned to accept his friends as people who groped in darkness like himself and found no solution to life except in love of their fellows.

The end came peacefully. Relatives and friends attended a simple funeral service, and his ashes were committed to the sea, from the same small research vessel where he had done his work.

Later I examined his papers for information that might help in preparing his work for publication. Among them were fragmentary jottings of philosophy, whimsey, and passion that made me realize with a keen sense of loss how poor our human communication is and how little we may know about the people that we live and work with for months and years.

In our failure to solve the riddle of human behavior, we shrug and mumble some platitude about human nature. Perhaps it was Gene's nature to be what he was. But I have often wondered what he might have been if his life had not been filled with the foreboding that is the natural consequence of a tragic family history of early disease and death. Perhaps he perversely spurned the human contacts that might have eased his way, in a pitiful effort to keep from getting too involved in a world of which he did not quite feel himself a part. Perhaps there was equal perversity in the slowness of the preparation for his thesis research. Some men who fear the future might hurry, but it was Gene's way to make sure that what he did, however little, should be right.

I have undertaken the completion of what was to have been Gene's dissertation. The data had been compiled. There were fragments of manuscript, and I had discussed much of the work with him and knew his opinions about it. Other friends helped. Georgiana Deevey completed the zooplankton counts that he had begun, and Shirley Conover examined the experimental phytoplankton material. I have discussed the data with many of his friends, here and in Woods Hole, and have profited by their advice.

Although many have helped, I feel that it is fitting to give Gene full authorship of his paper. The premature termination of his research will be obvious on reading the paper, but I feel that he obtained some very significant results and deserves the full measure of credit for them.

G. A. R.

Oceanography of Long Island Sound
1954-1955

Gordon A. Riley

Bingham Oceanographic Laboratory

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ABSTRACT

A general survey of Long Island Sound was carried out from March 1954 to November 1955 with biweekly sampling at a few stations in the central part and with approximately monthly coverage of the remainder of the area.

The eastern end of the Sound, which is adjacent to open coastal waters, was slightly cooler in summer and warmer in winter than the shallow and enclosed western portion. The latter had a total seasonal temperature range of about 25°C. The difference between surface and bottom temperatures was generally less than 5° in all parts of the Sound. The salinity at the western end ordinarily was 3-5 ‰ fresher than at the eastern end, although the immediate surface layer in the eastern end was markedly freshened during occasional floods of the Connecticut River. Previous papers have described a presumably normal seasonal variation in salinity with a spring minimum and an autumn maximum, but the latter was reduced in 1954 and virtually obliterated in 1955 by torrential rains accompanying hurricanes.

Oxygen was reduced in bottom waters during spring and summer; minimum values were about 40 % of saturation in the western end, 50 % in the central basin, and 85 % in the deeper and more turbulent waters at the eastern end. Phosphate and nitrate concentrations decreased from west to east, particularly in autumn and winter; however, there were no marked regional differences in the qualitative aspects of the seasonal cycles. Previous work has indicated that nitrogen is a more important limiting factor than phosphorus in the central region. Seasonal cycles observed during the 1954–55 survey suggest that this is true throughout the Sound, despite the fact that freshwater drainage supplies relatively more nitrate than phosphate.

The seasonal cycle of phytoplankton, as indicated by chlorophyll analyses, was qualitatively similar throughout the Sound except for minor differences in the timing of the cycle. There were large autumn flowerings in 1954 and 1955 whereas little or none had been observed in 1952 and 1953. The discussion indicates that these differences can be interpreted in terms of illumination, stability, and nutrient supply. Quantitatively there were large regional differences in the chlorophyll concentration. Proceeding from the western to the eastern end, there was a seven-fold decrease in concentration per unit volume, and the total crop per unit area of sea surface was also significantly smaller although the difference was only about two-fold.

It is not clear why the western end failed to develop a correspondingly larger zooplankton crop than the central basin. The concentration of phytoplankton in the eastern end was minimal for the support of *Acartia*, the dominant genus of copepods in most of the Sound. Hence it is not surprising that these forms tended to be replaced by coastal water species that are believed to have a higher degree of metabolic efficiency than species of *Acartia*.

INTRODUCTION

In March 1952 the Bingham Laboratory began an oceanographic survey of Long Island Sound. During the first two years, weekly observations were obtained at stations in the central part of the Sound, and the results were published in the Bulletin of the Bingham Oceanographic Collection, Volume 15.

Beginning in March 1954 and continuing until November 1955, the survey was expanded to general coverage of the Sound at less frequent intervals. A two-day cruise was made every two weeks, weather permitting, alternately covering the eastern and the western ends of the Sound. Thus most of the stations were occupied once a month, with a few in the central basin receiving biweekly coverage.

A preliminary and descriptive account of the physical and chemical data is given herein. The present work is intended primarily as background information for subsequent papers of a more specific nature. In addition to the papers in this volume, a more thorough analysis of physical oceanographic processes will be published subsequently, as well as other aspects of the survey that have not yet been examined fully.

Field work was carried out aboard the Shang Wheeler, a vessel belonging to the Milford Biological Laboratory of the U.S. Fish and Wildlife Service.

The author is deeply grateful to Victor L. Loosanoff, the Director of the Laboratory, for his continued cooperation, and to Captain Herman R. Glas for his loyal and helpful assistance in every phase of field operations.

METHODS

The area of operation and a typical cruise plan are shown in Fig. 1. About 15 stations were occupied per two-day cruise, most of them consisting of a Secchi disk record, a surface thermometer reading and a bathythermogram, and Nansen water bottle samples at two to four depths for measurements of salinity, oxygen, phosphate, nitrate, and chlorophyll. At about one-third of the stations, oblique zooplankton tows were made with a Clarke-Bumpus sampler, using either a No. 2 or a No. 10 net, and surface water samples were preserved with formalin for phytoplankton enumeration. On most cruises there were a few stations consisting only of a temperature reading and a surface bucket sample for chemical analysis. These included some open water stations as well as those at the Connecticut and Housatonic Rivers and occasionally in the Thames River for estimates of the amount of nitrate and phosphate contributed by the major river systems.

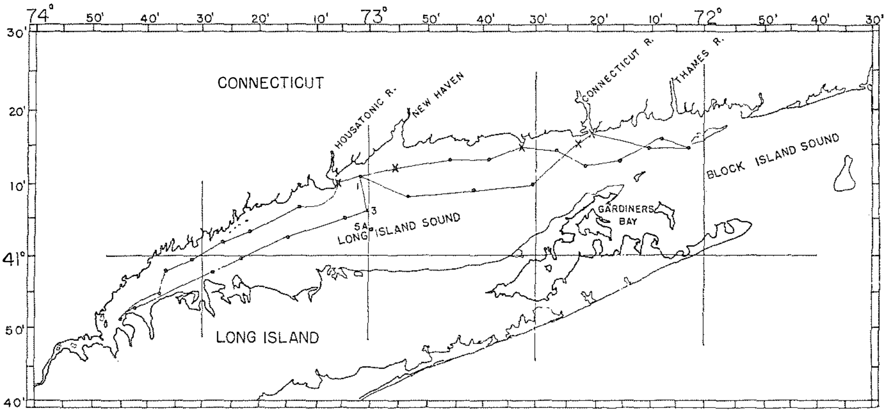

Figure 1. Chart of Long Island Sound showing a typical station pattern (cruise of October 27–28, 1955 to the western end of the Sound and November 8–9 to the eastern end). Routine stations, dots; surface bucket samples, x's. Numbers 1, 3, and 5A refer to stations occupied in subsequent years; these will be mentioned in other papers in this volume.

The chemical methods were the same as those used earlier in the survey (Riley and Conover, 1956); hence details need not be repeated. In brief, salinity was determined by titration; the Winkler method was used for oxygen and the Atkins-Dénigès method for phosphate. Nitrate was measured with strichnidine, essentially according to the method described by Zwicker and

Robinson (1944). For chlorophyll, 375 ml of sea water were filtered through No. 42 Whatman paper, and the acetone extract of the residue was measured in a Klett-Summerson photoelectric colorimeter, using a No. 66 filter. Errors of the method and calibration of the readings have been described in the paper cited above.

Samples collected during the first day of each cruise were analyzed for phosphate and nitrate during the evening, and the chlorophyll readings were obtained the following morning. Samples collected during the second day were analyzed on the day following the cruise. All samples for oxygen determination were stored in the dark and titrated on the day after the cruise. No evidence has been found that differences in the length of the storage period affected the results significantly.

THE PHYSICAL AND CHEMICAL ENVIRONMENT

Temperature. In order to present the data in summary form, the Sound was arbitrarily divided into a series of areas situated along the longitudinal axis, each area comprising 10′ of longitude and extending between the north and south shores. All stations within each area have been averaged.

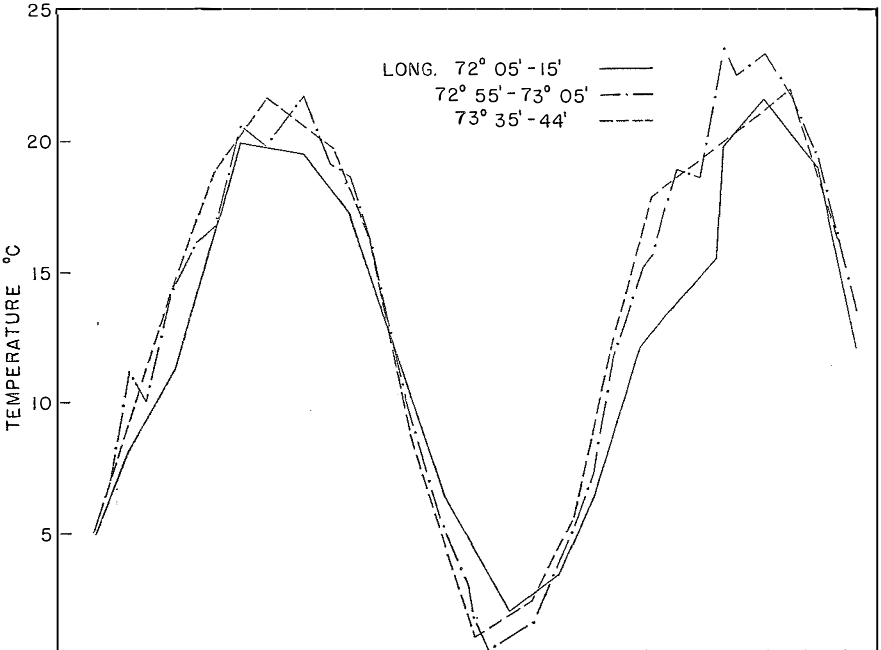

Figure 2. Surface temperature. Average of all stations within each of the areas noted on the graph.

Fig. 2 shows surface temperatures averaged by cruise and by area in three of the longitudinal strips, one being located near the eastern end, one in the middle, and one near the western end. These are sufficient to show the most important regional differences. Other variables as well as temperature will be illustrated in the same way.

The easternmost area is deeper than the others and is exposed to rapid interchange with open coastal waters. Hence it is not surprising that the annual temperature range was slightly less than in the other areas and that the seasonal progression lagged slightly. However, the horizontal distribution of temperature was relatively uniform compared with some of the other variables that will be considered later.

The vertical temperature gradients shown in Fig. 3 were fairly typical of the Sound as a whole. A negative temperature gradient was generally present from March until August, but differences of more than 5° have seldom been observed. Tidal mixing was strong enough to prevent the formation of a strong seasonal thermocline, and there was no immediately available source of cold bottom water. The adjacent inshore waters of Block Island Sound were also moderately stable, and all of this water, surface to bottom, was dense enough by virtue of its higher salinity to contribute to the flow of bottom water into Long Island Sound. Farther offshore there is a strong

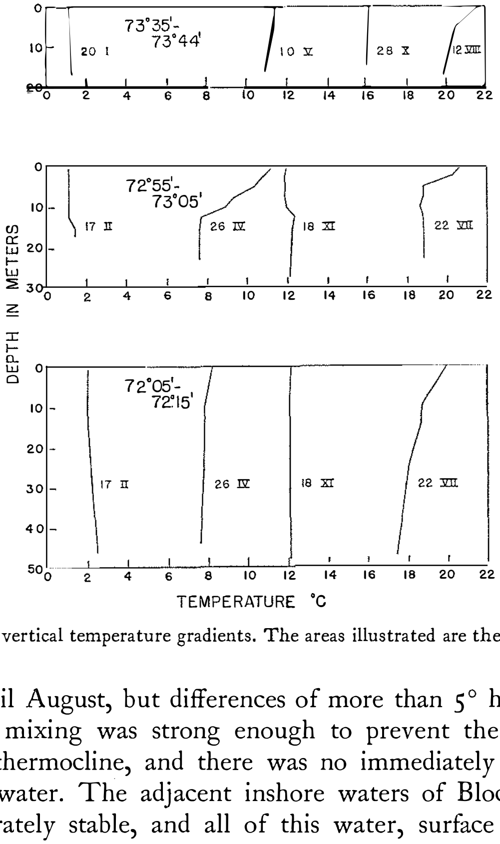

Figure 3. Average vertical temperature gradients. The areas illustrated are the same as in Fig. 2.

seasonal thermocline, but no evidence has been found that any of the offshore bottom water reaches Long Island Sound intact.

In the past, vertical temperature gradients in autumn have tended to be small and variable. It was common to find slight negative temperature gradients even though the water mass as a whole was cooling. In such cases the major cooling mechanism is presumed to have been vertical convection rather than eddy conductivity. In late autumn and early winter the surface salinity tended to decrease, making the water more stable, and positive temperature gradients increased in frequency and magnitude.

The sequence of events that has been described was slightly altered in 1954, and markedly so in 1955, by heavy rains in late summer and autumn which permitted the establishment and maintenance of positive gradients in salinity and temperature. This condition continued into midautumn in 1954 and throughout the autumn and winter of 1955.

Salinity. Fig. 4 shows average surface salinities in the three areas previously figured. The easternmost area usually had the highest salinity, but it was subject to rapid and extreme freshening whenever there was a flood in the Connecticut River. This was a normal occurence in April, following the spring thaw in northern New England. Unusually heavy rains were also capable of producing similar surface freshening. The atypical autumn freshening in November 1955 followed rainfall totalling about ten inches in the preceding three weeks. A similar case was observed in June 1952 (Riley, 1956).

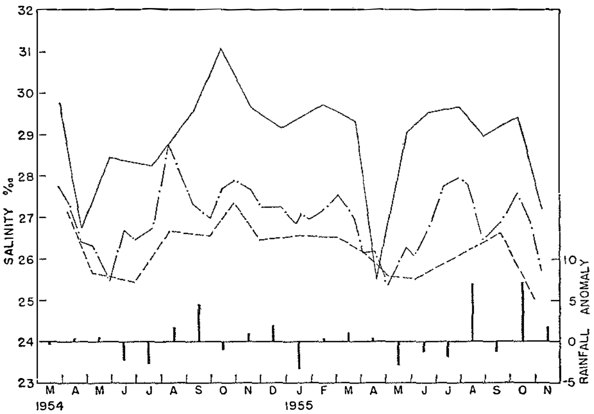

Figure 4. Average surface salinity. Areas and identifying symbols as in Fig. 2. The monthly rainfall in inches is shown as the departure from the normal rainfall for each month.

West of the mouth of the Connecticut River, spring freshening began earlier and lasted longer than in the eastern end, and the relative change was not so great. The total volume of river drainage into the central and western basins was only about a third that of the eastern narrows. However, there are indications that the circulation pattern becomes progressively more sluggish toward the western end, so that such drainage as exists is more effective in reducing the general level of salinity; also the effects of seasonal variations tend to be distributed over a longer time. Furthermore, there are qualitative differences in drainage in the western end. About half of the fresh water is derived from small rivers in Connecticut and southeastern New York where the snow cover usually is not continuous through the winter, so that there tends to be gradual freshening in winter and a less pronounced spring minimum.

The seasonal progression of salinity in the central basin during 1954 and 1955 was very irregular compared with the situation previously described (Riley, 1956) for 1952 and 1953, when the spring minimum was followed by a gradual and regular increase to a midautumn maximum, with an equally gradual decline during the late autumn and winter.

In the lower part of Fig. 4 the total monthly rainfall as recorded by the New Haven Weather Bureau has been plotted as departures from their long term monthly averages. A generally inverse relationship is apparent between salinity in the central basin and rainfall. In particular, the early summer was dry during both years and was followed by excessive rains. This combination of occurences had the effect of shifting the salinity maximum toward midsummer and of making it sharper than usual. The late summer and autumn rains were particularly effective in that they were hurricane torrents which drained into the Sound with minimum loss by evaporation and seepage. By contrast an almost equal excess of rainfall in August 1952, which was more evenly distributed through the month, had little effect on salinity.

Fig. 4 shows a further reduction in salinity and a flattening of the seasonal cycle in the western area, where the narrowing of the Sound intensifies the effects of freshwater drainage. There are also other possible sources of fresh water. An analysis of mass transport phenomena (Riley, 1956) has indicated a movement of about 1100 m3/sec into the western end of the Sound from the New York Harbor region. Six analyses have been made at the point where this water enters the Sound. The salinity averaged 0.29 °/₀₀ less than at the westernmost station in the Sound proper. While the data are obviously insufficient for accurate estimates, they suggest that the freshwater increment from the New York approaches may be about the order of magnitude of river drainage into the area under consideration.

The small streams that drain into the Sound from Long Island differ from those of the Connecticut and New York mainland in that seasonal variations in flow are relatively slight. Their volume in summer often exceeds total rainfall within the geographical limits of the drainage basin, presumably because they are fed by groundwater seepage from more distant areas. This raises the further question of whether direct and undetectable seepage from the sandy Long Island soils may have a significant effect on the waters of the Sound. It is a question that cannot be answered at the present time, but it will need to be borne in mind in connection with the later discussion of the sources of nutrient supply.

Fig. 5 compares surface and bottom salinities in the eastern end and in the central basin. The eastern bottom water, which showed a slight seasonal variation similar to that of the adjacent waters of Block Island Sound, was little affected by flood conditions, so that temporarily there were large vertical salinity gradients and strong stability; at other times in 1954–55 a vertical salinity gradient of lesser magnitude was generally present. The gradients tended to decrease slightly from the eastern end toward the central basin, and there was a closer relationship between seasonal trends of surface and bottom waters. Similar conditions existed throughout the western half of the Sound.

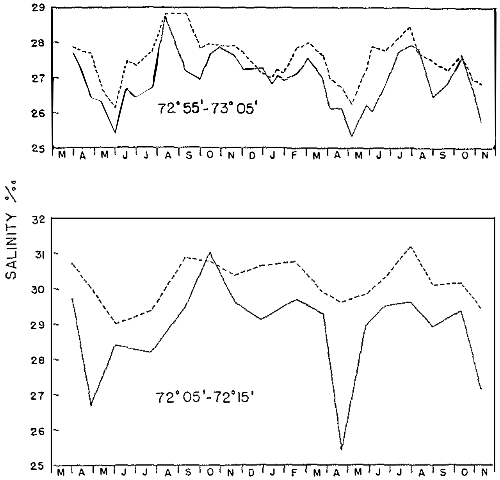

Figure 5. Comparison of salinity at the surface (solid lines) and bottom (broken lines) in the central and eastern areas.

Freshwater drainage and the two-layer transport system favored development and maintenance of a vertical salinity gradient throughout the Sound. However, in previous years (1952–53) autumn mixing has been strong enough to destroy the gradients frequently. Thus the magnitude of the autumn gradients in 1954 and 1955 may be regarded as an unusual phenomenon associated with abnormal rainfall.

Oxygen. In a later paper the distribution of oxygen will be examined carefully in an attempt to determine rates of biological production and comsumption in different parts of the Sound. For present purposes only brief mention is required. The seasonal cycle in the central part has been described previously by Riley and Conover (1956), and essentially similar results were obtained in this area during the 1954–55 phase of the survey. A similar seasonal cycle has also been found in the western end, but the reduction of oxygen in the bottom water in summer was more pronounced than elsewhere; minimum values recorded were about 40 °/₀ of saturation as compared with about 50 °/₀ in the central basin.

In the deeper and more turbulent waters of the eastern end, the oxygen at the bottom was at least 85 °/₀ of the surface saturation value at all stations. All waters from surface to bottom tended to be slightly undersaturated throughout the year. The reduction in the surface layer probably was the result of rapid mixing with deep water of slightly smaller oxygen content. The existence of a small deficit in the whole water column, in winter as well as in summer, also suggests that this water mass was mainly derived from the deeper layers offshore, although the source cannot be identified with certainty by its temperature and salinity characteristics.

Phosphate. Fig. 6 shows that the general level of phosphate concentrations increased from east to west, particularly in autumn and winter. Otherwise there were no marked regional differences in seasonal cycles. Enrichment experiments by S. A. M. Conover (1956) indicated that phosphate was not an important limiting factor in the central basin. The form of the seasonal cycles suggests that Conover's conclusion is applicable to the Sound as a whole, although it has not been tested experimentally.

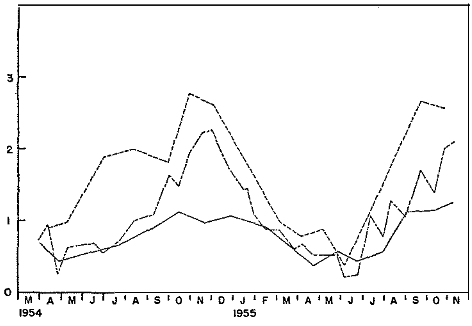

Figure 6. Surface phosphate in μg–at P/l.

It was common to find a slight vertical phosphate gradient in spring and summer. Typical values for the difference between bottom and surface concentrations were about 0.1 μg-at P/l in the eastern end, 0.2 to 0.3 in the central basin, and 0.3 to 0.5 at the western end. Previous work indicated that biological activities were capable of reducing the surface concentration about

0.03 μg-at/l in a day's time and of increasing the amount in the bottom water correspondingly. The lack of pronounced gradients therefore was due to a moderately rapid rate of vertical mixing. The gradients in autumn and winter varied from slightly negative to positive, the latter occasionally showing differences of as much as 0.5 μg-at P/l between surface and bottom. Riley and Conover (1956) suggested that positive gradients were the logical consequence of the kind of transport pattern that exists in the Sound, which causes rich western water to flow over the layer of poor water that moves in from the east.

Nitrate. The nitrate cycles in Fig. 7 present a picture of poverty as compared with phosphate. The N : P ratio by atoms at the time of the midwinter maximum has ranged between 5 : 1 and 8 : 1 in various years and in different parts of the Sound, or about one-third to one-half the normal ratio in Atlantic oceanic waters. From the end of the winter flowering until August or September there was little or no nitrate anywhere in the water column except for a small but noticeable increase in April of each year in the easternmost area.

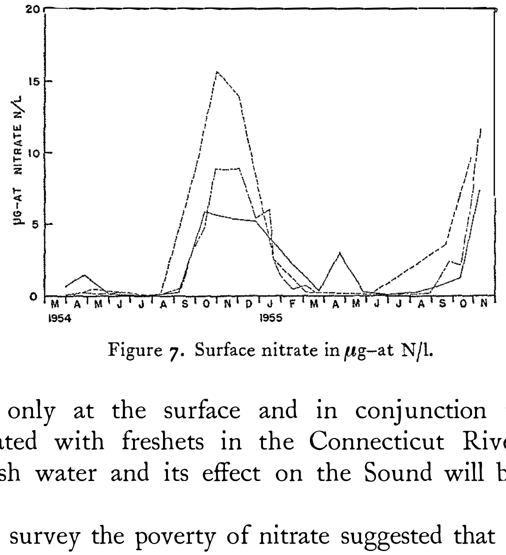

Figure 7. Surface nitrate in μg–at N/l.

This occured only at the surface and in conjunction with the reduced salinity associated with freshets in the Connecticut River. The nutrient content of fresh water and its effect on the Sound will be discussed in the next section.

Early in the survey the poverty of nitrate suggested that nitrogen might be an important limiting factor with respect to phytoplankton growth, and this was confirmed by enrichment experiments (S. A. M. Conover, 1956). Because of the apparent importance of the nitrogen cycle, it seemed desirable to undertake a more complete study of the subject. The results are given by Harris (in this volume). It is sufficient for the moment to say that his work confirms earlier conclusions that nitrogen is the key element in the system. However, it is also shown that ammonia is a more important source of nitrogen than is nitrate during most of the season of active phytoplankton growth.

Freshwater Nutrient Sources. On most cruises surface samples were taken a short distance upstream from the mouths of important rivers for evaluation of freshwater sources of phosphate and nitrate. The rivers were sampled on the ebb tide whenever possible, but limitations of time occasionally prevented this.

Table I shows the salinity and the concentration of phosphate and nitrate in the river samples. The phosphate concentration generally was equal to or less than that of adjacent Sound waters and will not be considered further. Nitrate was nearly always greater in the river water, although the amount varied from time to time.

Salinity data show that the samples (Table I) represent varying admixtures of river and Sound waters. Combining these figures for river water with observations of salinity and nitrate at the nearest station in Long Island Sound proper, algebraic estimates were obtained of the amount of nitrate that would be expected in river water of zero salinity. The results are indicated as N′ in Table I. This was done for all samples except a few from the Housatonic River in which the salinity was so nearly the same as that of the outside waters that large errors were possible.

The rivers had a seasonal cycle of nitrate somewhat similar to that of the Sound, with a winter maximum and a summer minimum. However, it is uncertain as to whether freshwater biological cycles were important in this respect. Seasonal variations in runoff may have been the controlling factor. Clearly the floods in the late summer of 1955 were accompanied by a rapid increase in nitrate, a situation quite different from the pattern of the previous summer.

In 1954 Lohr and Love published chemical analyses of reservoir and other water supplies of potential commercial usage. Their data included about 45 analyses in the Long Island Sound watershed. Most of their nitrate values for surface waters fell within the range described above, the average being 10.0 μg-at N/l. Probably the small rivers represented by these analyses supply essentially the same amount of enrichment as the large ones that have been measured routinely. There were also ten analyses of well waters from the New York mainland and from the western end of Long Island with a total range of 8 to 610 μg-at N/l and a mean value of 210. In view of the large potentiality for enrichment by groundwater seepage, it is unfortunate that its volume of flow cannot be estimated.

Under most circumstances the nitrate output from rivers appeared to be incorporated rapidly into the biological system. The major exception was the period of spring freshet in the Connecticut River, when it appeared that more than half of the nitrate was transferred out of the Sound before it could be absorbed by the phytoplankton. During the late summer flood recorded on September 1, 1955, the data indicate that about 80 % of the nitrate from the Connecticut River was no longer present as such when the water left the Sound

TABLE I. Analyses of Salinity (S) in parts per mille and Phosphate and Nitrate in μg-at/l of P and N, respectively, near the Mouths of the three largest Rivers that discharge into the Sound. N′ is an Estimate of the amount of Nitrate-N in River Water of Zero Salinity. For further Explanation see text.

	Connecticut River				Thames River				Housatonic River			
	S	P	N	N′	S	P	N	N′	S	P	N	N′
1954												
Mar. 30	1.42	0.54	37.0	38.8	15.93	0.81	9.2	19.0	–	–	–	–
Apr. 12	–	–	–	–	–	–	–	–	14.87	1.03	13.2	28.9
Apr. 26	–	–	–	–	11.27	0.70	9.9	16.0	–	–	–	–
Apr. 27	0.43	0.81	15.6	15.8	–	–	–	–	–	–	–	–
May 11	–	–	–	–	–	–	–	–	0.28	–	5.9	5.9
June 1	6.39	0.74	12.6	16.5	21.72	0.31	0.2	0.8	–	–	–	–
July 2	–	–	–	–	–	–	–	–	26.08	0.70	0.0	0.0
July 22	–	–	–	–	26.23	1.62	0.0	0.0	–	–	–	–
July 23	11.46	0.86	2.3	3.8	–	–	–	–	–	–	–	–
Aug. 13	–	–	–	–	–	–	–	–	20.03	1.28	1.8	5.7
Sept. 9	–	–	–	–	20.17	0.36	8.4	24.4	–	–	–	–
Sept. 10	19.05	0.97	3.5	8.0	–	–	–	–	–	–	–	–
Oct. 1	–	–	–	–	–	–	–	–	27.54	1.51	2.0	×
Oct. 14	16.41	1.23	11.6	19.1	–	–	–	–	–	–	–	–
Oct. 15	–	–	–	–	21.49	1.31	15.3	36.8	–	–	–	–
Nov. 19	9.86	1.06	17.8	23.4	18.50	0.96	12.1	18.6	–	–	–	–
Dec. 2	–	–	–	–	–	–	–	–	1.40	1.37	17.4	17.9
Dec. 27	1.58	0.73	17.4	17.9	–	–	–	–	–	–	–	–
1955												
Jan. 20	–	–	–	–	–	–	–	–	26.44	1.51	4.1	×
Feb. 18	11.75	1.38	21.0	32.6	–	–	–	–	–	–	–	–
Mar. 3	–	–	–	–	–	–	–	–	7.95	1.44	17.0	23.6
Mar. 24	5.00	1.03	16.7	20.2	–	–	–	–	–	–	–	–
Apr. 6	–	–	–	–	–	–	–	–	4.96	1.70	21.9	27.0
Apr. 21	0.22	0.66	7.4	7.4	–	–	–	–	–	–	–	–
May 6	–	–	–	–	–	–	–	–	16.07	1.11	2.9	7.7
May 27	6.68	0.82	10.6	13.8	21.96	0.58	0.2	0.6	–	–	–	–
June 7	–	–	–	–	–	–	–	–	26.57	0.42	0.1	×
June 23	23.41	0.58	0.2	0.8	–	–	–	–	–	–	–	–
July 12	–	–	–	–	–	–	–	–	24.67	0.93	0.1	0.4
July 29	17.20	0.58	2.2	4.6	–	–	–	–	–	–	–	–
Aug. 9	–	–	–	–	–	–	–	–	15.26	0.40	9.4	20.6
Sept. 1	12.08	0.91	4.9	8.8	–	–	–	–	–	–	–	–
Sept. 21	–	–	–	–	–	–	–	–	11.41	1.00	6.9	10.3
Oct. 12	12.51	1.14	6.5	11.2	–	–	–	–	–	–	–	–
Oct. 27	–	–	–	–	–	–	–	–	6.96	1.10	17.1	20.0
Nov. 9	0.52	0.67	12.9	12.9	–	–	–	–	–	–	–	–

through the eastern passes. In the central and western basins, virtually no surface enrichment could be detected at any time except in the immediate vicinity of river mouths.

QUANTITATIVE ASPECTS OF THE SEASONAL CYCLE OF PHYTOPLANKTON

Routine chlorophyll analyses will be used to evaluate the general features of seasonal and regional variations in phytoplankton. Cell counts and the discussion of species composition will be reserved for a later paper.

Just before the beginning of this two-year survey, routine observations in the central part of the Sound had revealed a winter diatom flowering which reached its peak in mid-February 1954. The scarcity of phytoplankton and nitrate throughout the Sound in March and April of that year suggested a widespread postflowering condition. The ensuing events are summarized in Fig. 8, which shows average chlorophyll in the three areas that have been discussed previously in connection with other variables.

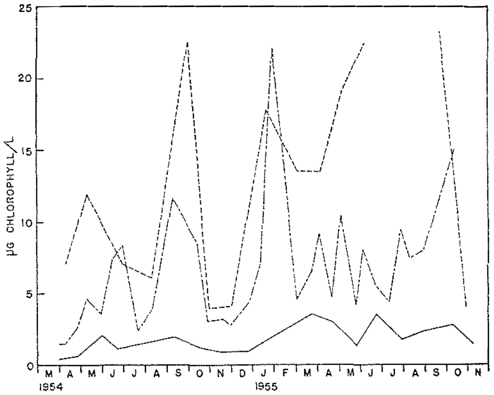

Figure 8. Surface chlorophyll in μg/l.

The most outstanding feature of the observed distribution during 1954 and 1955 was the vast difference in the chlorophyll concentration between one end of the Sound and the other, such that the minimum concentration in the western end approximated flowering levels in the eastern end. However, since the eastern end is deeper than other areas, it will be seen later that regional variations in the quantity of chlorophyll per unit area of sea surface were not nearly as large as the differences in concentration per unit volume.

The seasonal cycle in the central basin for 1954 and 1955 will be considered first because this area was sampled more frequently than the others and because data from 1952 and 1953 are available for comparison. The irregular summer curve, with a series of flowerings of moderate size, appears to be normal; the general level of chlorophyll concentrations in the summer of 1954 was lower than that in the other three years of the investigation.

The autumn flowerings in 1954–55 were more pronounced and of longer duration than those in 1952 and 1953. As pointed out earlier, there was excessive late summer and autumn rainfall during 1954 and 1955, and the large quantities of nitrate observed in freshwater drainage probably aided the early establishment of the flowerings. However, nitrate enrichment was not a likely explanation of the entire sequence of events. In all four years, the autumn regeneration of nitrogen was well underway by mid-September, and the nitrate situation was not markedly better in 1954 and 1955 than in the preceding two years.

In a previous discussion of the autumn season by S. A. M. Conover (1956), it was suggested that light intensity is the most important limiting factor, and present results appear to be a special case which strengthens the general conclusion. In 1952 and 1953 there was virtually no stability in the water column in late September and October, but stability was maintained until mid-October in 1954, and even later in 1955, because of abnormal surface dilution. This stability was accompanied by pronounced vertical gradients in chlorophyll, which also was quite different from the observations of the first two years. In short, it is proposed that vertical stability promoted a flowering by maintaining the phytoplankton in a surface stratum where the fading autumn light was still sufficient to support growth, whereas the same amount of light might be insufficient if the cells were rapidly circulating through the whole vertical column.

Subsequent data for 1956 are worth mentioning in this connection, although they are largely reserved for a later publication. The early summer was cool; the temperature gradually rose and finally reached its seasonal maximum in September, a month later than usual. Thermal stability was also preserved into early September, and at that time the beginning of nutrient regeneration in the bottom waters coincided with the onset of a large autumn flowering. The latter was limited to the upper 5–10 m, and the surface concentration was the highest that has yet been observed in an autumn flowering. Rainfall and river discharge were below normal. These results in 1956 strongly support the theory that vertical stability is a prime requisite, irrespective of whether thermal or haline conditions create the stability. A nutrient supply is also necessary, but it appears to be immaterial whether an external source of enrichment is present or not.

Some aspects of the problem still remain obscure. Throughout the investigation a definite pattern has been repeated in which nitrate gradually increased to a concentration of 3–5 μg-at N/l over a period of several weeks in late August and September; then the flowering began if other conditions were suitable. The initial increase in nitrate implies either a reduction in phytoplankton growth or an increase in the regeneration rate, or both. It is not certain just what happened at this point, and it is equally unclear as to why the phytoplankton did not respond more quickly to the initial increase in nutrients. The obvious suggestion of a physiological lag is not altogether satisfactory because the phytoplankton was able to grow rapidly enough throughout the summer to make use of all available nitrate.

After an unusually short period of late autumn poverty in 1954, the winter diatom flowering got underway in January 1955 and reached its peak about February 1. Peaks in previous years had been recorded in early March 1953 and mid-February 1954. Differences between 1953 and 1954 were described by S. A. M. Conover (1956) as being the result of temperature-controlled competition between two of the dominant species (*Skeletonema costatum* and *Thalassiosira nordenskiöldii*). This led to a pronounced difference in the radiation level that was required for the inception of a flowering, depending on which species was favored by the temperature that prevailed at the time. However, the situation appeared to be somewhat simpler in 1955. The number of hours of sunshine in January was the highest in a 55-year series recorded by the New Haven Weather Bureau, and the estimated radiation for January 1955 was about the same as February values for 1953 and 1954. This seems to be sufficient reason for an early flowering, regardless of species composition.

The flowering was of moderate size, the maximum chlorophyll concentration in 1955 being less than in 1953 but greater than in 1954. This seems rather surprising in view of the fact that the winter stock of nitrate in 1955 was not much more than half the maximum of the three previous years. However, it will be apparent later (Harris, in this volume) that considerable quantities of nitrogen were present in other forms in 1955; apparently these were available for phytoplankton growth or were gradually made available during the winter and early spring. It is possible, although it remains to be established, that the total nitrogen stock was normal and that failure to achieve the usual level of the nitrate maximum was due to the unusually short regeneration time between the autumn and winter flowerings.

The flowering passed its peak in 1955 before the nitrate supply was completely exhausted, and this probably was due to heavy weather and to a temporary reduction in radiation in February. During February and March the chlorophyll concentration fluctuated considerably, but generally it remained above the postflowering level of the preceding two years. Some nitrate remained in the water, and again referring to the work of Harris, there were other significant sources of nitrogen in the system.

At the present writing four flowerings and five postflowering periods have been observed since 1952. These are hardly sufficient for broad generalization, but the elements of a pattern are evident. First, a major flowering has occured each year, with its peak sometime between January and March.

Second, the postflowering observations of various years reveal an intergradation between two opposite syndromes: free nitrate plus chlorophyll plus zooplankton, or low concentrations of all three. The former situation tended be associated with a slow, cold spring. The implications are obvious. If unfavorable weather arrests the flowering so that production is spread over a long period, it provides maximum benefit for the zooplankton population. A quick flowering with little postflowering growth provides more food than is needed in the beginning and offers little chance for a successful second brood.

In all of the waters between the eastern passes and Long. 72° 30′W, during 1954–55 the largest chlorophyll concentrations were obtained in late March. With monthly sampling intervals there is no assurance that the peak of the flowering was observed. However, the steady and gradual decline in nitrate from December through March argues strongly against the occurence of a short diatom burst of large magnitude at any time during the winter. Rather it suggests steady but unspectacular growth. This is to be expected in an area in which the surface layer was continually seeded by the flowering population from the central basin but in which the water was too deep and turbulent to be a likely locale for an early flowering.

There was a second flowering in May and June of each year in the eastern part of the Sound; these were small in absolute magnitude, but the one in 1955 was almost as large as the March flowering of the same year. Small increases also occurred in early autumn, coinciding with much larger flowerings in the central basin.

Chlorophyll concentrations were large in the western basin as compared with the eastern end of the Sound or by any other standards. The data suggest that there were three major flowerings during each of the two years, for although the series of observations was begun too late to observe a winter flowering in 1954, there is hardly any doubt that one had occurred. The May-June flowerings were primarily dinoflagellate blooms. In 1955, replacement of winter diatoms by spring dinoflagellates took place with little decline in total population, so that there was a continuous state of flowering for about five months. There was a marked vertical gradient in chlorophyll during the late spring blooms, which is presumed to reflect the ability of dinoflagellates to maintain a preferred depth.

A decline occurred in the midsummer population in 1954. No data were obtained in this area in the summer of 1955. The westernmost observations were at Long. 73° 32′W, and there a midsommer minimum was found.

The autumn flowerings in 1954–55 were larger than the maximum observed population during the winter diatom blooms, although there is no assurance that any of the flowerings were sampled precisely at the climax. Since these were years of widespread autumn flowerings throughout the Sound and since it is known that they do not always occur in the central basin, it must remain an open question as to whether an autumn flowering is a consistent event in the western end. However, present experience indicates that the autumn regeneration of nutrients begins early there and that the shallow depth makes the seasonal decline in radiation somewhat less severe in its inhibiting effect. Thus an autumn flowering appears to be a more likely event in the western end of the Sound than elsewhere.

REGIONAL VARIATIONS IN TOTAL PHYTOPLANKTON AND ZOOPLANKTON

The chlorophyll observations were averaged by cruises for all stations in each of the 10′ strips of longitude, first by combining similar depths at all of the stations in each area and then by averaging the concentrations at all depths to obtain an estimate of the mean chlorophyll in the water column as a whole. The results are summarized in Table II, which includes (a) information on maximum concentrations during flowering periods, (b) the minimum observed concentration (late autumn, early winter, or spring postflowering period), and (c) the annual mean.

Estimates of the maximum and minimum populations obviously are rough approximations because the monthly interval between sampling was too long for accurate description of short term events. The annual means, which have a more dependable degree of precision, show a consistent increase in concentration from the eastern passes to the central region; between Long. 72° 45′

TABLE II. MEAN CONCENTRATION OF CHLOROPHYLL (μg/l) IN THE WATER COLUMN AS A WHOLE AT A STATION IN THE RACE (eastern entrance to the Sound) AND AT ALL STATIONS IN THE LONGITUDE RANGES LISTED.

Area	Maximum		Minimum	Anunal Mean
	Winter Flowering	Autumn Flowering		
Race	4.1	3.0	0.3	1.7
72° 05′–15′	4.5	2.3	0.4	1.9
15′–25′	4.4	3.1	0.8	2.4
25′–35′	6.4	5.9	1.2	3.2
35′–45′	11.7	5.8	1.6	4.9
45′–55′	13.5	13.0	2.1	5.9
55′ to 73° 05′	19.0	14.5	1.7	6.2
73° 05′–15′	17.4	10.0	1.5	5.7
15′–25′	21.1	12.1	1.2	5.8
25′–35′	16.6	12.1	1.1	6.4
35′–44′	14.5	20.2	3.5	9.2
44′–	17.4	16.6	3.5	11.8

and 73° 35′W the population was relatively uniform, and then it increased again in the constricted western portion. Thus the over-all range in average concentrations varied by a factor of 7 : 1. Maximum and minimum populations exhibited a more or less similar range.

The total chlorophyll underlying a unit area was roughly computed as the product of the mean annual concentration and the mean depth of water in each area. The depth decreased from east to west, so that the gradient in the total phytoplankton crop was markedly less than the range in concentrations per unit volume. Total chlorophyll increased from 50 mg/m^2 in the eastern end to 122 in the area between Long. 72° 45′ and 72° 55′W. In the remainder of the Sound there were irregular variations between 84 and 121 mg/m^2.

The zooplankton collections were oblique tows which sampled most of the water column except at the deep stations, and it is believed that the collections give a reasonably accurate picture of the average concentration of zooplankton in the water column. Displacement volumes were determined on all samples that were sufficiently free of phytoplankton to warrant measurement, and the results were compiled as milliliters of zooplankton per cubic meter of water strained.

The zooplankton observations were much less complete than the chlorophyll measurements. In order to estimate annual means, it was necessary to combine several areas in some cases and to interpolate in order to fill a few gaps in the seasonal cycle. Results are shown in the first part of Table III. The No. 10 net hauls were used for the calculation because they were generally larger than the No. 2 catches and more nearly represented the total zooplankton population.

The data showed no large or clearly significant regional variations in zooplankton concentrations, although there was a slight indication of a decrease toward the eastern end. However, again because of regional differences in depth, the estimates of total crop per unit area gave quite different results from the comparison of concentrations per unit volume. In this case, the zooplankton crop was clearly larger at the eastern end than elsewhere.

Comparison of Tables II and III suggests that the moderate concentration of phytoplankton in the eastern end was about as effective in maintaining the zooplankton as the large concentration in the western end. Inquiry into this problem is facilitated by estimates of feeding capacity which are compiled in Table III.

R. J. Conover (1956) determined feeding rates of *Acartia clausi* and *A. tonsa* under controlled conditions of temperature and food supply which included most of the naturally observed range of the two variables. Since *Acartia* is the dominant genus of copepods in most of the Sound, Conover applied his experimental results to a general consideration of food problems; his methods will be continued here. The daily filtration capacity under average conditions was estimated to be 85 l/ml of displacement volume of zooplankton. This factor was applied to the observed zooplankton volume in each area, and the results are listed in Table III as the filtration capacity of the population as a whole. The product of the filtration capacity and the mean concentration of phytoplankton (Table II) then provided an estimate of daily ingestion of phytoplankton. This was recorded in Table III as milligrams of phytoplankton organic matter ingested, using conversion factors derived from Harris and Riley (1956). The percentage of the phytoplankton crop that is estimated to have been consumed each day varied in the different areas between 4.5 and 6 %. This is a credible amount, since the daily production of phytoplankton is believed to average about 7 % of the standing crop.

TABLE III. REGIONAL DISTRIBUTION OF ZOOPLANKTON (annual mean displacement volume) AND ESTIMATES OF FEEDING RATES.

Area	Zooplankton Volume (ml/m³)	Zooplankton Volume (ml/m²)	Filtration Capacity (l)	Phytoplankton Org. Mat. Ingested (mg/m²)	Total Ingestion, % of Zoopl. Org. Mat.
72° 05′–25′	0.55	15	1270	340	23
72° 25′–45′	0.60	13	1100	590	46
72° 45′ to 73° 15′	0.73	14	1190	940	67
73° 15′–25′	0.68	11	930	730	66
73° 25′+	0.69	7	590	730	104

The final column in Table III shows the estimated food intake of zooplankton as a percentage of their own organic content. The figure given for the central part of the Sound is only slightly different from R. J. Conover's (1956) estimate of 58 % ingestion for 1952 to 1954. His work indicated that the Acartias have an unusually high metabolic rate, requiring a daily food intake of 29 % of ther body weight; about 17 % was believed to be used in growth and the remainder was assumed to be unassimilated waste.

The calculations indicate that the food supply in the western end was potentially able to support a more rapid growth rate than that in the central region. The fact that this did not result in a larger population is not understood. It is possible that there was in fact a larger growth rate which was counter-balanced by a larger rate of predation. It is perhaps equally likely that the growth rate was not greatly increased by a superabundance of food and that the population was limited by other density-dependent factors as yet undiscovered.

The eastern half of the Sound was marginal for the support of the Acartias. The estimated 23 % daily ingestion of organic matter in the area farthest to the east was less than Conover's calculated mean respiratory requirement. The intermediate region between Long. 72° 25′ and 72° 45′W possibly could provide metabolic requirements, but effective growth would appear to require an impossibly high degree of efficiency in assimilation unless they were able to get considerable sustenance from detritus and other sources of organic matter not included in the estimate.

Although the Acartias have sometimes been abundant in the eastern end of the Sound, there is a distinct tendency for them to be replaced by other species which are dominant in the open waters to the eastward but which are minor elements in the central and western sections of Long Island Sound. The normal interchange of water masses is sufficient reason for these species to be common elements in the plankton in the eastern end. However, the present discussion suggests that this is not the only reason for their abundance. Most of the coastal water species apparently have a lower metabolic rate than the Acartias and can grow effectively with a smaller concentration of food organisms (Deevey, 1952; R. J. Conover, 1956). Thus it seems likely that they are physiologically equipped for dominance over Acartias in such waters.

It has not been fully determined as to why the coastal water species failed to achieve dominance over the Acartias in the central and western parts. This would be expected in view of their greater feeding efficiency unless some other factor or factors were distinctly unfavorable. Conover has suggested that they tend to be excluded by low salinity. Qualitative aspects of the food supply, or even its great abundance, might also be undesirable for these species.

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Гордон А. Райле

Океанография пролива Лонг Исланд Соунд, 1954–1955. Краткий обзор

Общее обозрение пролива делалось от Марта 1954 до Ноября 1955 года с двухнедельным сбором в нескольких местах центральной части пролива и месячным сбором в других частях.

Восточный конец пролива, прилегающий к открытым прибрежным водам океана, несколько холоднее летом и теплее зимой чем мелкая и более закрытая западная часть, где общее сезонное различие температуры равнялось приблизительно 25°C. Разница температуры поверхностнаго и придоннаго слоя в общем была меньше 5°C во всех частях пролива. Соленость у западнаго конца обыкновенно меньше чем у восточнаго конца на 3–5 $^0/_0$ несмотрл на то что в последнем соленость поверхностнаго слоя значительно уменьшается во время случайных наводнений реки Коннектикут. В прежних работах описано сезонное колебание солености с весенним минимумом и осенним максимумом как нормальное явление. Но осенний маскимум был понижен в 1954 г. и совсем исчез в 1955 г. благодаря пролевным дождям сопровождавшим ураганы.

Кислород уменьшался в придонных водах весной и летом с минимумом насыщения в 40 $^0/_0$ в западной части, 50 $^0/_0$ в центральной части и 85 $^0/_0$ в более глубоких и безпокойных водах восточнаго конца в особенности осенью и зимой. Но заметных качественных сезонных различий не было. Прежния работы показали что азот как ограничивающий фактор важнее чем фосфор в центральной части пролива. Сезонные циклы наблюденные в 1954–1955 г. приводят на мысль что это верно для всего пролива несмотря на факт что сток пресной воды снабжает больше азотных чем фосфорнокислых солей.

Сезонный цикл фитопланктона, как видно из анализа хлорофила, качетсвенно тот же во всем проливе за исключением незначительных различий в его сроке. Большой осенний расцвет наблюдался в 1954 и 1955 г., тогда как в 1952 и 1953 г. расцвет был незначительный или совсем отсутствовал. В обсуждении указано что эти различия могут быть приписаны освещению, устойчивости и количеству пищи. Были и местные количественные различия в концентрации хлорофила. Его количество уменьшалось от западнаго до восточнаго конца пролива в семь раз, а весь сбор на ту же единицу поверхности уменьшался только в два раза.

Остается не ясным почему западный конец пролива не произвел соответственно большего зоопланктона чем центральная часть. Концентрация фитопланктона у восточного конца была минимальной для поддержания жизни Acartia, доминируюощаго рода копеподов во всем проливе. Поэтому не удивительно что виды Acartia уступали видам прибрежных вод обладаюощим более целесообразным метаболизмом.

The Nitrogen Cycle in Long Island Sound

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ABSTRACT

Data were obtained from October 1954 to June 1955 on concentrations of nitrate, nitrite, ammonia, particulate nitrogen, and dissolved organic nitrogen at five stations distributed through the length of Long Island Sound. The seasonal cycles were qualitatively similar in different parts of the Sound except for minor differences associated with variations in the times of flowerings. However, there was a strong horizontal gradient, with maximum concentrations of all fractions at the western end of the Sound.

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[1] Eugene Harris carried out the field work and experiments described herein and wrote a small part of the manuscript. After his tragic death in February 1956, I undertook the completion of the paper. Insofar as possible I have adhered to his concept of the meaning of the data, although it was inevitable that problems should arise during the writing that I must deal with after my own fashion. G.A.R.

The winter maximum of inorganic nitrogen, mainly in the form of nitrate, was almost entirely removed from the water column during the late winter diatom flowering. The removal was accompanied by an increase in particulate nitrogen, which attained maximum concentration during the postflowering period. Its subsequent decline coincided with a slight resurgence of ammonia. However, much of the particulate nitrogen in the water column appeared to have been lost temporarily by sedimentation on the bottom, so that by midspring the sum of all fractions was only 15 % of the midwinter stock.

The concentration of inorganic nitrogen in late spring and early summer was seldom more than 2 μg-at N/l, mainly present as ammonia. Experiments with natural plankton populations showed that ammonia was readily utilized by phytoplankton and was produced rapidly by the excretory processes of zooplankton. Although the nitrogen cycle as a whole was complex, resulting in most of the nitrogen being bound in refractory forms, it is clear that the simple processes of plant utilization of ammonia and its regeneration *in situ* by bacteria and zooplankton proceeded almost as rapidly as the phosphate cycle, and the ammonia cycle constituted a large percentage of the total nitrogen turnover.

The average daily nitrogen requirement of phytoplankton in the central part of the Sound was estimated to be 0.5 to 0.6 μg-at N/cm^2 of sea surface. This was only a little less than the amount available in the water mass at any one time during the season of active growth, which emphasizes the necessity for rapid turnover in order to maintain productivity. Roughly half of the requirement is believed to have been supplied by zooplanktonic excretion and one-tenth by bottom animals; the remaining two-fifths can be attributed to bacterial regeneration in the water column and on the bottom and to external sources of enrichment.

Enrichment by freshwater drainage during the winter and spring was about 0.04 μg-at N/cm^2 each day when averaged for the Sound as a whole. However, 75 % of the fresh water was localized in the eastern end, so that the effective enrichment elsewhere was only about 0.01 μg-at. Transport into the western end from the New York Harbor area was important locally, although enrichment by transport was only a tenth of that of river drainage. At the eastern end, the outflow of impoverished surface water and its replacement by inflowing bottom water of higher nitrogen content produced a net daily enrichment roughly estimated as 0.06 μg-at N/cm^2 in the Sound as a whole during the spring period. In autumn, when regeneration exceeded utilization, there were indications that a significant amount of nitrogen was lost from the Sound by horizontal diffusion.

INTRODUCTION

A descriptive account of the nitrate cycle in Long Island Sound by Riley and Conover (1956) suggested that nitrogen may be an important factor limiting plant growth during the spring and summer. Shirley A. M. Conover (1956) enriched natural surface water populations with nitrate, phosphate, iron, and manganese, singly and in combination. During the postflowering period of March 1954, only nitrate enrichment returned the diatom population to a flowering level. In a similar experiment in June 1954, nitrate again produced better growth than any of the other substances tested.

However, Harris and Riley (1956) found that the nitrogen content of net catches of phytoplankton was nearly constant throughout the year. Ketchum and Redfield (1949) had shown that laboratory cultures of algae in nitrogen-deficient media could exist with as little as 50 % of the normal nitrogen content, so that the deficiency in Sound waters appeared to be comparatively mild. While this did not contradict the experimental evidence of nitrogen limitation, it suggested that other sources of nitrogen which had not been examined made this limitation less severe than was indicated by nitrate concentrations alone.

In further examination of these problems, a study of the nitrogen cycle was begun with the following aims in view: (a) to analyze on a seasonal basis and in different parts of the Sound as many of the nitrogen fractions as were feasible with present analytical techniques; (b) by experiments with natural phytoplankton populations to check the previous conclusions about nitrogen limitation and to determine rates of absorption and preferences for particular ions; and (c) to determine rates of supply by animal excretion, bacterial regeneration, and by any other significant sources.

METHODS

Two-day cruises were made at intervals of approximately two weeks, covering alternately the eastern and western halves of the Sound. Nitrate and nitrite analyses were obtained at all stations. On the second day of each cruise, additional samples were taken at three stations for measurements of ammonia, of combined nitrogen in particulate form, and in some cases for measurements of part of the dissolved organic fraction. Thus biweekly samples were obtained in the central basin at positions which varied somewhat from cruise to cruise but which fell within the hatched area shown in Fig. 1. Routine station positions marked by dots were chosen for full-scale nitrogen sampling at approximately monthly intervals.

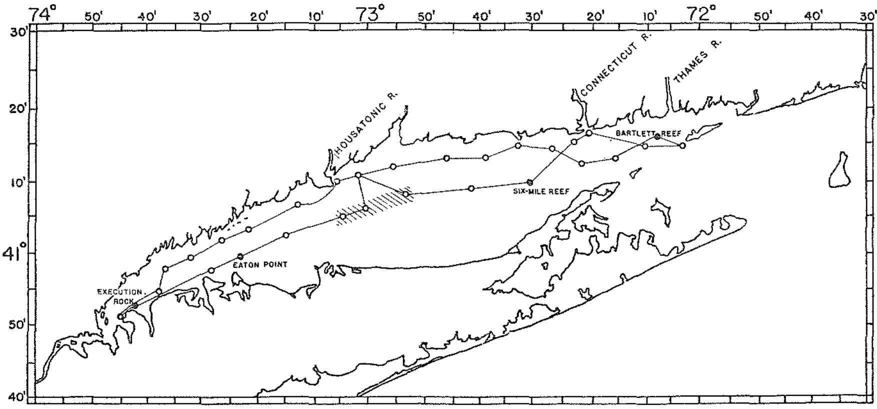

Figure 1. Chart of the area of operations and a typical cruise plan. Routine stations are shown as circles. Dots and hatched area indicate positions where samples were taken for investigation of the nitrogen cycle. These are accompanied by geographical place names used to identify the stations in the text.

Nitrate was determined by means of the strichnidine method of Zwicker and Robinson (1944), which was slightly modified in that the amount of strichnidine in the reagent was reduced to half the concentration originally stipulated. Nitrite was analyzed according to the Griess-Ilosvay reaction, as described by Robinson and Thompson (1948). A Klett-Summerson colorimeter with a No. 54 filter was used to read both the nitrate and nitrite solutions; in the latter case a suitable correction was made for the turbidity of the water.

For measurements of particulate nitrogen, a one-liter sample of sea water was filtered through an HA millipore filter (pore size 0.5μ) on shipboard immediately after collection. Occasionally it was impossible to filter a whole liter because of clogging, but in such cases a smaller volume was sufficient for analysis. The material, carefully removed from the filter by rubbing and washing with distilled water, was temporarily stored in a refrigerator in a few milliliters of distilled water. Analysis by the micro-Kjeldahl method was carried out within two or three days.

About midway in the filtration process a 100 ml screw cap bottle was rinsed and filled with the sea water filtrate and stored in the refrigerator for ammonia analysis of the water. This was completed on the following day according to the procedure of J. P. Riley (1953).

On a number of occasions, samples of the filtered sea water were also subjected to an acid hydrolysis, results of which showed that there was a significant amount of combined nitrogen in dissolved form or in small particulate matter which could be liberated in this way. The ammonia still was first cleansed by blank distillations. A 50 ml sample of filtered sea water was then introduced into the flask along with 10 ml of Na-metaborate buffer, and the ammonia was distilled from the sample; the sample was then transferred to a Kjeldahl flask, 5 ml of ammonia-free distilled water being used to rinse the last of the sample into the flask, and 2 ml of conc. H_2SO_4 were added. The sample was then digested and the amount of nitrogen was determined by the micro-Kjeldahl method. A duplicate run with reagents and distilled water was used for a blank correction. The results of this test are designated dissolved organic nitrogen, although it seems unlikely that all of the dissolved fraction could be determined by this procedure.

Sampling and Analytical Errors. Errors in the nitrate method have been discussed by Riley and Conover (1956). The accuracy of the nitrite method is satisfactory and needs no further mention. On the other hand, the ammonia method requires considerable practice, and the degree of accuracy claimed for the method by J. P. Riley (1953) was not fully attained. Table I shows ten sets of duplicate analyses obtained during the course of zooplankton experiments in which the standard deviation of the difference between pairs was $\pm$ 1.08 μg-at N/l.

TABLE I. ANALYTICAL ERRORS IN THE AMMONIA ANALYSIS (μg-at NH_3–N/l).

Paired Samples		Difference between Pairs
6.8	7.8	1.0
8.2	8.1	0.1
4.8	5.7	0.9
10.8	9.3	1.5
4.8	5.0	0.2
8.3	9.3	1.0
5.5	5.5	0.0
2.0	1.7	0.3
5.3	9.2	3.9
3.1	3.8	0.7

In routine station data on ammonia, and especially in the dissolved and particulate organic fractions, there were frequently irregularities in vertical distribution of much larger magnitude than the ordinary analytical errors given in Table I. Altogether about 50 stations were occupied, with two to four depths sampled at each station. The maximum amount of variation among the depths sampled at individual stations is tabulated in Table II.

TABLE II. VERTICAL VARIATIONS IN NITROGEN LISTED AS PERCENT FREQUENCY OF OCCURRENCE OF DIFFERENCES OF THE MAGNITUDE SHOWN IN THE LEFT-HAND COLUMN.

μg-at N/l	NH_3	Dissolved Organic N	Particulate N
0–1	42	33	37
1–3	42	14	29
3–10	10	20	18
10+	6	33	16

Thus at 6% of the stations there were vertical variations in ammonia of more than 10 μg-at N/l, and the frequency of large differences was even greater in the case of particulate and dissolved organic nitrogen. About half of the large values were obtained from samples taken near the bottom, so that the results were not altogether unreasonable; the other half were found at both surface and mid-depth. Although the possibility of accidental contamination cannot be ruled out in any particular case, the data as a whole suggest that the distribution was very irregular and was subject to large sampling errors. This is not altogether unexpected in the case of particulate nitrogen. Cooper (1948) has documented a somewhat analogous situation in analyses of iron distribution, and Goldberg *et al.* (1952) have emphasized the discontinuous nature of particulate iron and suspended matter in general. However, another explanation must be sought for variations of a similar magnitude in the soluble fractions. One possibility is that the patchiness of plankton is associated with the development of small foci of intensive accumulation of metabolic products. It will be shown later that the zooplankton population is capable of excreting ammonia very rapidly and that the development of a dinoflagellate flowering coincided with a marked increase in dissolved organic nitrogen.

THE SEASONAL CYCLE

In the central part of the Sound the biweekly samples included the surface water, a mid-depth sample at 5 or 10 m, and a near-bottom collection at 15 to 25 m. Because of large sampling errors, the data are presented in smoothed form by showing seasonal cycles as averages of surface and mid-depth determinations.

Fig. 2 combines all of the data into a single graph, with the organic nitrogen plotted above the base line and the inorganic forms below. The upper line is the Kjeldahl determination of particulate nitrogen. This can be divided

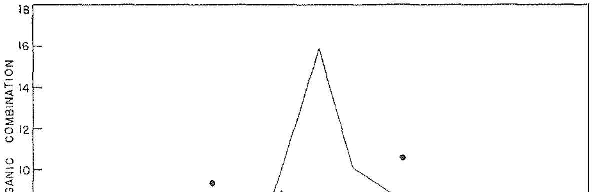

Figure 2. Seasonal cycle of the various nitrogen fractions in the central part of the Sound. For explanation see text.

roughly into planktonic and nonplanktonic fractions, since the nitrogen content of the plankton has been determined in relation to chlorophyll concentration and zooplankton volume (Harris and Riley, 1956) with sufficient consistency to establish conversion factors and since data on chlorophyll and zooplankton are available for each station. Estimates of phytoplanktonic and zooplanktonic nitrogen are plotted additively in Fig. 2, and the difference between total particulate nitrogen and the combined planktonic fractions is labeled bacteria and detritus. Superimposed on the graph are the points representing the quantity of dissolved organic nitrogen that is liberated by acid hydrolysis. The number of points is insufficient to warrant drawing a seasonal curve.

The nitrite, nitrate, and ammonia data are plotted additively below the base line. In compiling these data it has been assumed that the strichnidine test measures the sum of nitrate and nitrite. Therefore, the nitrate values that have been plotted represent the difference between the results of the strichnidine test and the Griess-Ilosvay nitrite.

The study of the nitrogen cycle began during the early stage of the usual autumn increase in nitrate, which was accompanied by a decline in particulate nitrogen. The nitrate maximum in the fall of 1954 was unusually low (Fig. 2), a more typical figure in the three previous years being 15–20 μg-at NO_3N/l. It has been suggested by Riley (in this volume) that the short period between the autumn and winter flowerings did not allow time for the usual amount of regeneration. This question cannot be fully settled in the absence of complete data for other years, but clearly a large fraction failed to be converted to nitrate, for the total observed nitrogen was 24 μg-at/l in late December 1954.

The decrease of inorganic nitrogen during the next month and a half from 10.7 to 0.6 μg-at was slightly more than matched by an increase in particulate nitrogen from 4.4 to 16.0 μg-at. There is a suggestion here of continued regeneration of inorganic nitrogen from the dissolved fraction or of direct utilization of the latter by phytoplankton.

The postflowering decline of particulate nitrogen was accompanied by regeneration of ammonia and a slight increase in nitrate. The phytoplankton then became stabilized at a subflowering level until the inorganic nitrogen was again exhausted; during this period the zooplankton population achieved the highest level of the year and one of the largest spring populations that has ever been observed.

There was a period of two and a half months between the peak of the flowering and the minimum that followed in mid-April of 1955. In 1953 and 1954 the decline had been essentially continuous and was completed within a month to six weeks; both of these earlier flowerings obviously had been terminated by nitrogen depletion. It is less likely that this was the case in 1955. On January 31, when the maximum chlorophyll concentration was recorded, a small but significant amount of nitrate remained in the water. There followed a three-week period in which solar radiation dropped below the high January level; also there were two severe storms in February. If the flowering was halted by a combination of moderate nutrient depletion and temporarily adverse physical conditions, this would seem to be sufficient reason for the decline to be less cataclysmic than that previously observed and for it to be further prolonged by recycling of the nitrogen. Furthermore, the large zooplankton crop that developed suggests that a long slow flowering is more beneficial to the animal population than a large one that is quickly finished.

All of the nitrogen fractions that have been measured totalled 19.5 μg-at N/l in late March; this was only slightly less than the early winter maximum. But by mid-April the total was reduced to only 3 μg-at, after which it increased to about 6 μg-at and remained at that level through June 1955. The spring decrease in total nitrogen was general throughout the Sound and is therefore to be regarded as a fundamental part of the biological cycle rather than a product of the exchange of water masses at a particular location. Most of the observed facts can be explained as sedimentation of particulate matter on the bottom, a lag in its decomposition, and the subsequent release of its nitrogen content to the water. The existence of the sedimentation process is supported by nine analyses of water collected one or two meters above the bottom during the period from February 18 to April 6. Particulate nitrogen varied from 9.7 to 33.5 μg-at N/l and averaged 17.4, a figure well above the usual range of values for the surface and mid-depths as shown in Fig. 2.

The scanty data on dissolved organic nitrogen are not sufficient to describe its seasonal cycle with confidence. The drastic reduction that appeared to take place around the first of April is open to question. What appeared to be a sudden change may have been due in part to sampling errors. However, the generalized picture of a reduction in dissolved organic nitrogen in spring was widespread and consistent.

The ammonia fraction in spring and early summer was generally at least equal to the combined nitrite and nitrate fractions, and in one case it was an order of magnitude larger. The tendency toward an inverse relationship between phytoplankton and ammonia is the first indication that has been found of a causal basis for oscillations in the size of the phytoplankton population which commonly occur throughout the spring and summer.

In May and June, both the inorganic and particulate fractions were similar to the concentrations observed at the beginning of the survey in October 1954. It seems likely that the summer is a period of low-level fluctuations and that the part of the cycle that has been described is the most varied and interesting part. The largest gap in the data is of course the dissolved organic fraction; it has been imperfectly described, and its behavior is little understood. Data to be introduced later will indicate that the spring and summer fluctuations of this fraction deserve careful study.

Fig. 3 shows the monthly observations at the two stations in the eastern half of the Sound, and data for the two western stations are plotted on the same scale in Fig. 4. At three of the four stations in Figs. 3 and 4 the values plotted are again averages of surface and mid-depth observations; however, in most cases only two samples were taken at the westernmost station, for which the average of surface and bottom observations is used.

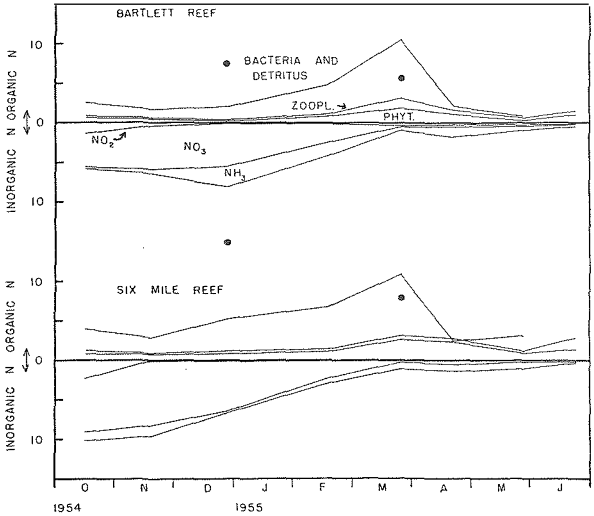

Figure 3. Seasonal cycle of nitrogen at the two stations in the eastern part of the Sound.

Early winter data showed regional differences in both the total nitrogen stock and the time when the maximum occurred; these are listed in Table III.

The major features of the seasonal cycle were similar at all stations. Minor variations were correlated with differences in phytoplankton cycles described

TABLE III. Maximum Winter Nitrogen Stock in µg-at N/l at Individual Stations (mean of surface and mid-depth levels).

Station	Date	Inorganic	Inorganic + Particulate	All Fractions
Bartlett Reef.......	Dec. 27	8.1	10.2	17.7
Six-mile Reef......	”	6.5	11.6	26.3
Central L. I. Sound.	”	10.8	15.2	24.6
Eaton Point.......	Dec. 3	15.3	19.5	–
Execution Rock....	Oct. 29	24.1	30.0	–

by Riley (in this volume). In the eastern end there was a long, slow increase in particulate nitrogen from November or December until late March, with a corresponding decrease in the inorganic fractions. Although the flowering culminated later here than elsewhere in the Sound, it was apparent that active growth was proceeding throughout the late winter. No marked increase in ammonia was observed after the end of the flowering; however, ammonia continued to be the most important source of nitrogen through the spring and early summer.

At the western stations the peak of the flowering may have been missed, although the inorganic nitrogen data leave little doubt that there was a major flowering during late January or early February. Later events here differed from those in the rest of the Sound only in that a high level of plant production was maintained throughout the spring.

On June 7 there was a dinoflagellate flowering in most of the western half of the Sound. The maximum observed chlorophyll was at the Execution Rock station. The relation that was found between chlorophyll and nitrogen is shown in Table IV. The chlorophyll data suggest that the phytoplankton was swarming near the surface; at some of the other stations on the same cruise samples were taken at one or two intermediate depths, and the maximum concentration was invariably at the surface. Table IV shows that the particulate nitrogen fraction at the surface was large on June 7, but the disparity between surface and bottom concentrations was not as great as in the case of chlorophyll. The bloom appeared to be deficient in nitrogen, since the measured amount in the particulate fraction was less than the estimated amount based on the average ratio of chlorophyll to nitrogen in net plankton as determined by Harris and Riley (1956). This is shown in Fig. 4, where the high and patently false phytoplankton estimate is indicated by a dotted line.

The large concentration of dissolved organic nitrogen, particularly at the surface, was in marked contrast to analyses in early May, a month before, when the average concentration was about 0.1 μg-at N/l. At other stations on June 7, the dissolved organic nitrogen ranged from 0.0 to 5.7 and averaged 30% less than the particulate fraction.

TABLE IV. CHLOROPHYLL (μg/l) AND NITROGEN (μg-at/l) AT STATION 1608, NEAR EXECUTION ROCK, ON JUNE 7, 1955.

Depth in meters	1	25
Chlorophyll	42.7	6.9
Particulate N	10.2	5.2
Dissolved organic N	20.3	5.7
NO_2–N	.01	.00
NO_3–N	.06	.01
NH_3–N	.85	.00

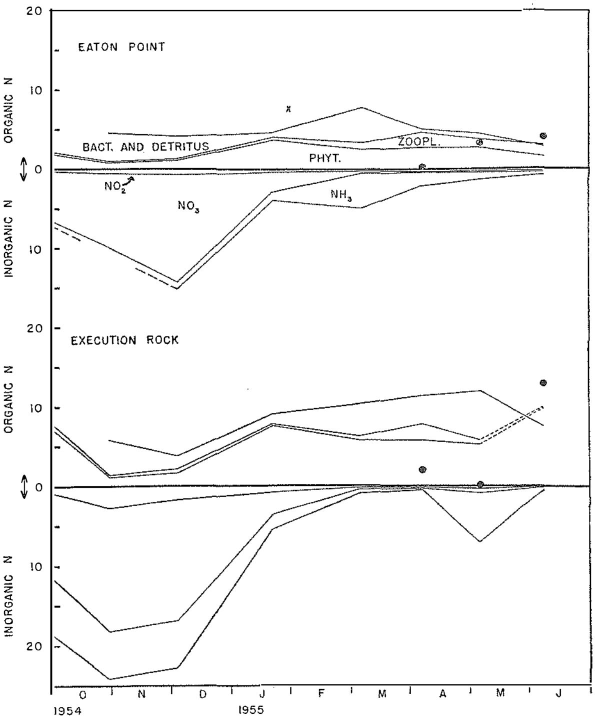

Figure 4. Seasonal cycle of nitrogen at the two stations in the western part of the Sound.

The inorganic nutrient supply was virtually nil, the only figure of any importance being the surface ammonia concentration. In the collection a month earlier, the ammonia concentration had been unusually high, with values of 2.6 and 12.9 μg-at N/l at surface and bottom, respectively. There was also a concentration of 1.2 μg-at NO_3-N at the bottom.

Thus the presence of abundant nutrients set the stage for a flowering. There is no certain evidence as to the origin of the dissolved organic matter that accompanied it, but the fact that it increased in proportion to the chlorophyll and that the nitrogen content of the phytoplankton decreased correspondingly, strongly suggests that it was a decomposition or a secretion product of the bloom itself.

EXPERIMENTS

Sixteen experiments were undertaken from January 21 to June 23, 1955. Experiments 1, 2, 4, 11, 13, and 16 were various types of enrichment experiments designed to test the response of natural phytoplankton populations to varying kinds and amounts of nitrogen addition. Experiment 3 was set up to measure the regeneration of inorganic nitrogen in a sample of stored sea water; it was not completed and will not be mentioned further. Experiments 5 through 10 and 12 measured the ammonia excretion of catches of natural zooplankton in relation to phosphate excretion and oxygen consumption. Finally, 14 and 15 were similar excretion experiments on two common and important members of the bottom community, the polychaete *Nephthys incisa* and the lamellibranch *Yoldia limatula.*

Zooplankton and Bottom Fauna. The experimental zooplankton was obtained by towing a No. 2 net near the surface. Samples of the catch were poured into one-liter glass stoppered bottles. The bottles were flushed thoroughly and were then completely filled with freshly collected sea water, a siphon covered with silk netting being used to prevent loss of zooplankton. Water was also kept for chemical determination of initial experimental conditions. The zooplankton was kept in black cloth bags in a tub of water on deck for the duration of the experiment, which was usually four hours. The temperature was taken frequently, and the water was changed as often as necessary to maintain a normal surface water temperature. At the conclusion of the experiment, glass beads were added to the bottles to facilitate mixing, and samples were then drawn off for duplicate determinations of oxygen, phosphate, and ammonia. The water for ammonia tests was filtered through millipore filters as soon as possible after the end of the experiment and was kept in a refrigerator until the tests were made the following day.

Table V lists the date and duration of an experiment, the area sampled, and other pertinent data. Table VI shows the experimental results converted to

TABLE V. LIST OF EXPERIMENTS ON ANIMAL EXCRETION AND OXYGEN CONSUMPTION.

Exp. No.	Date	Time	Location	Number of animals	Dry weight (mg)
Zooplankton					
5 (1)	Apr. 6	1200–1600	Eaton Point	1510	11.6
(2)	Apr. 6	1200–1600	Eaton Point	1530	13.9
6 (1)	Apr. 22	1000–1400	Bartlett Rf.	3180	21.4
(2)	Apr. 22	1000–1400	Bartlett Rf.	1630	19.1
7 (1)	May 6	1215–1615	Eaton Point	3880	12.7
(2)	May 6	1215–1615	Eaton Point	6270	15.8
8 (1)	May 27	1015–1315	Bartlett Rf.		
(2)	May 27	1335–1740	Bartlett Rf.	2490	6.1
9	May 27	1315–1730	Six-mile Rf.	3180	6.2
10	June 1	1055–1455	Central LIS	2980	6.1
12	June 7	1320–1805	Eaton Point	3840	11.6
Nephthys incisa					
14	June 23	1800–2200	Central LIS	6	229.1
Yoldia limatula					
15	June 23	1810–2210	Central LIS	10	320.4*

* Decalcified.

TABLE VI. Experimental Determinations of Oxygen Consumption and the Production of Ammonia and Phosphate in μg-at of O_2, N, and P per mg dry wt per Day.

Exp. No.	Temp.	O_2 Consumption		Excretion		O:N	O:P	N:P
		ml	μg-at	NH_3	PO_4			
5(1)	4.5–5.5	.14	12.7	3.1	.14	4.1	88.	21.4
(2)		.13	11.4	3.3	.21	3.4	54.	15.7
6(1)	7–8	.09	7.9	1.35	.16	5.8	49	8.4
(2)		.08	6.9	.72	.10	5.1	87	6.9
7(1)	12.5–14	.23	19.9	1.89	.72	10.5	28	2.6
(2)		.18	16.0	1.14	.19	14.0	84	6.0
8(1)	16–18	.21	18.4	5.4	.43	3.4	43	12.6
(2)		.33	28.8	4.7	.60	6.1	48	7.8
9	17.5	.36	31.6	2.0	.14	15.8	232	14.7
10	17.5–18.5	.56	49.0	3.8	1.30	12.9	38	2.9
12	15.4–16.2	.23	20.2	1.65	.18	12.2	112	9.2
14	16.7	.0135	1.18	.059	.0049	20	240	12.1
15	16.7	.012	1.05	.049	.0039	21	269	12.6
Means								
Zooplankton		.23	20.0	2.60	.37	7.7	54	7.0
Bottom fauna		.013	1.11	.054	.0044	20.5	252	12.3

daily rates per mg of dry weight of animal tissue. The species composition of the zooplankton is given in Table VII.

Experiments 5 and 7, performed in duplicate with aliquots of the same catch, provide an indication of the general magnitude of experimental errors. Experiment 6 was set up with two catches obtained only a short distance from each other, but they proved to be radically different in species composition; hence the experiment cannot be regarded as a duplicate as intended. Experiment 8 represents two successive experiments on the same plankton sample.

Table VI shows that the respiratory and excretory rates of bottom fauna were different from those of zooplankton both in absolute magnitude and in some of the atomic ratios. The difference in magnitude is not remarkable in view of the size differences of the animals involved, but the atomic ratios require some discussion. Harris and Riley (1956) found a mean N : P ratio of 15.7 : 1 in phytoplankton and 24.6 : 1 in zooplankton. Animals living on phytoplankton and retaining an excess of nitrogen in accordance with their tissue composition would be expected to have an excretory N : P ratio of less than 15.7 : 1. Although the bottom fauna and perhaps half of the zooplankton experiments fall within a reasonable range of 12 : 1 or more, there are five or six values 8 : 1 or less that seem excessively low.

The mean phosphorus content of the phytoplankton was 0.35 μg-at/mg organic matter. Assuming the latter to be about half carbon, the C : N : P

TABLE VII. PERCENTAGE COMPOSITION OF EXPERIMENTAL ZOOPLANKTON MATERIAL.

Exp. No.	5		6		7		8	9	10	12
	(1)	(2)	(1)	(2)	(1)	(2)				
Acartia clausi	77.5	77.8	3.9	42.9	98.8	98.6	85.0	95.5	28.2	4.2
Pseudocalanus minutus	4.6	2.6	42.6	–	–	–	–	–	–	–
Temora longicornis	5.3	9.8	27.4	38.5	–	–	–	–	58.4	65.6
Acartia tonsa	0.7	–	–	–	–	1.4	–	0.6	–	–
Centropages hamatus	10.6	9.2	5.8	–	0.6	–	–	1.3	1.3	–
Eurytemora americana	1.3	–	–	–	–	–	–	–	–	–
Centropages typicus	–	–	0.6	–	–	–	–	–	–	–
Clytemnestra rostrata	–	–	0.6	–	–	–	–	–	–	–
Oithona similis(?)	–	–	0.6	–	–	–	–	–	–	–
Pseudodiaptomus coronat.	–	–	–	–	–	–	–	–	0.7	..–
Copepod nauplii	–	–	3.2	0.9	0.6	–	1.1	1.9	–	1.6
Evadne nordmanni	–	–	0.6	–	–	–	–	–	0.7	–
Poden polyphemoides	–	–	–	–	–	–	–	–	–	0.5
Barnacle nauplii	–	–	4.5	3.6	–	–	–	–	1.3	–
Crustacean larvae	–	–	–	–	–	–	–	–	6.7	1.0
Sagitta elegans	–	–	0.6	0.9	–	–	–	–	–	–
Hydromedusae	–	–	2.6	2.6	–	–	–	–	–	–
Gastropod veligers	–	–	0.6	0.9	–	–	–	–	–	–
Rotifers	–	–	–	–	–	–	–	–	–	26.6
Polychaete larvae	–	–	–	–	–	–	–	–	–	0.5
Invertebrate eggs	–	–	6.4	4.4	–	–	4.6	–	–	–
Fish eggs	–	0.6	–	–	–	–	8.1	0.6	2.7	–
Unidentified	–	–	–	3.5	–	–	1.2	–	–	–

ratio by atoms would be about 119 : 15.7 : 1. A maximum estimate of the amount of oxygen required to oxidize this phytoplankton would be of the order of 300 atoms, which assumes that all of the nitrogen and phosphorus is present in bound form in protein and lipid. Some portion of these elements probably exists in an inorganic state; nevertheless the minimum estimate of the oxygen requirement, based on the carbohydrate conversion factor, is about 230 atoms of oxygen to one of phosphorus; only the bottom fauna and one zooplankton experiment fell within this likely range, and most of them were nearly an order of magnitude lower. The minimum O : N ratio would be 14.7 : 1, which again is higher than the experimental average, although the discrepancy is not so extreme.

Unless there are extraneous sources of error in these experiments, the results can only mean that the zooplankton were ingesting more phytoplankton than they could utilize either for growth or for energy and that the phosphate and ammonia were being returned to solution more rapidly than the carbon was oxidized. In this connection it should first be pointed out that the data on oxygen consumption were in accord with previous studies. R. J. Conover (1956) reported that the mean oxygen consumption of the Acartias in Long Island

Sound is about 0.028 ml o^2/mg wet weight of animal tissue in a day, which is equivalent to 0.27 ml/mg dry weight. This value falls approximately in the middle of the range observed during the present series.

Conover also determined grazing rates experimentally and calculated rates of production; the question now arises as to whether his data will support a conclusion that zooplankton ingest enough phytoplankton to supply the phosphate and ammonia that appeared during the present experiments.

Conover's grazing experiments indicated that, with a phytoplankton concentration approximating the annual mean in the central part of the Sound and at the annual mean temperature, the Acartias were capable of eating 0.57 g of phytoplankton carbon per gram of zooplankton carbon in a day. This may be restated for present purposes as 0.46 mg organic matter per mg dry weight of zooplankton. He assumed 80 °/₀ assimilation, and from this value he subtracted the experimentally determined respiratory requirement. The difference, amounting to 16.6 °/₀ of the animals' weight per day, was postulated to represent zooplankton production.

The validity of this figure may be checked in another way. Conover's measurements show that the volume of *Acartia clausi* increased from about 1.3×10^{-4} mm^3 (Stage I nauplius) to about 0.04 mm^3 for an adult female 0.84 mm long. An average daily increase of 16.6 °/₀ would require a growth period of 34 days. The observed generation time was four to six weeks during the spring. Thus Conover's figure seems reasonable for the life cycle as a whole. However, it may over-estimate the productivity of the large animals, since the field data suggest that the naupliar stages proceed more rapidly than the copepodites.

A daily production of 16.6 °/₀ of zooplankton with a nitrogen content of 89 µg/mg dry weight would require a daily impoundment of 1.06 µg-at N/mg dry weight. The phytoplankton food supply, previously estimated as averaging 0.46 mg organic matter, contained about 2.5 µg-at N. The difference, about 1.4 µg-at, represents potential excretion, although there is not much likelihood that all of it would be converted to ammonia immediately. This figure is little more than half of the experimental average given in Table VI.

However, the present work has shown that the measured particulate nitrogen is almost always greater than the amount estimated to be contained in living plankton. This so-called bacteria and detritus fraction cannot be ignored as a possible nitrogen source. The matter is best considered by examining individual experiments. Table VIII first shows the amount of ammonia excreted by the total zooplankton sample during a four-hour experiment; when the actual exposure period was longer or shorter, the result was corrected to a four-hour standard. The column entitled growth requirement is the amount of nitrogen that would be retained if the animals were increasing their mass 16.6 °/₀ each day, and the sum of the two columns is then the total nitrogen required in order to keep growth and excretion at a normal level.

TABLE VIII. NITROGEN EXCRETION AND ESTIMATED GROWTH REQUIREMENT COMPARED WITH NITROGEN AVAILABLE IN THE FOOD. ALL FIGURES IN μg-at N.

Exp. No.	Excretion	Growth Requirement	Total N Required	Ingestion, Phyt.	Prec. 4 hrs Tot. N	Avail. in Exp.
5(1)	6.0	2.1	8.1	1.8	5.6	2.6
(2)	7.6	2.5	10.1	2.3	6.8	3.0
6(1)	4.8	3.8	8.6	2.1	5.4	2.4
(2)	2.3	3.4	5.7	1.9	4.8	2.4
7(1)	4.0	2.3	6.3	6.1	12.3	4.2
(2)	3.0	2.8	5.8	7.6	15.3	4.3
8(1)	5.5	1.1	6.6	0.5	12.9	17.9
(2)	4.9	1.1	6.0	?	?	19.6
9	2.2	1.1	3.3	1.4	5.8	3.6
10	3.9	1.1	5.0	0.9	–	–
12	3.8	2.1	5.9	3.9	8.7	4.1

R. J. Conover (1956: figs. 26, 28) has evaluated the grazing rate of *Acartia clausi* at a series of temperatures, and his data will be used to estimate feeding rates in the present study, although this introduces a possible source of error in experiments in which *A. clausi* was not the dominant species. These rates, together with the mean quantities of phytoplankton and particulate nitrogen (excluding the amount in the zooplankton itself) at the stations where the experiments were initiated, provided estimates of feeding during the four hours preceding the experiment.

The validity of comparing nitrogen excretion with pre-experimental ingestion depends upon the rate of overturn. If it requires more than four hours from the time an item of food is ingested until excretion is completed, then a quantitative comparison of the two sets of figures is justified; if the cycle proceeds more rapidly than this, the excretion represents a correspondingly shorter feeding period. However, in the latter case one would expect total excretion to be supplemented by feeding during the course of the experiment. Unfiltered sea water was used, and a significant amount of particulate nitrogen was present. Assuming that feeding continued in experimental bottles at the same rate as that previously postulated, the total amount of nitrogen ingested during four hours may be expressed as

$$N = N_0\,(1 - e^{-4KW/24}), \qquad (1)$$

where N_0 is the particulate nitrogen in the water at the beginning of the experiment, K is the feeding rate at any given temperature as expressed by Conover in terms of ml of water filtered per mg dry weight of zooplankton in 24 hours, and W is the weight of zooplankton in the experiment.

The results of this calculation are shown in the last column of Table VIII. Examining this table as a whole, it may be seen that the nitrogen content of the phytoplankton was generally insufficient to supply the zooplankton requirements. The total available particulate nitrogen exceeded the requirement except in experiments 5 and 6.

The amount of particulate nitrogen that was available during the course of the experiment was in most cases greater than the observed excretion but less than the total estimated requirement. Thus it was capable of providing a significant supplement if the turnover was sufficiently rapid for this material to begin to be excreted during the experiment.

The term "excretion" has been used in a general sense, denoting all ammonia production. It is possible that it was produced both by true excretion and by liberation from semidigested faecal material excreted during the course of the experiment. Further studies by more exacting methods are needed to clarify the physiological meaning of the results. The time factors involved in ingestion, assimilation, and excretion also remain to be worked out, and while the above discussion suggests that the errors are not extreme, a more careful study under controlled conditions of feeding would be desirable.

Analyses were performed on the day after the experiment, and organic products of zooplankton activity may have suffered further degradation in the meantime. Such errors would be least in the case of ammonia determinations, since the samples were filtered immediately after the end of the experiment; they would be greatest in the case of phosphate, in which the whole water was analyzed. It remains an open question as to whether this factor contributed to the low N : P ratios that were observed.

It is somewhat questionable to use freshly caught zooplankton for experiments because of the possibility of injury during the tow and of subsequent death in the course of the experiment. This possibility was reduced to a minimum by using only actively swimming animals poured from the upper part of the bottle containing the tow. Most of the animals appeared to be active at the end of the experiments; in the one case in which there was a double experiment with a total duration of over seven hours, the second series differed little from the first.

In short, there are several aspects of the problem that deserve more careful attention. Nevertheless, the results that have been obtained are believed to be the first experimental contribution that has been made on the role of zooplankton in the nitrogen cycle in the sea, and the results will be used, with some necessary qualifications, in the further analysis of the quantitative aspects of the cycle.

Phytoplankton. For phytoplankton enrichment experiments a carboy of surface water was taken, usually at the last station of a cruise. After thorough mixing, the water was siphoned into a series of quart bottles, some of which contained appropriate nutrient salts while others were light and dark controls. All of bottles were suspended in a wire basket in Milford Harbor at a depth of one meter for an exposure of four to six days. The water was then analyzed for chlorophyll content and for one or more of the nutrient salts, and samples were preserved in formalin for cell counts.

Experiments 1, 2, and 4 tested the relative effects of nitrite, nitrate, and ammonia on chlorophyll production and cell multiplication. The amount of enrichment was in each case 20 μg-at N/l; all of these experiments, including the light and dark controls, were set up in dublicate.

Experiment 11 was designed to determine the relations of nitrite concentration in the medium, nitrite uptake, and phytoplankton increase. There was a graded series of nitrite enrichment ranging from 0.5 to 20 μg-at N/l as well as the usual controls. A bottle was also enriched with 20 μg-at NO_3-N and one with NH_3-N for comparative purposes. There were no duplications in experiment 11.

Experiments 13 and 16 compared nitrate and ammonia enrichment in triplicate. The chlorophyll analyses from these two experiments are listed in detail in Table IX to illustrate the amount of variation that may be expected in replicates. The remainder of Table IX shows averaged chlorophyll data for all of the experiments.

The biological material was heterogeneous both as to species composition, as will be seen later, and as to physiological state. Experiment 1 used material that was taken during the winter diatom flowering, which probably was slightly past its peak at the inshore position that was sampled, since the nutrient supply was nearly exhausted. The chlorophyll data give the impression that

TABLE IX. CHLOROPHYLL CONCENTRATIONS IN μg/l IN ENRICHMENT EXPERIMENTS. INITIAL CONCENTRATION IS LABELED I, LIGHT BOTTLE, L, AND DARK BOTTLE, D. OTHER COLUMNS REPRESENT THE ADDITION OF 20 μg-at N/l OF THE ION LISTED.

Exp. No.	I	L	D	NH_3	NO_3	NO_2
			Individual analyses			
13	10.1	9.2	6.8	34.9	11.2	–
	–	14.5	7.0	36.9	15.0	–
	–	–	–	38.2	16.1	–
16	14.0	10.4	4.3	24.1	7.9	–
	–	11.0	3.5	23.6	17.1	–
	–	–	–	11.7	15.1	–
			Averages			
1	7.6	16.7	14.7	23.6	25.8	26.2
2	2.5	2.5	2.7	6.5	7.9	9.7
4	8.1	7.1	7.5	12.0	10.5	7.6
11	2.3	2.6	2.3	12.1	5.0	7.0
13	10.1	11.8	6.9	36.7	14.1	–
16	14.0	10.7	3.9	19.8	13.4	–

the phytoplankton was still in an active state of growth; the increase that occured in the dark bottle is common in such cases, but the cell counts, which will be discussed later, suggest a more senescent condition. Experiments 2 and 4 represented the quasi-steady state of the spring period in which there was little change in control bottles and only moderate response to enrichment. Material for experiments 11 and 13 was taken during the development of a small, early summer flowering, and there was a strong response to enrichment, particularly in the case of ammonia. Experiment 16 began near the peak of this flowering, and the cells probably were in a senescent condition. The chlorophyll showed a serious decline in control bottles and only slight response to nutrient addition.

Of the three nitrogen sources examined, ammonia was superior in the majority of cases and was not markedly inferior in the remainder. Much of the physiological literature indicates that nitrate is more readily utilized than nitrite, but the present series shows no clearcut difference between the two ions with respect to chlorophyll production. The only pronounced difference was in the rate of uptake. Its effect on phytoplankton production, if any, was not visible within the time limits of the experiments. In experiments 1, 2, 4, and 13 virtually all (92 to 99 %) of the nitrate was absorbed during the experimental period. Experiment 11 was not analyzed, and in 16 the absorption was only 33 % of the amount available. In ordinary net phytoplankton, the chlorophyll content in μg was 1.65 times the nitrogen content in μg-at during the spring flowering and 0.95 in summer (Harris and Riley, 1956). Thus the

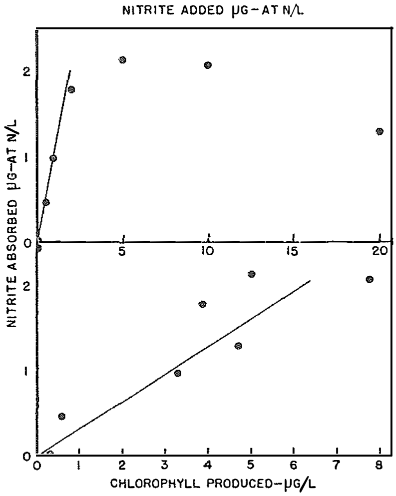

Figure 5. Experimental measurements of nitrite absorption by phytoplankton in relation to the amount present at the beginning of the experiment and the chlorophyl production in experimental bottles.

absorption of 20 μg-at of NO_3-N during the experiment was potentially capable of increasing the chlorophyll content 20 μg, more or less, but this was achieved only in experiment 1. At other times there was a great excess of nitrogen.

Nitrite absorption in the first four experiments (1, 2, 4, 11) varied from 1.3 to 9.6 μg-at N/l; the graded series of nitrite concentrations in experiment 11 is plotted in Fig. 5. Clearly the absorption of nitrite is more closely related to chlorophyll production than to the amount of nitrite available in the medium. The results support Harvey's (1953) contention that the absorption of nitrite is qualitatively different from that of nitrate, and they do not conflict with his theory that this utilization depends upon a transitory product of growth in the light. However, the nitrite uptake in relation to chlorophyll production averaged three times the normal nitrogen-chlorophyll ratio in plankton.

The terminal ammonia concentration was determined only in experiment 13. It was found that all of the 20 μg-at that were available had been utilized, but the chlorophyll increase was more than sufficient to require complete utilization. Thus the experiment had no bearing on the question of whether ammonia can be absorbed in excess against future need.

TABLE X. Total Cell Counts (millions per liter) in Enrichment Experiments. Figures marked with an Asterisk represent single Counts. Others are Averages of Experiments Performed in Duplicate or Triplicate. Columns are Labelled as in Table IX.

Exp.	I	L	D	NH_3	NO_3	NO_2
1	9.7*	13.0	9.4	11.3	10.4	9.9
2	2.5*	6.1	6.5	10.6	5.7	6.8*
4	1.2*	2.8*	2.5	2.9	2.5	2.7
11	–	0.7*	.3*	1.2*	0.7*	1.3*
13	2.7*	8.7*	3.5	21.6	14.5	–
16	1.4*	4.8	2.5	2.4	4.0	–

Table X summarizes the total cell counts that were made in connection with the enrichment experiments. They show little evidence, except in experiment 13, that nitrogen addition significantly affected the cell count. Nutrients were absorbed in excess of ordinary requirements, and the increase in chlorophyll suggested an improved physiological state. One would expect cell division to follow, but it was not observed within the time limit of the experiments, except in No. 13. It is probably significant that experiment 13 was begun at a time when the phytoplankton was already in an active state of growth, increasing toward the peak of a small summer flowering. *Skeletonema costatum* was almost entirely responsible for the observed cell increase, although it had been outnumbered by dinoflagellates at the beginning of the experiment. *S. costatum* is the most important diatom in the Sound; it was present in all of the experiments and was the dominant species in the first two. Its growth in experimental bottles generally was superior to that of other diatoms, particularly with addition of ammonia. However, its behavior varied so much from one experiment to another that generalizations about this species, or any other diatom, are speculatory.

The June flowering was dominated first by *Peridinium trochoideum* and then by *Prorocentrum triestinum.* Experiment 11 was begun during the early days of this flowering when diatoms were still dominant, although there were some 38,000 cells/l of *Peridinium trochoideum.* This species increased rapidly in three bottles containing 1–5 μg-at NO_2-N/l, reaching a maximum concentration of 416,000 cells/l in the bottle with 2 μg-at. In these three bottles there were also 27–38 thousand cells/l of *Gymnodinium variable*, although the quantity at the beginning of the experiment was so small that the species was not included in the routine counts. Nor was it found in more heavily enriched bottles. *P. trochoideum* also failed to produce significant growth with larger concentrations of nitrogen, and it seriously declined in the bottle enriched with nitrate; in subsequent experiments, all with 20 μg-at N/l added, this species approximately doubled in two ammonia enrichments in experiment 16 but declined in the other ten cases. There was no indication that any other dinoflagellate profited significantly by strong nitrogen fertilization.

The nitrite experiment does not have a direct bearing on the observed *Peridinium* flowering, because there was virtually no nitrite in the water. However, the flowering was preceded by an increase in ammonia (Fig. 2) of the same range as the effective NO_2-N concentrations. On the other hand, S. A. M. Conover (1956) noted that in the spring and early summer of 1952, when there were nitrate concentrations of 1–5 μg-at N/l, diatoms were dominant. These various observations are provocative although much of the meaning remains obscure. It is possible that they contain the key to the problem of competition between diatoms and dinoflagellates.

QUANTITATIVE ASPECTS OF THE NITROGEN CYCLE

The Internal Biological Cycle. The sum of all inorganic nitrogen fractions in the central part of the Sound decreased 10 μg-at/l during the 53-day period from December 27, 1954 to February 18, 1955, or 0.10 μg-at N/l^{-1} day^{-1}. This may be regarded as a minimum estimate of the rate of absorption by phytoplankton during the period of the diatom flowering. In addition, experimental evidence indicates that ammonia was excreted by the zooplankton. From the amount of zooplankton present at the time, it is estimated that this source of supply amounted to 0.11 μg-at NH_3-N/l in a day. Other possible sources were bacterial regeneration *in situ* and the upward transfer of regenerated materials from the bottom. However, the bacteria have not been studied, and vertical transfer could not be determined readily during the winter period of strong turbulence. Thus it is possible to say only that the daily utilization was more than 0.3 μg-at N/l.

After February 18 vernal warming set in. It was then possible to determine vertical exchange by analyzing the seasonal temperature progression and hence to obtain a more complete picture of nitrogen utilization by the application of standard physical oceanographic procedures.

At any fixed locus in the Sound, a nonconservative concentration may be altered by a combination of several processes: (a) a net biological rate of change which is the resultant of the opposing processes of plant growth and of the utilization of the products of growth by animals and bacteria, and (b) a rate of change resulting from the physical exchange of water. Riley (1956 b) presented a physical oceanographic analysis of the changes in oxygen and phosphate in the central part of the Sound, using a simplified equation

$$\frac{\delta N}{\delta t} = R + \frac{A}{\varrho} \cdot \frac{\delta^2 N}{\delta z^2}, \qquad (2)$$

in which $\delta N/\delta t$ is the rate of change of a nonconservative concentration N at any given depth z; R is its net biological rate of change; and A is the coefficient of vertical eddy diffusivity. This simplified version assumes that advection and horizontal diffusion can be ignored, and Riley suggested that this is allowable provided sufficient data are averaged to minimize the sampling errors.

In the present case eq. (2) again will be used for detailed treatment of nitrogen data from the central part of the Sound, but the effects of transport and horizontal diffusion will also be examined in a later section. For purposes of numerical calculation, the equation was rewritten in finite difference form so that it could be applied to a series of depths sampled at successive intervals of time. Coefficients of vertical eddy conductivity were calculated from the observed temperatures and were used as an approximation of A in eq. (2).

During the period from February 18 to June 23, 1955, there were eight sets of analyses at the surface, at mid-depth (5 or 10 m and averaging 7 m) and near bottom (averaging 20 m). These were combined into a single estimate of the average net rate of change at 7 m. The method of calculation was the same as that described by Riley (1956 b) and need not be repeated. Results are listed in the first two lines of Table XI. The rates of change of ammonia and of the combined nitrate and nitrite fractions were negative; that is, utilization by plants exceeded regeneration by consumers, and the results are so designated in this table.

The first two items in Table XI show only the amount of nitrogen brought to the 7 m level by vertical turbulence and consumed there. In addition, the phytoplankton utilized part of the small inorganic nitrogen stock that was present in the water on February 18, and the difference in concentration between

TABLE XI. MEAN DAILY RATES OF CHANGE OF NITROGEN BETWEEN FEBRUARY 18 AND JUNE 23, 1955 AT A MEAN DEPTH OF 7 M IN CENTRAL LONG ISLAND SOUND.

	μg-at N/l	Percent
Net utilization of NH_3	.064	17.3
Net utilization of NO_2, NO_3	.014	3.8
Nitrogen stock	.007	1.9
Excretion by zooplankton	.285	77.0
Total	.370	100.

the beginning and end of the period is given in the third line in terms of mean daily consumption. The total utilization by phytoplankton is equal to the sum of these three items plus regeneration *in situ* by bacteria and animals. Of these only zooplankton can be estimated. The figure shown is based on the average observed population, which was 1.13 ml/m3, or about .11 mg dry weight per liter, and on the average experimental regeneration rate given in Table VI.

Although the total in Table XI falls short of total utilization, the data serve to establish an order of magnitude and to show also the relative importance of different nitrogen sources. It was previously reported (Riley and Conover, 1956) that nitrate and nitrite were relatively insignificant sources of nitrogen except in autumn and winter. This is confirmed in the present study, and in addition it would appear that the system is mainly supported by a rapid and direct exchange of ammonia between phytoplankton and zooplankton.

Similar methods have been used to estimate nitrogen utilization at the other four stations, but the sampling errors were too large to inspire confidence in the results. The largest value, obtained at the Execution Rock station in the western end, indicated a productivity about twice that of the central basin. Otherwise there was no consistent trend from west to east.

Riley (1956 b) obtained an estimate of total phosphate utilization in the central part of the Sound by combining physical oceanographic calculations of net utilization with a few assumptions about other aspects of the biological system. This can be expanded into a treatment of the nitrogen cycle with the aid of conversion factors derived from the present study. There are enough possibilities of error both in the original analysis and in the assumptions so that a high degree of accuracy cannot be claimed for the results. However, two purposes will be served: (a) to estimate utilization and regeneration at all levels instead of at a single mid-depth stratum, and (b) to determine the order of magnitude of regeneration by bacteria and other members of the consumer population.

Estimates of total phosphate utilization by phytoplankton had been obtained as averages for the periods listed in the first column of Table XII. The average N : P ratio in the phytoplankton produced was 15.7 : 1 (Harris and Riley, 1956), which provides a suitable factor for converting the phosphate data to

TABLE XII. Balance Sheet of Nitrogen Utilization and Regeneration During the First Two Years of the Survey. All Figures are Listed as Daily Change in Nitrogen in μg-at N/cm^2, which Includes a cm^2 water Column 20 m long and the Mud Surface at the Bottom of the Column.

	Phytoplankton Utilization	Obs. Rate of change	Zooplankton Excretion	Residual Regeneration*	Total Regeneration
III 5–V 21, 1952	.42	.025	.34	.054	.425
V 21–VIII 19	.72	–.017	.59	.064	.703
VIII 19–XI 17	.60	.273	.68	.144	.873
XI 17, 1952–II 10, 1953..	.20	.036	.05	.136	.236
II 10–III 16.............	1.79	–.84	.20	.700	.95
III 16–V 18.............	.33	.004	.25	.034	.334
V 18–VIII 25	.68	.027	.25	.407	.707
VIII 25–XI 18	.31	.201	.32	.141	.511
XI 18, 1953–I 25, 1954...	.31	.122	.05	.332	.432
I 25–II 24	1.33	–.91	.20	.170	.420
Means					
1952–3	.610	–	.404	.156	.610
1953–4	.507	–	.218	.239	.507

* Allowance has been made for .05 μg–at N/cm^2 excreted by bottom organisms.

estimates of nitrogen utilization which are shown in the second column of Table XII. Next is shown the average daily change in the nitrate-nitrite concentrations in the water column; while this does not constitute the total inorganic fraction, it is of course the nitrate that is mainly concerned in the large autumn increase and the decrease during the flowering. The small errors due to lack of ammonia data have little significance for present purposes. Now this observed rate of change may be written

$$\frac{\delta N}{\delta t} = -U + R_1 + R_2 \cdots + R_n, \tag{3}$$

in which $-U$ is the rate of utilization of nitrogen N by phytoplankton, and the series of R's represents the rates of regeneration of the various animal and bacterial consumers. This statement is permissable when all biological processes within the vertical column are totaled, provided horizontal exchanges can be ignored. It is apparent then that total regeneration can be obtained by adding phytoplankton utilization and the rate of change of inorganic nitrogen. The result is shown in the last column of Table XII.

Regeneration by zooplankton was determined from average estimates of zooplankton respiratory rates (Riley, 1956 b) and from the average relation between oxygen consumption and ammonia excretion in Table VI. A generalized estimate of excretion by benthic infauna also may be obtained from the *Nephthys incisa* and *Yoldia limatula* experiments given in Table VI. Sanders (1956) reported that the infauna totaled about 9 g/m^2 or 0.9 mg/cm^2 dry weight, and hence it could be expected to produce about 0.05 μg-at NH_3-N per day. In the absence of information on seasonal variation, this figure was applied to all of the data, although there probably should be a seasonal correction.

The remainder of the regenerative processes, determined by difference, are listed as residual regeneration in Table XII. It is also inherent in the method that errors in any of the other estimates will be reflected in this column. Seven of the estimates fall within a fairly narrow and reasonable range of 0.03 to 0.17 μg-at N/cm^2. The three large values are open to suspicion, and likely possibilities of error should be mentioned. First, all physical oceanographic calculations of autumn and winter utilization by phytoplankton are much less accurate than spring and summer values because the vertical temperature gradients were small and variable. Two of the three excessively large values occurred during this period, and all values obtained at this time were a little larger than would be expected during a period when the activity of bacteria and animals is reduced by low temperature. Second, there is some evidence that the ratio of excretion to respiration in zooplankton may increase during periods of phytoplankton abundance. If this is correct, part of the residual regeneration during flowering periods might be allocated more properly to the zooplankton column.

There is no obvious reason for error in the one unusually high summer regeneration value. The zooplankton population was small during 1953 and was obviously incapable of utilizing as much food as did the population of 1954. Possibly in 1953 a larger proportion of the phytoplankton population sank to the bottom and was utilized there. The data also suggest a slight reduction in over-all productivity during the second year. This is part of the chain of events which on the one hand is a cause of lowered zooplankton production and on the other hand is a natural consequence of the reduced rate of turnover associated with regeneration from the bottom.

Problems of Transport and Horizontal Diffusion. Since the preceding analysis has dealt with the nitrogen cycle in limited areas of the Sound, ignoring the effects of transport and horizontal diffusion, the question arises as to whether this over-simplification has introduced serious errors. Solution of the problem awaits a full-scale investigation of the circulation of the Sound, which will be published later. However, some preliminary results can be reported at the present time.

Riley (1956 a) described the two-layer transport system that exists in the Sound, with quantitative estimates of summer transport, and preliminary analyses have been made of transport exchange in 1954 and 1955 utilizing the principles of salt continuity. Results were essentially in agreement with previous estimates based on measured currents, although there were increases of 50 to 100 % in certain seasons.

Although the analysis was preliminary and tentative and hardly warrants detailed description at the present time, it provided a yardstick for measuring the relative importance of the various physical parameters in determining the distribution and rates of flux of nitrogen. The results may be summarized as follows: (1) If the transport is no more than twice the measured summer values as described by Riley (1956a), its effect on nitrogen flux will not exceed 10–20 °/o of the vertical flux due to eddy diffusivity that was described in the preceding section. While this is not negligible, it probably is no more serious than random errors involved in the calculation of biological rates of change from coefficients of vertical eddy diffusivity. (2) The physical oceanographic analysis indicated that coefficients of horizontal eddy diffusivity are of the order of 10^6 to 7×10^6 cm²/sec. If this is correct, the effect of horizontal diffusion on nitrogen distribution is about 10 to 70 °/o of the transport effect. (3) Although the horizontal flux appears to be relatively unimportant in determining biological rates of change, it needs to be examined further in connection with the general problem of nitrogen balance in the Sound. This will be taken up in the next section.

Sources of Nitrogen Enrichment. During the late winter and spring period, freshwater drainage into the Sound averaged about 1000 m³/sec. This water contained, on the average, about 15 μg-at NO_3-N/l as indicated by data in the preceding paper by Riley (in this volume). If the fresh water were thoroughly mixed throughout the Sound, there would be a daily net gain of 0.04 μg-at NO_3-N/cm² of sea surface, or about 5 to 6 °/o of the total phytoplankton requirement.

However, 75 °/o of the total drainage enters the eastern end. Previous indications are that the accompanying enrichment is largely confined to the area east of Long. 72° 30′W, although there could be a delayed and indirect effect if the consumption of nitrate were followed by transfer of the nitrogen in particulate form into the central part by way of the bottom transport layer.

The total daily nitrate enrichment that was available in the surface layer at the eastern end averaged 0.18 μg-at/cm², or roughly one-quarter to one-half of the phytoplankton requirement. However, observations have revealed a significant amount of nitrate in the freshened surface layer leaving the Sound in times of flood, so that the generalized average for freshwater enrichment exceeds actual utilization.

In the main body of Sound waters west of Long. 72° 30′W, the average enrichment was only 0.009 μg-at N/cm² in a day. In one sense these figures are minimal since there may be significant amounts of other nitrogen compounds in fresh water, but in all other respects they are maximal because they represent the annual peak in both freshwater outflow and its nitrate concentration.

Transport estimates have indicated an inflow into the western end of the order of 1100 m³/sec (Riley, 1956a). A few analyses have been made at the point of inflow (Lat. 40° 48.2′N, Long. 73° 47.3′W), and routine data have been obtained at a position intermediate between the one just given and Execution Rock Station. Nitrogen values at these two stations almost invariably have been higher than at Execution Rock, and the maximum values frequently have been at the surface. This is indicative of a source of enrichment either from pollution in the New York Harbor area or from groundwater seepage. During the period from February to June 1955 the average surface water nitrate was 2.5 μg-at N/l as compared with 0.7 μg-at at Execution Rock. Assuming a transport of 1100 m3/sec, the total enrichment would be an order of magnitude lower than that supplied by all freshwater drainage. However, it could be a very important source of local enrichment in the constricted western portion of the Sound and might well be the major factor involved in the apparent richness of that area.

The exchange transport at the eastern end is potentially capable of either enriching or impoverishing the Sound, depending on the concentrations and horizontal gradients that are involved. The usual equation for an analysis of this kind of problem is

$$F = VN - \frac{A_x}{\varrho} \cdot \frac{\delta N}{\delta x}, \qquad (4)$$

where the flux F of nitrogen through one cm² of the cross-sectional area at the eastern end is expressed in terms of current speed V, the coefficient of horizontal eddy diffusion A_x, and the nitrogen concentrations N along the longitudinal axis x. However, in the present case, mass transport estimates have been obtained, so that the advective flux is more simply determined as the product of transport volume and nitrogen concentration. The flux due to eddy diffusivity will be determined according to the last term in equation (4).

Table XIII shows total nitrogen (combined soluble, particulate, and dissolved organic fractions) in the surface and bottom layers at the two routine stations in the eastern part of the Sound, averaged for the periods from October 15 to December 27, 1954 and from February 18 to June 23, 1955. The station at Bartlett Reef will be used for estimates of advective exchange.

TABLE XIII. Average total Nitrogen in μg-at N/l at Six-mile Reef and Bartlett Reef Stations.

	Six-mile	Bartlett
Autumn		
Surface layer	27.4	16.4
Bottom layer...........	43.0	18.3
Spring		
Surface layer	15.1	1.8
Bottom layer	16.8	14.2

According to Riley (1956a), the summer values for surface and bottom transport at the longitude in question are respectively 18,400 and 17,000 m^3/sec. Preliminary analysis indicates approximately a 50% increase in basic transport exchange and 1000 m^3/sec of freshwater drainage during the periods in question, so that the revised estimate is 27,600 and 25,500 m^3/sec in the surface and bottom layers respectively. Application of these figures to the station data in Table XIII gives the estimates of transport flux in the first two lines of Table XIV.

TABLE XIV. EXCHANGE OF NITROGEN IN *g*-at/sec AT THE EASTERN END OF THE SOUND. POSITIVE FIGURES INDICATE GAIN OF NITROGEN BY THE SOUND; NEGATIVE ONES, LOSS. THE FINAL LINE IS THE ESTIMATED MEAN DAILY ENRICHMENT OR IMPOVERISHMENT CALCULATED AS μg-at N/cm^2 OF SEA SURFACE IN THE SOUND AS A WHOLE.

	Autumn	Spring
Transport – surface layer ...	– 453	– 326
bottom layer ...	467	362
Diffusion – both layers	– 30	– 6
Net change	– 16	30
μg-at N/cm^2	– 0.043	.075

For the area between the Bartlett and Six-Mile Reef stations, an unpublished examination of the salinity balance has indicated a diffusion coefficient of about 2×10^6 g cm^{-1} sec^{-1}. As a sample calculation, and denoting that part of the flux which is due to eddy diffusion as F', the rate of transfer in the surface layer in autumn is given by

$$F' = \frac{-A_x}{\varrho} \frac{\delta N}{\delta x} = \frac{-2 \times 10^6}{1.02} \frac{(27.4 - 16.4) \times 10^{-3}}{3.3 \times 10^6} =$$

$$= -0.065 \ \mu\text{g-at } N \text{ cm}^{-2} \text{ sec}^{-1}.$$

Note that the axis has been directed westward so that the signs will conform with the notation in Table XIV. The gradient has also been multiplied by 10^{-3} to express concentrations as μg-at N/cm^3. The surface layer has an estimated cross-sectional area of $2.24 \times 10^5/m^2$ so that the total transfer is –15 g-at N/sec. In the bottom layer, with a cross-sectional area of 1.12×10^5 m^3, an additional loss of 15 g-at was obtained by a similar calculation. The same physical parameters were used to estimate the loss by diffusion in spring, but the results were relatively insignificant because of the decrease in the nitrogen gradient. In the remainder of Table XIV, the net change due to the combined processes of transport and diffusion has been determined and then converted to an estimate of average daily enrichment per unit area of surface in the entire Sound. This seems to be a reasonable way to express the results, because continuation of the transport system and gradients into the Sound insures a general rather than a local enrichment effect.

The results tend to confirm an earlier theory (Riley and Conover, 1956) that transport exchange enriches the Sound during the spring and summer but reverses the process during the autumn regeneration period. Enrichment by horizontal exchange seems to be approximately the same as the freshwater drainage effect. However, it would be unwise to regard the results as anything more than an order-of-magnitude estimate. They represent a relatively small difference between large numbers which are themselves subject to considerable sampling error.

Discussion. The total nitrogen stock in the central part of the Sound in late December 1954 was about 25 μg-at/l. Of this original stock, only about 15 °/o remained in the water column by midspring. The concentration of inorganic nitrogen in the water column averaged 0.87 μg-at N/l from March 25 to June 23, and this was little more than one day's needs for phytoplankton growth. Experiments showed that about half of the need was supplied by zooplankton excretion, about one-tenth by bottom fauna. Thus the ammonia-phytoplankton-animal relationship constituted the major activity of the nitrogen cycle by virtue of its rapid rate of turnover, despite the fact that it contained only 15 °/o of the total nitrogen in the system.

Part of the remaining requirement was satisfied by external enrichment. However, analyses in the preceding section indicated that the combined enrichment by horizontal exchange and freshwater drainage was seldom more than 20 °/o of the daily requirement and was often much less.

The role of the bacteria has not been examined directly, but it may be deduced from the foregoing discussion that they supplied some 20 to 40 °/o of the daily phytoplankton requirement. Since their substrate contained 85 °/o of the nitrogen stock, it would appear that their rate of turnover of nitrogen was an order of magnitude lower than that of animals. This is not entirely unexpected. Not only were they charged with the degradation of stable materials that the animals had failed to assimilate, but previous experiments indicate that their rate of decomposition of fresh plankton is slow.

Von Brand, *et al.* (1937) demonstrated that the bacterial liberation of ammonia from dead plankton proceeded rapidly at first and then more slowly. The process virtually stopped in 8 to 20 days, at which time some 20 to 35 °/o of the nitrogen originally present in the plankton remained undecomposed or in bacterial cells. The ammonia was then transformed to nitrite and the nitrite to nitrate, the whole process generally requiring two or three months.

Field data obtained during the present survey strongly suggest a similar sequence of events in nature. Fig. 2 showed that on two occasions there was an increase in ammonia some two to four weeks after a bloom. To regard this as the first stage of bacterial decomposition of a bloom seems more reasonable than any other hypothesis that can be proposed. The subsequent slow decomposition of refractory materials has not been described adequately either in experiments or in nature; however, existence of such a stage is hardly in doubt since much of the nitrogen stock remained out of circulation during the spring and summer.

The ultimate oxidation of ammonia to nitrite and nitrate was obvious only in autumn and winter. The fact that little nitrate was present at other times does not prove that it was not formed. However, the slowness of the oxidation as described in experiments by von Brand, *et al.* (1937), coupled with present evidence that phytoplankton readily utilized ammonia, indicates that most of the ammonia was used before it could be oxidized.

There remain some questions of a hypothetical nature that may be mentioned chiefly as problems for the future. If the zooplankton experiments have been interpreted correctly, these animals waste more food than they utilize. Although the unused materials are quickly converted to a form suitable for renewed plant growth, this in a sense only tends to multiply and perpetuate the waste. It would be interesting to know how the Sound compares in this respect with other regions. Harvey, *et al.* (1935) reported that English Channel zooplankton excreted semidigested food during the spring flowering, but they found no evidence of waste at other times. Riley (1956b) compared published data for the English Channel with data for Long Island Sound and concluded that the Sound was less efficient in animal production. The standing crop of phytoplankton and the net daily production were estimated to be two to four times those in the English Channel, whereas the zooplankton crop in the Sound was only a third larger.

This comparison implies that maximum efficiency in zooplankton production will be attained with a moderately low concentration of phytoplankton and that a reduction in plant production in the Sound might simply reduce waste without impairing zooplankton productivity. However, the facts do not altogether bear this out. Table XII showed that an apparent reduction of 20 °/₀ in total phytoplankton productivity during 1953 was accompanied by a 40 °/₀ reduction in the zooplankton crop. Riley (1956b) suggested that a qualitative difference in food might have been responsible rather than a decrease in total quantity. Diatoms were less abundant during 1953, and experiments by R. J. Conover (1956) had shown that diatoms were eaten more effectively than the nannoplankton which dominated the population that year. Conover's experiments also indicate that *Acartia clausi* and *A. tonsa*, the dominant copepods in the Sound, had unusually high respiratory rates as compared with some oceanic species, and hence they were fundamentally inefficient. If this is so, it is also possible that the role of zooplankton in the Long Island Sound nitrogen cycle is relatively more important, as compared with the role of bacteria, than in some other waters. This question needs further study, and so does the whole problem of zooplankton production efficiency.

The role of bacteria also needs to be examined more closely. Harvey (1955:68) and others have suggested that the quantity of bacteria in oceanic waters seems insufficient to carry out all of the functions that have been ascribed to them. One explanation, although not the only possible one, is that animals carry out a considerable proportion of these functions. Certain theoretical advantages of animal dominance of the regenerative processes seem great enough to suggest that adaptation may move toward the development of an association that will exploit these advantages to the fullest degree.

The important difference between the two types of regeneration is the time factor. The time required for a zooplankton organism to return excess nutrients to the water is not known precisely, but for practical purposes it is negligible compared with the lag of several weeks that is involved in bacterial decomposition. From the quantitative standpoint, rapid regeneration increases the rate of turnover of essential nutrients and promotes high productivity.

Qualitatively the differences may be equally significant, but the variety of possible results requires consideration of particular cases. During a spring diatom flowering the animal population tends to increase, although not rapidly enough to use all of the available food. If animal metabolism rapidly returns the nutrients to the water, the late stages of the flowering will be bolstered and will provide food at a time when the expanding animal population needs it most. This situation strongly damps any tendency toward oscillation of the plant and animal populations, so that both will tend to converge toward a steady state.

Next consider a hypothetical opposite extreme in which animals, although present, do not affect the nutrient supply significantly. A spring flowering in shallow water would be followed by poverty until bacterial decomposition of the flowering liberated its nutrient content, and then another flowering would be possible. Even in Long Island Sound, where bacteria are believed to be less important than zooplankton, these nutrient surges were clearly apparent in early March and late May (Fig. 2); the March surge in particular over-expanded the zooplankton population, which was then decimated in the poverty that followed.

From the standpoint of population dynamics, the nutrient-phytoplankton relationship is analogous to a prey-predator reaction in which the phytoplankton has the role of the predator. Volterra's (1928) classical treatment of prey-predator oscillations has been reworked along various lines, and the theory of Wangersky and Cunningham (1957) is pertinent to the present discussion. They have introduced the concept of a time lag in the reaction of an organism to its environment and have demonstrated that differences in the length of the lag control the degree of damping of the oscillations. The present case is an unusual one, in that the time lag in the growth of prey (a nutrient) tends to be longer than that of the predators when nutrient production is controlled by bacteria. However, it must be intuitively obvious as well as mathematically demonstrable that a reduction in the time lag of the prey will reduce the damping effect on the oscillations of the predator population.

A somewhat different series of events is expected in oceanic waters, but the tenor of the conclusions is the same. When zooplankton graze in the surface layer and return part of the intake to the same waters, one can expect a higher rate of turnover than in the case of cells dying and decomposing as they sink into deep water. However, drastic population oscillations are not so likely in oceanic waters because the return of nutrients to the surface layer by vertical diffusion is relatively slow and uniform.

It is common in temperate and subtropical waters during the summer to find the maximum phytoplankton concentration in the thermocline region, well below the level of optimal light intensity. Zooplankton feeding in this layer during the day will excrete part of the ingested nutrients in the impoverished surface zone at night, producing a net upward transfer of nutrients – a biological convection – which may exceed physical transfer by diffusion. This is an example (a few more also could be cited) of a situation in which vertical migration may be postulated to have long-term advantages by promoting the productivity or stability of the prey population; from a short-term point of view, however, it would seem more desirable for the animals to stay with a phytoplankton swarm until it is consumed. Many investigators have pondered the selective advantages of the migratory habit and have failed to arrive at any solution, at least with respect to near-surface populations. Thus the subtle, long-term advantages deserve mention, speculative though they be.

Optimum productivity and stability of the whole marine association would seem to require an ideal situation in which the quantity of animals is sufficient to perform all functions of nutrient regeneration of which animals are capable and in which a modest population of bacteria is available to carry on the remainder of the decomposition process. Toward this end there are certain natural checks and balances. The tendency of bacteria to grow on the surface of organisms and detritus insures both a heavy consumption rate by predators and the maintenance of a seed population on the bodies of predators and surviving prey. The limited surface area available (ZoBell and Anderson, 1936), and probably antibiotics and bacteriophage (Wood, 1953) as well, combine to keep the bacteria well below the potential population density that can be achieved in experiments which are designed to permit them to utilize all of the available supply of organic matter in sea water. These natural checks no doubt reduce the rate of oxidation of dissolved organic matter, but they also help to maintain a supply of particulate food for animals.

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Евгений Гаррис

Азотный цикл в проливе Лонг Исланд Соунд
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С Октября 1954 года до Июня 1955 года данные по концентрации азотных и азотистых солей, аммиака, азота частичнаго вещества и раствореннаго азота органическаго происхождения боли получены на пяти станциях разбросанных по всей длине пролива Лонг Исланд Соунд. Сезонные циклы были Качественно тождественны во всех частях пролива за исключением незначительной разницы в сроке расцвета. Однако, значительный горизонтальный градиент с максимальной концентрацией был найден во всех пробах взятых в западном конце пролива.

Зимою максимум неорганическаго азота, преимущественно в форме солей азотной кислоты, вполне отсутствовал в воде во время поздняго зимняго расцвета. Его отсутствие сопровождалось увеличением азота частичнаго вещества достигавшаго максимума концентрации после периода расцвета. Однако большое количество азота частичнаго вещества в воде было потеряно благодаря осаждению на дно так что в средине весны сумма всех фракций составляла только 15 % суммы зимних фракций.

Концентрация неорганическаго азота поздней весной и ранним летом редко превосходила 2 микрограмма на N/l главным образом в форме аммиака. Опыты над планктоннымн населениями показали что аммиак легко потребляется фитопланктоном и быстро замещается выделительными процессами зоопланктона: Хотя в общем азотный цикл сложен, превращая большинство азота в стойкие соединения, ясно что обычные процессы его использования растениями и последующей регенерации бактериями и зоопланктоном идут с тем же темпом как в фосфатном цикле и представляют значительный процент общаго азотнаго оборота.

В средней части пролива суточная потребность в азоте для фитопланктона составляет 0.5–0.6 микрограммов иа N/см^2 поверхности воды. Зто только немного меньше количества находящевося в воде в любое время сезона активнаго роста, что подтверждает необходимость в быстром обмене для поддержания продуктивности. Принято что около половины необходимаго азота снабжается выделением зоопланктона, а одна десятая придонными животными. 2/5 могут быть приписаны в воде и на дне бактериям и внешним природным источникам.

Приток азота в пресной воде во время зимы и весны составляет около 0.04 микрограммов на и/см^2 в сутки для всего пролива. Однако приток 75 $^0/_0$ в пресной воде находится на восточном конце пролива, тогда как в других местах он равняется приблизительно 0.01 $^0/_0$ на N/см^2. На западном конце приток азота из гавани Нюиорка значителен в местном отношении, но только $^1/_{10}$ его имеет своим источником речную воду. У восточнаго конца пролива отток обедненной поверхностной воды и ея возмещение притоком донной воды с более высоким процентом азота дает суточное обогащение оцененное приблизительно в 0.06 микрограммов на N/см^2 всего пролива во время весны. Осенью, когла регенерация превосходит потребление, значительное количество азота исчезает в проливе благодаря горизонтальной диффузии.

Transparency of Long Island Sound Waters

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ABSTRACT

A total of 888 Secchi disc readings in Long Island Sound were converted to estimated extinction coefficients by application of the Atkins-Poole formula and were analyzed in relation to various factors which affect transparency. An equation has been developed which adequately expresses autumn and winter extinction coefficients throughout the Sound in terms of chlorophyll concentration of the phytoplankton, wind speed, vertical stability of the water column and total depth of water. In late spring and summer there was additional extinction which was probably due to organic detritus; this was indirectly expressed as a function of the oxygen deficit in subsurface waters on the grounds that maintenance of a deficit in the presence of strong vertical mixing is indicative of availability of such materials. Another indirect relation was added to the equation by correlating silt effects during floods with reduction in surface salinity. Only about half of the silt correc-

tions had a satisfactory degree of accuracy; also four other small groups of data showed serious discrepancies between observed and computed extinction coefficients. These were mainly from morphometrically atypical locations where there was reason to expect an unusual abundance of suspensoids or dissolved organic material. Discordant results constituted 6 °/₀ of the total number of observations.

INTRODUCTION

Long Island Sound is a moderately turbid body of water in which most of the Secchi disc readings of transparency fall within the general range of 1–5 m. On rare occasions values of as little as 0.2 m have been obtained during heavy plankton blooms or when the rivers were in flood. The maximum value thus far recorded is slightly more than 9 m. Usually the largest readings are found in the eastern end of the Sound, which is relatively deep and is subject to rapid interchange with open coastal waters.

A preliminary analysis of 460 transparency observations in the central basin of Long Island Sound (Riley, 1956) indicated that phytoplankton is responsible for about one-third of the total light extinction. The remainder is due to a conglomeration of other factors: the water itself, dissolved and particulate organic matter, and silt and bottom sediment in suspension. The latter appeared to be particularly important since there were significant statistical relations between transparency and such variables as depth, stability, wind, and tidal speed, all of which might be expected to influence the rate of suspension of bottom materials.

The elements of the quantitative treatment may be expressed in three equations. First, the Secchi disc readings were converted to extinction coefficients according to the Poole and Atkins (1929) formula

$$K = \frac{1 \cdot 7}{D}, \tag{1}$$

where K is the extinction coefficient per meter, and D is the Secchi disc reading in meters. The effect of phytoplankton was postulated to be

$$f(C) = .0088\,C + .054\,C^{2/3}, \tag{2}$$

in which $f(C)$ is that part of the total extinction coefficient K which is due to phytoplankton and in which C is μg of chlorophyll per liter. The equation, developed empirically by comparing plant pigment concentrations with transparency in both oceanic and neritic waters, was found to be a reasonably accurate expression (with certain possible exceptions to be noted below) throughout variations in chlorophyll concentration of four orders of magnitude. This accuracy seemed to justify applying the equation to the problem even though the fundamental meaning was obscure.

The calculated effect of phytoplankton as estimated from eq. (2) was subtracted from the extinction coefficients as determined from eq. (1), and the residuals so obtained were used to evaluate effects of other factors. The result was

$$K = f(C) - .01\,d + .018\,\frac{W}{.3 + \Delta\sigma_t} + .013\,v + .0063\,f(\mathrm{O_2}) + .05\,, \qquad (3)$$

where d is the depth of water in meters; W is the mean wind speed in miles per hour during the week preceding the observation; $\Delta\sigma_t$ is the mean increase in density from surface to bottom at the beginning and end of the week; v is the average tidal current in cm/sec; and $f(\mathrm{O_2})$ is defined as the percent undersaturation of the bottom water or the percent difference between surface and bottom when the former is undersaturated. Reasons for most of these terms are obvious, but the last one requires some explanation. There was an increase in residual extinction coefficients in summer which was significantly correlated with the oxygen deficit and which was thought to be basically due to the presence of considerable quantities of decomposed organic detritus that accumulated in the summer.

Subsequent to the preliminary publication, the survey has been broadened to general coverage of the Sound. The total number of observations has been doubled, and a greater range of conditions has been investigated, particularly with respect to total depth of water, current velocity, bottom types, and silt effects associated with freshwater drainage.

With some hesitation the problem has been reopened. It seemed likely that the increased quantity and variety of the combined data would improve the empirical analysis substantially. On the other hand, a quantitative analysis would be more worthwhile if it could be constructed within a framework of sound theory. The complex processes of suspending sediment and maintaining it in suspension are not likely to be thoroughly understood for some time. Nor is it likely that the correct mathematical expressions for these processes will be derived by empirical prospecting. But in spite of these objections, it is believed that the results are helpful in understanding the transparency problem and may be of some use to anyone who chooses to undertake a more definitive study.

RELATIONSHIP OF TRANSPARENCY WITH STABILITY AND DEPTH OF WATER IN THE CENTRAL PART OF LONG ISLAND SOUND

The first step in the analysis of physical processes was to convert Secchi disc readings to estimated extinction coefficients according to eq. (1) and to subtract the probable effect of phytoplankton as indicated by eq. (2). The residual extinction coefficients were then grouped for further analysis. The first major group to be dealt with comprises 415 residual coefficients in the central part of the Sound between Long. 72°45′ and 73°05′W which were taken during periods when the oxygen deficit in the water column was less than 10 $^{0}/_{0}$ of the saturation value. Observations associated with oxygen of more than 10 $^{0}/_{0}$ are reserved for later examination of the summer increase in extinction coefficients that was postulated in the INTRODUCTION. The first group consists mainly of autumn, winter, and early spring data in which the residual coefficients are believed to be primarily associated with mixing processes. It was subdivided according to depth and stability, and Table I shows the average residual coefficients in each group.

The stability E is approximated by

$$E = 10^{-3}\frac{\Delta\sigma t}{\Delta z}, \qquad (4)$$

where $\Delta\sigma_t$ is the increase in density between surface and bottom and Δz is the depth in meters.

Table I shows that increasing stability has little or no effect on transparency at the shallow stations sampled, and conversely, increasing depth has little effect in water of indifferent stability. But the combination of increasing depth and stability produced a significant reduction. The results may be regarded as a first approximation of the effect upon transparency of the sediment that can be carried in suspension under the normal regime of winds and tidal currents in this area, as modified by variations in depth and stability. However, further examination of the data showed considerable variations in wind and current from one group of data to the next, and some of the variations tended to be systematic. For example, strong winds tended to be associated with slight stability. Hence it was necessary to analyze the effects of wind and tide and make any corrections for their variations that might be required.

TABLE I. MEAN RESIDUAL EXTINCTION COEFFICIENTS (corrected for Extinction by phytoplankton) IN RELATION TO DEPTH AND STABILITY. THE DESIGNATION U,I MEANS SLIGHTLY UNSTABLE OR INDIFERENT STABILITY.

Stability	Depth Ranges in Meters					
	3–5	6–10	11–15	16–20	21–25	26–35
U,I	.56	.47	.58	.58	.51	.50
0–500 × 10^{-8}	.51	.54	.65	.49	.41	.41
500– 1,000	.51	.55	.54	.45	.42	.43
1,000– 2,000	.56	.65	.47	.38	.26	.31
2,000– 5,000	–	.57	.55	.33	.35	.28
5,000–10,000	.55	.37	.41	.28	.26	.23
> 10,000	.54	.30	–	–	.23	–

EFFECT OF WIND AND TIDAL CURRENTS

In the preliminary study of the problem (Riley, 1956) a method was described for estimating the average speed of the tidal current from the predicted range in the height of the tide. The same practice will be continued here, together with the use of data averaged over a period of one week prior to the transparency observation. The total range of mean weekly tidal speeds in the present analysis is 13 to 26 cm/sec.

The wind data are daily averages in miles per hour obtained by the New Haven office of the U.S. Weather Bureau about half a mile inland from the northern shoreline of the Sound; thus they are at best rough estimates of the effective wind speed over the water.

The stress of the wind is commonly stated to be proportional to the cube of the wind speed at low velocities and to the square of the speed with moderate to high winds (Sverdrup, *et al.*, 1942:490). It is proposed here to use the square of the wind speed throughout because the quality of the data does not warrant elaborate treatment and because it is mainly the strong winds that are significant for present purposes. Thus the daily Weather Bureau averages were squared, and the squares were averaged over periods of one week prior to the transparency observation.

The wind and tidal data were then compared statistically with residual extinction coefficients, again grouping these according to depth and stability. The quantity of data was not sufficient for the extensive grouping of the previous section, but two depth ranges were examined, namely 3 to 15 and 16 to 35 m, with four stability ranges within each of these two depth groups. Table II shows the partial correlations that resulted from the analysis; *i.e.*, the simple correlations have been corrected for any interrelation existing between wind stress and tidal speed.

More than half of the correlations with wind are statistically significant. Variations in tidal currents are slightly significant only in deep and relatively stable water, although the previous investigation of this problem indicated

TABLE II. CORRELATIONS OF RESIDUAL EXTINCTION COEFFICIENTS WITH TIDAL SPEED V AND THE SQUARE OF THE WIND SPEED W^2. TWO ASTERISKS INDICATE THAT THE CORRELATION IS SIGNIFICANT TO THE 1% LEVEL OF PROBABLITY OR LESS; ONE ASTERISK, THE 5% LEVEL.

	3–15 m		16–35 m	
10^8E	v	W^2	v	W^2
0–1,000	.035	.088	–.147	.451**
1,000–2,000	.102	.214	.048	.255
2,000–5,000	–.141	.550**	.172	.593**
5,000 +	.034	.443**	.463*	'597**

that the over-all correlation with tidal speed is significant. Present results do not warrant inclusion of this factor, but the problem will be reconsidered later, when the summer observations are brought into the analysis.

By the usual statistical methods, correlations and standard deviations were used to derive coefficients of wind stress which are shown in the first part of Table III. The last part of this table shows two other sets of data that were introduced to extend the scope of the analysis. However, in both of these the quantity of data was minimal for application of correlation techniques, and the results have a lower order of validity than others. Also, the last set of data is questionable for other reasons. In order to examine as great a depth of water as possible, observations from the eastern end of the Sound were utilized. However, the latter is an area with a decidedly different regime of currents and sediments, which introduces another possible source of error in the results.

TABLE III. WIND STRESS COEFFICIENTS. IN EACH SET OF DATA, GROUPED ACCORDING TO DEPTH AND STABILITY, THE PRODUCT OF THE STRESS COEFFICIENT s AND THE SQUARE OF THE OBSERVED WIND SPEED REPRESENTS THE STATISTICALLY COMPUTED EFFECT OF WIND ON THE EXTINCTION COEFFICIENT. DEPTH AND STABILITY RANGES ARE LISTED, TOGETHER WITH THE MEAN DEPTH AND STABILITY WITHIN EACH GROUP.

Depth Range (m)	Mean Depth (m)	Stability Range; Mean Stability; Coefficients (s)				
		Range 10^8E	0–1,000	1,000–2,000	2,000–5,000	5,000 +
3–15	8	Mean 10^8E	230	1,500	3,400	12,400
		s	.0006	.0019	.0065	.0031
16–35	22	Mean 10^8E	410	1,580	3,280	7,360
		s	.0024	.0013	.0038	.0017
3–5	3.6	Range 10^8E	U,I	0–5,000	5,000 +	–
		Mean 10^8E	0	2,360	17,100	–
		s	.0015	.0037	.0040	–
42–100	55	Range 10^8E	0–1,000	1,000–2,000	2,000–5,000	–
		Mean 10^8E	810	1,610	3,190	–
		s	–.0015	.0012	.0004	–

Three generalizations may be derived from Table III: (a) Low stability is accompanied by low positive values for the wind stress coefficient, except for one anomalous negative value at the eastern end of the Sound. (b) In stable water the correlations tend to decrease with increasing depth. (c) In the two sets of data that have the highest degree of statistical validity, maximum values for the coefficients are found in waters of intermediate stability.

The results that have been obtained are qualitatively reasonable. With indifferent stability, extinction coefficients are relatively large, as shown in

Table I. Tidal currents and light winds are sufficient to maintain abundant sediment in suspension, so that an increase in wind stress has little further effect. With moderate stability, the rate of suspension of sediment is repressed under normal circumstances, but the stress of strong wind is effective, so that the value for the wind stress coefficient increases. With a further increase in stability, even strong winds are ineffective, so that the coefficient decreases again, and it is reasonable for this effect to be most pronounced in deep water.

It is desirable for use in later analyses to express the observed relationship in mathematical form, even though the equation would be likely to have no more than empirical significance. The general shape of the curve suggested that the points might be fitted by a modified version of the logistic of Pearl and Reed, such as

$$s = \frac{k_1 - k_2(1 - e^{\gamma E})}{1 + e^{\alpha - \beta E}}, \qquad (5)$$

where s is the wind stress coefficient, α, β, and γ are constants for a particular depth, k_1 is the upper asymptote of the sigmoid logistic curve, and $k_1 - k_2$ is a secondary asymtote at a lower level that is approached as the stability E increases without limit.

The equation proved to be a reasonably good fit for the three sets of wind stress coefficients that had been calculated for the central part of the Sound. Moreover, the constants used to compute the upper three curves in Fig. 1 fitted into a consistent scheme in which: $k_1 = .018$; $k_2 = .0125 + \log z/300$;

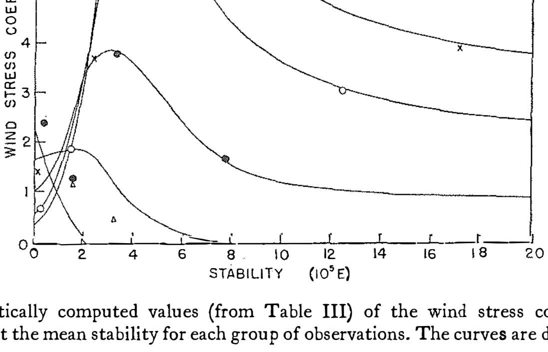

Figure 1. Statistically computed values (from Table III) of the wind stress coefficient s plotted against the mean stability for each group of observations. The curves are derived from eq. (5).

$\alpha = 4.9 - 1.5 \log z$; $\beta = (1.72 - .41 \log z)\, 10^5$; $\gamma = (.165 + .0115\, z)\, 10^5$; here z is the mean depth of the observations as given in Table III. While the physical derivation of the wind stress effect remains obscure, it would be rather remarkable for this consistency to be obtained if eq. (5) did not possess some measure of physical validity. Of course the constants cannot be expected to have general application even if the form of the equation is reasonably correct, because the magnitude of the wind stress effect will depend in part upon the character of the bottom sediments that are available for suspension. Thus it is not surprising that the data from the eastern end of the Sound, where the bottom is harder than elsewhere, do not fit closely with the scheme that has been outlined. The bottom part of Fig. 1 shows curves that have been calculated for depths of 50 and 100 m. Generality of application would require the points to approximate the 50 m curve. This is not so, although the existence of one patently erroneous value in Table III is sufficient warning that the statistical estimates are not very reliable.

GENERAL STATEMENT OF PHYSICAL PARAMETERS

Table I indicated that the residual extinction coefficient is a function of depth and stability, and it is possible that this function might be expressed in precise terms if the regime of mixing processes is constant or if adequate corrections can be made for variations in the rate of mixing. From the preceding section it would appear that the effect of variations in tidal speed is relatively insignificant in the present analysis and that the wind variations can be expressed adequately by eq. (5). Therefore, it is proposed for purposes of further study that

$$K' = s\,(W^2 - 60) + f\,(z, E); \tag{6}$$

here K' is the residual extinction coefficient; s is the wind stress coefficient from eq. (5); W^2 is the mean squared wind speed during the week preceding the observation, from which is subtracted the average squared wind speed for the observations as a whole, so that the wind effect is treated as a deviation from the mean condition; and $f(z,E)$ is a function of depth and stability which is now to be evaluated.

For each of the groups of data in Table I, the appropriate correction was made for wind effect. The revised values need not be listed in tabular form since the general features of Table I were not seriously altered. It was apparent there that the combined effect of increasing stability and increasing depth was much greater than either one by itself. Preliminary plotting and inspection indicated that the greatest likelihood for success in curve fitting lay in an exponential function involving the product of z and E. By a process that included correlations of the logarithms of the variables and trial and error for appropriate choices of constants, the equation

$$f(z,E) = .200 + .375\, e^{-x} \qquad (7)$$

was evolved, in which

$$x = \frac{z^{9/5}(100 + E \times 10^5)^{2/3}}{39{,}200}. \qquad (8)$$

Fig. 2 shows that eq. (7) is a reasonable fit for the upper and lower depth ranges; at intermediate depths there was considerable scatter. In defense of these results it is pointed out that the intermediate ranges represent a relatively narrow band of water near the coast which is subject to onshore and offshore movement with transient winds. Its variable past history is potentially a cause of random scatter. Observations in water of greater depth than 15 m represent a larger and more stable water mass; the shallow 3–5 m range was at a station in the protected waters of New Haven Harbor.

Summarizing the work thus far, eqs. (2), (6), and (7) may be combined into a generalized statement of the extinction coefficient, namely

$$K = .0088\,C + .54\,C^{2/3} + s(W^2 - 60) + .375\,e^{-x} + .200, \qquad (9)$$

where s and x are functions of depth and stability defined by eqs. (5) and (8). Eq. (9) is statistically a good fit for 415 extinction coefficients in the central part of the Sound, taken mainly in autumn, winter, and early spring.

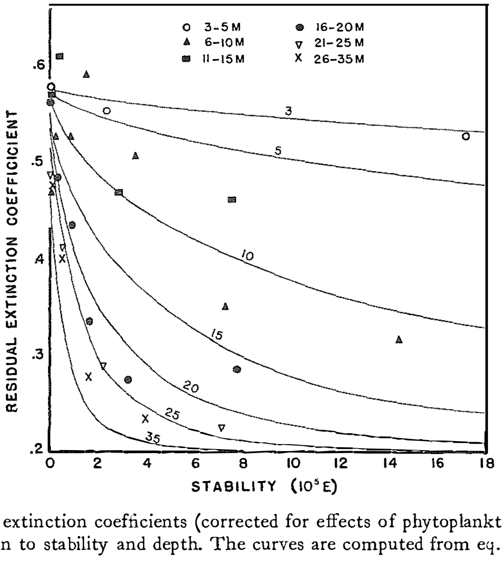

Figure 2. Residual extinction coefficients (corrected for effects of phytoplankton and wind stirring) in relation to stability and depth. The curves are computed from eq. (7).

OTHER DATA IN THE CENTRAL PART OF THE SOUND

Next to be considered are 135 observations taken primarily in summer and late spring, in which there was an oxygen deficit in the water column amounting to 10 °/₀ or more of the surface saturation value. As before, the extinction coefficients were calculated from the Secchi disc readings according to eq. (1), and from these values were subtracted the estimated effect of phytoplankton and mixing processes according to eq. (9). The difference between observed and calculated coefficients averaged .085, or 14 °/₀ of the total extinction. The standard deviation of the difference was ± .143. Thus the existence of a systematic difference between winter and summer observations tends to be confirmed, although it is quantitatively less important than the random errors. The problem then is to determine whether there are phenomena in summer which will account for some or all of the systematic difference and the individual variations around it.

First, it has been noted (Harris and Riley, 1956) that there is a seasonal variation in the relation of chlorophyll to phytoplankton dry weight, so that it seemed somewhat questionable to use a single chlorophyll coefficient as a year-round estimate of extinction by phytoplankton. If the coefficient needs to be revised in summer, this should be revealed by correlating chlorophyll with residual extinction coefficients during this period of the year when all chlorophyll percentages are low. However, the result was an insignificant value of –.068.

Next there is the question of the effect of organic detritus upon extinction coefficients. From qualitative examination it is known that the amount of detritus is large in summer, but it is difficult to obtain suitable quantitative measurements for direct comparison. The oxygen deficit has been used (see Introduction) as an indirect index on the grounds that the maintenance of a deficit in the presence of moderately strong tidal mixing is possible only when there is an abundant supply of detritus in the water. Although the use of this index is not ideal, it is justified by the existence of a small but significant ($P < .01$) correlation of .278 with the residual coefficients. The equation is

$$f(O_2) = .004\, \Delta\, O_2 - .013\,, \qquad (10)$$

where $f(O_2)$ is the postulated indirect effect of oxygen on the extinction coefficient and $\Delta\, O_2$ is the percentage reduction in oxygen as previously defined in the Introduction. The relationship obtained here is only slightly different from results of the previous analysis which were summarized in eq. (3).

There was some slight indication in the winter observations of a relation between tidal speed and extinction coefficients under conditions of high stability. Since the water column tends to be more stable in summer, the problem needs to be reopened.

TABLE IV. AVERAGE RESIDUAL EXTINCTION COEFFICIENTS GROUPED ACCORDING TO MEAN TIDAL SPEED AND STABILITY.

Tidal Speed (cm/sec)	Stability (10^8E) 0–5,000	5,000–10,000	10,000 +
< 18	–.09	.00	–.04
18–20	.00	.03	.04
> 20	.04	–.01	.08

Table IV suggests that the residual coefficients increase with increasing tidal speed, and this effect is most pronounced when the water is very stable. The effect is not sufficiently marked to warrant much attention, but it is statistically significant and may be expressed by the regression equation

$$f(v, E) = .015\,(v - 19) + 480\,E - .024, \tag{11}$$

in which the effect of variations in mean tidal speed v is given in terms of deviations from the mean value of 19 cm/sec in the central part of the Sound.

By combining eqs. (9), (10), and (11), the systematic difference between winter and summer observations is eliminated. Otherwise the accuracy of the analysis is not much improved. The correlations, although significant, have relatively low numerical values, and the corrections introduced by eqs. (10) and (11) reduce the standard deviation of the residual extinction coefficient only about 10 %. Eq. (10) has a slightly higher order of validity than (11), and it will be used in further analyses. However, it is admittedly little better than merely increasing the constant in eq. (9) to .285 for summer use.

Some of the variation that remains is probably systematic. Ordinarily three to five observations were taken during each day at sea. Examining individual days, it is found that about half of the time all of the residuals for a single day were either positive or negative. It is unlikely that this type of distribution would be obtained by chance. Probably there were particular days when factors that have not been taken into account tended to make all of the waters a little more or less transparent.

WESTERN LONG ISLAND SOUND

A total of 167 transparency observations have been obtained in the area west of the central basin (west of Long. 73° 05′W). As in the analysis of the central part of the Sound, these were divided into two groups on the basis of the presence or absence of a significant oxygen deficit. Eq. (9) was applied to the latter and a combination of (9) and (10) to the former. The results are shown in Table V.

Calculated values are slightly too large in winter and too small in summer. The only serious discrepancies appear in the examination of individual observa-

TABLE V. COMPARISON OF OBSERVED AND CALCULATED EXTINCTION COEFFICIENTS IN THE WESTERN PART OF LONG ISLAND SOUND.

	Number of Observations	Mean Extinction Coefficients	
		Calculated	Observed
Autumn-Winter...	103	.724	.675
Spring-Summer...	64	.715	.788
All data	167	.721	.718

tions. Ten out of twelve summer observations west of Long. 73° 35′W were higher than the calculated values, the average difference being .19. This is a small area that is subject to admixture of discolored water from the New York Harbor region. The discoloration appears to be mainly dissolved material rather than detritus, although the subject has not been examined carefully.

One other set of discordant results was obtained during a single cruise in May 1955, when all extinction coefficients exceeded the calculated values by amounts ranging from .19 to .41. The surface waters had an abundant population consisting mainly of diatoms, the most important species being *Skeletonema costatum* and *Nitzschia seriata*. Possibly the postulated chlorophyll function was inadequate on this particular occasion. However, it seems more likely that some other factor temporarily increased the extinction coefficients, because both of the species mentioned have been common constituents of other flowerings which were adequately accounted for by the chlorophyll equation.

These two types of discrepancies together accounted for 80 °/₀ of the difference between the calculated and observed values for spring and summer extinction coefficients.

EASTERN LONG ISLAND SOUND

The eastern part of the Sound is oceanographically diverse, so that the data must be examined piecemeal. The deep water in the vicinity of the passes is relatively clear except at times of freshet. The presence of silt of terrestrial origin is correlated with a reduction in surface salinity, and inspection of the data indicated that it was advisable to set aside, for later examination of the silt problem, all observations in which the increase in salinity from surface to bottom was more than 2 °/₀₀.

Aside from these there are 93 observations between Long. 72° 00′ and 72° 30′W and 45 between 72° 30′ and 72° 45′W to be considered here. The area was divided in this way because, from the morphometric standpoint, the central basin may be regarded as extending eastward to about Long. 72° 30′W, while beyond this point the Sound narrows and deepens, with rapidly increasing tidal currents and a hard bottom.

As in the preceding section, eqs. (9) and (10) were used to calculate extinction coefficients, and these are compared with observed values in Table VI. Good agreement was obtained in deep waters (21 to 70 m) in the eastern quarter of the Sound. This is somewhat unexpected in that the equations were derived for a very different type of physical environment. Fair agreement was obtained at five stations in water of less than 20 m. Thirteen observations (labeled Long Sand Shoal) were markedly higher than the calculated values; these were taken at a single location, 41° 14′N, 72° 28′W, near the western tip of a shoal which arches west and slightly south from the mouth of the Connecticut River. River water enters the area on the ebb tide, and although the water is not obviously muddy except in times of flood, it seems likely that the high turbidity at this station is due to silt which is kept in suspension by strong, scouring tidal currents until it is finally dissipated offshore.

TABLE VI. COMPARISON OF OBSERVED AND CALCULATED EXTINCTION COEFFICIENTS IN THE EASTERN PART OF THE SOUND. WINTER AND SUMMER OBSERVATIONS ARE COMBINED IN EACH AVERAGE. FOR FURTHER EXPLANATION SEE TEXT.

	Number of Observations	Mean Extinction Coefficients	
		Observed	Calculated
72°00′ to 72°30′W			
Deep Stations	75	.390	.387
Shallow Stations			
Long Sand Shoal	13	.68	.48
Others	5	.39	.46
72°30′ to 72°45′W			
Falkner Island Station	18	.82	.54
Others	27	.49	.52

Table VI shows another aberrant station located north of Falkner Island at 41° 12′N, 72°40′ W. This again is in a semienclosed basin between a shoal and the Connecticut shore. River influences in this case are negligible. Tidal currents are relatively weak, and there is a soft mud bottom. Eight of the observations at this station showed marked discrepancies ranging from .34 to .91 and averaging .61. In the other ten the difference between observed and calculated coefficients was –.14 to .20, with a mean of .02.

The situation as a whole suggests that about half of the time there are special circumstances which have not been treated in the equations and which produce high turbidity by stirring up bottom sediments. The data have been searched without success for evidence of a consistent relation with the direction and speed of the wind or with the phase of the tide at the time of the observation. It is possible that local eddies or the passage of tidal currents across the shoals produce a patchy distribution of mud in suspension, so that it is largely a matter of chance as to the type of water that is sampled at any one time.

The other stations in this longitude range were in open waters of the Sound in depths of 16 to 30 m. There was reasonable agreement between observed and calculated extinction coefficients.

REDUCTION IN TRANSPARENCY BY SUSPENDED SILT

As pointed out earlier, there were a few obvious cases of reduction in transparency by suspended silt during floods. These were accompanied by reduction of surface salinity, and it was possible to separate them for further analysis by arbitrarily choosing all cases in which the increase in salinity between surface and bottom exceeded 2 °/₀₀. Of course it is not expected that there will be a precise relationship between turbidity and surface freshening, because the silt load probably varies from time to time; also dissipation of silt from the surface layer by a combination of turbulence and sinking is likely to proceed faster than dissipation of fresh water by turbulence alone.

There were 33 observations available for analysis, mostly in the eastern half of the Sound and most of them associated with the outflow from the Connecticut River. They ranged from very muddy water with an extinction coefficient of 8.5 (Secchi disc 0.2 m) to relatively clear waters in which it was questionable as to whether the silt effect was significant.

The first procedure in the analysis was to estimate the effects of other parameters by means of eqs. (9) and (10). The values so obtained were subtracted from observed extinction coefficients, and the remainders were compared statistically with the salinity gradients. In order to have a negligible effect with small gradients of less than 2 °/₀₀ and a very pronounced effect with larger gradients, it seemed likely that a power function of the salinity gradient would be required for good representation. Accordingly, a least squares fit was applied to the logarithms of the variables with the result that

$$f(S) = .02(\Delta S)^{9/5}, \tag{12}$$

where $f(S)$ is the postulated effect of silt on the extinction coefficient, and ΔS is the difference in salinity between surface and bottom. By combining eqs. (9), (10), and (12), total extinction coefficients were reconstructed and compared with observed values (see Fig. 3). Although the correlation is significant, there is too much scatter for satisfactory prediction. Some of the reasons for this scatter may be seen in Fig. 4, which shows the difference between observed and calculated values in relation to the longitude of the observation. The cruise of June 4 to 6, 1952, indicated by x's in the figure, was made during the heaviest flood that has been examined during the course of the survey, and the results are particularly instructive. Very high values were found in the vicinity of the Connecticut River, and visibly muddy water extended all the way to the eastern passes, where the last station sampled had an extinction coefficient

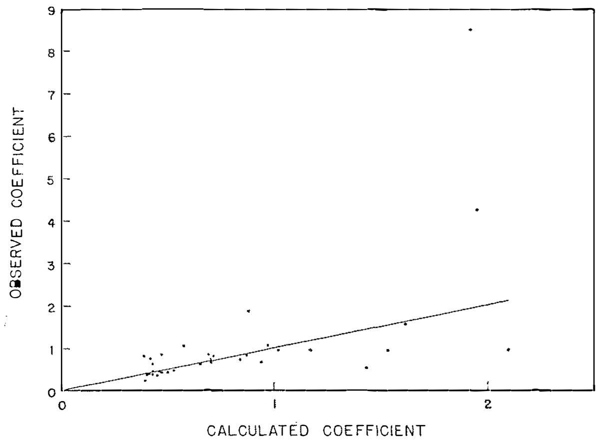

Figure 3. Relation between observed extinction coefficients and values computed from eqs. (9), (10), and (12) under conditions in which the transparency is reduced by suspended silt.

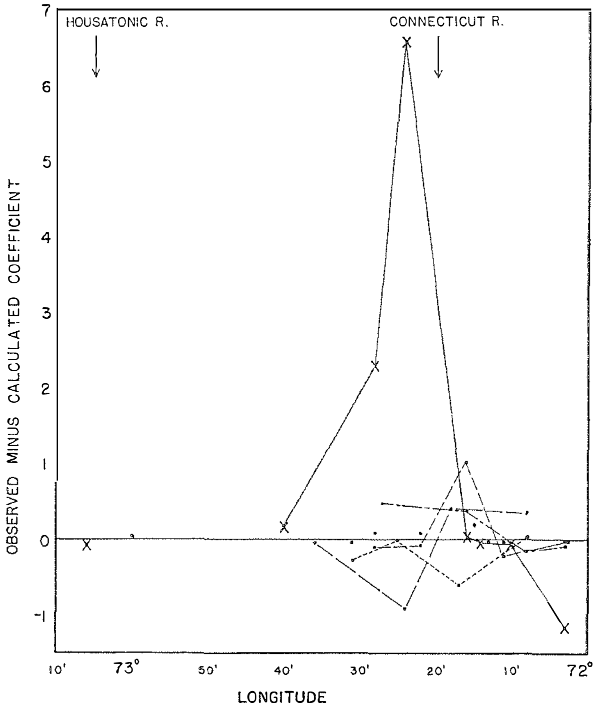

Figure 4. Difference between observed and computed extinction coefficients in relation to longitude and position of freshwater sources of silt. Symbols denote different cruises. For further explanation see text.

of .95. This is approximately four times the average for nonflood conditions at the station in question. The freshened surface layer was moving out of the Sound rapidly, and there was little admixture with the underlying saline water. But the silt must have been sinking away from the surface rapidly because by the time the water reached the passes the silt content, although still visible, was much less than the average relationship expressed by eq. (12). Similar tendencies can be observed in other cruises, with maximum values near the mouth of the river.

DISCUSSION

Summarizing briefly, equations have been developed for the central water mass of Long Island Sound which express most of the variation in extinction coefficients in terms of readily measurable physical and biological parameters. The errors of the analysis are such that the difference between observed and computed coefficients had a standard deviation of ±.13, or slightly under 70 % of the mean value for the extinction coefficient in this part of the Sound.

In applying the equations to the remainder of the Sound there were a few large discrepancies: (a) In one cruise to the western end during a late spring bloom, all computed values were too low. (b) They were also too low at most of the summer stations in the western tip of the Sound; this probably was due to an unusual abundance of dissolved "yellow substance", although the matter has not been examined thoroughly. (c) Two stations in the eastern half of the Sound, both located in atypical morphometric situations, had similarly low calculated values at least part of the time; these were believed to be due to an unusual availability of river silt or bottom sediment. (d) Extinction coefficients were increased in time of flood by the silt load, which could not be precisely predicted; half of the observations fell within ±.15 of the calculated value, but some of the deviations were extreme. Althogether, there were 56 cases of major discrepancy, or 6 % of the total number of observations.

In the other 94 % of the data, there were no systematic errors greater than .06 in the averages for particular areas. This is not a result that was to be expected. The fact that the equations can be applied to a fairly wide variety of physical environments is indicative of a certain balance in physical relationships which is recognized qualitatively. (For example, increasing tidal currents in the eastern end of the Sound are accompanied by a decrease in the amount of soft sediments that are available for suspension). But the quantitative validity of such relationships hardly could be assumed *a priori*. Despite the general applicability of the equations in Long Island Sound waters, they could not be applied safely to other areas without careful examination of observational data. It seems unlikely that eq. (7), in particular, could be used in all shallow waters, and the sediment effects that the equation predicts would have to become vanishingly small in deep oceanic waters.

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Прозрачность вод пролива Лонг Исланд Соунд
Краткий обзор

888 измерений диском Секки были испльзованы для подсчета коеффициентов исчезновения по формуле Аткинса-Пуля и анализированы на их соотношение с разными факторами оказывающими влияние на прозрачность. Выработано уравнение удовлетворительно представляющее коеффициенты исчезновения осенью и зимою для всего пролива в связи с хлорофильной концентрацией фитопланктона, скоростью ветра, устойчивостью вертикальнаго столба воды и ея глубиной. Поздней весной и летом добавочное исчезновение было установлено', обусловленное вероятно органическим детритом. Оно проявлялос косвенно как функция недостатка в кислороде в подповерхностном слое воды на том основании что поддержание его недостатка в присутствии сильнаго вертикальнаго перемешивания указывает на присутствие органическаго детрита. Другое косвенное соотношение было включено в уравнение путем корреляции влияния ила во время наводнений с уменьшением солености поверхностнаго слоя воды. Приблизительно только половина поправки на влияние ила приводило к удовлетворительной точности. Четыре маленькия группы других данных вели к серьозным различиям между наблюденными и подсчитанными коеффициентами исчезновения. Эти данныя были получены в морфометрически не типичных местонахождениях где можно было ожидать чрезвычайное изобилие взвешенных или растворенных органических веществ. Такие противоречивые результаты составляли 6 % общего числа наблюдений.

Note on Particulate Matter in Long Island Sound

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ABSTRACT

Measurements were made of total particulate matter, organic matter, ash, and chlorophyll in the surface water at a station in the central part of Long Island Sound. Total organic matter varied within relatively narrow limits of 1.2 to 3.1 mg/l during the one-year period of study, as contrasted with a 20-fold variation in chlorophyll. The chlorophyll content of the organic matter ranged from 0.13 to 0.90 %, averaging 0.35 %, as compared with 0.93 % in net phytoplankton collections. This suggest that a considerable fraction of the organic matter occurs as detritus or as organisms containing little or no chlorophyll. Results are discussed from the standpoint of zooplankton nutrition.

Harris (in this volume) obtained experimental results indicating that the ingestion of phytoplankton by the zooplankton population was insufficient to maintain the observed metabolic turnover of phosphorus and nitrogen. Except during periods of major phytoplankton augmentation, the total particulate nitrogen was considerably in excess of the amount that reasonably could be expected to exist in living organisms. The measured ammonia excretion could be rationalized only on the assumption that some of the nonliving particulate nitrogen in the water was assimilated.

There have been other indications, of a more indirect type, that considerable quantities of organic detritus are present in the water and that these are being utilized, particularly during late spring and summer. Riley (1956), in calculations of seasonal variations in production and consumption on the basis of oxygen and phosphate observations, found that there was an excess of production over consumption in winter and early spring, with the balance being restored by an excess of consumption in the water column and on the bottom from May until midautumn. Riley and Schurr (in this volume) found an increase in light extinction during the spring-summer period of stability which was postulated to be due to suspended detritus and which was correlated with the degree of development of the oxygen deficit.

In further examination of this problem, a series of measurements has been made of the weight of particulate matter, organic and inorganic, in the surface water in the central basin of Long Island Sound. On 14 occasions during 1956 and early 1957, surface samples of 2.5 l were taken at a station located at Lat. 41° 03.5′N, Long. 72° 59′W. This station, situated in about 35 m of water in the south-central part of the Sound, was well away from any immediate sources of freshwater drainage so that particulate matter of nonpelagic origin was minimal.

Each water sample was filtered through an HA millipore filter (pore size 0.5 μ), and after several rinses with distilled water the residue was washed and rubbed from the filter into a crucible containing a few milliliters of distilled water. The contents were then dried at 100° C, weighed, ignited, and weighed again. The difference on ignition is assumed to approximate particulate organic matter.

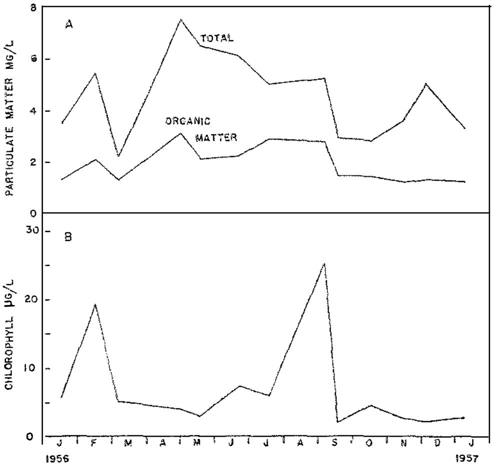

Figure 1. *A*. Seasonal cycle of total particulate matter and organic matter (difference on ignition) at a station in central Long Island Sound. The difference between the two curves represents ash. *B*. Chlorophyll in μg/l at the same station.

Results are shown in Fig. 1 A; Fig. 1 B is the seasonal cycle of surface chlorophyll at the same station. The total organic matter varied within relatively narrow limits of 1.2 to 3.1 mg/l, as contrasted with an approximately 20-fold variation in chlorophyll. The percentage of chlorophyll in individual samples ranged from 0.13 to 0.90 % of the total organic matter, averaging 0.35 %. Previous analyses of net phytoplankton by Harris and Riley (1956) gave a larger average chlorophyll content of 0.93 % and a total range of 0.26 to 1.47 %. These results suggest that a considerable fraction of the organic matter exists as detritus or as organisms that contain little or no chlorophyll, although the relative amounts of the different fractions must vary widely from time to time. During the February and September flowerings, the phytoplankton fraction probably constituted more than 70 % of the total organic matter.

From the end of April until July the phytoplankton was estimated to average only 37 °/₀ of the total. These figures were obtained by applying the conversion factors of Harris and Riley (1956) for net plankton to the population as a whole. This is an acceptable procedure for flowering periods, but it is more questionable for other times, when a large fraction of the population consists of species which are small enough to escape the net. Nevertheless, results tend to confirm previous indications that particulate organic matter exceeds the amount that would be expected merely on the basis of chlorophyll analyses; this is particularly true in late spring and summer.

All investigators have recognized the fact that surface waters contain detritus, which sometimes may be a significant source of food for zooplankton. Long Island Sound is a special case only in that the quantity of detritus appears to be very large and bears remarkably little resemblance to the seasonal cycle of phytoplankton. Its suitability as food remains open to question. On the one hand there is experimental evidence that the zooplankton can assimilate more nitrogen than is found in phytoplankton. On the other hand, the seasonal imbalance between production and consumption suggests that at least part of this material has a slow rate of degradation. Organic matter that has been in suspension for several months or that has been resuspended after a sojourn on the bottom is likely to contain little digestible material other than attached bacteria.

In short, neither phytoplankton analyses nor total sestom measurements give a clear picture of the amount of food that is avilable to the animal population at any one time. Chemical methods or biological assays need to be developed to determine the assimilable fraction.

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Гордон А. Райле

Заметка о частицах вещества в проливе Лонг Исланд Соунд

Краткий обзор

Сделаны измерения всего частичного вещеста, органического вещества, золы и хлорофила в поверхностном слое воды на станции в центральной части пролива. Общая масса вешества колебалась в сравнительно узких пределах от 1.2 до 3.1 мг/l в продолжении целаго года и значительно отличалась от массы хлорофила, которая колебалась в двадцать раз больше. Содержание хлорофила органических частиц колебалось от 0.13 до 0.90%, в среднем 0.35%, по сравнению с его массой в фитопланктоне собранном сетью, равнявшейся 0.93%. Это ведет к предположению что значтельное количество органическаго вещества состоит из детрита или происходит от организмов содержащих мало хлорофила или вовсе не содержащих его. Обсуждение результатов изследования сделано с точки зрения питания зоопланктона.

Dissolved Carbohydrates in Long Island Sound

1956-1958

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ABSTRACT

Water samples from Long Island Sound were analyzed for carbohydrate content through a complete yearly plankton cycle. No carbohydrate was found during the spring diatom bloom, and significant amounts of dissolved carbohydrates appeared only toward the end of a July dinoflagellate bloom. The amounts found (0.5–1.5 mg/l) were an order of magnitude less than those found in bacteria-free pure cultures of the same organisms.

INTRODUCTION

The role of dissolved organic materials in the nutrition of marine organisms has been a matter of contention since the time of Pütter (1907). Recent work has placed less emphasis on the food value of dissolved materials and more on their possible functions as toxins, hormones, vitamins, and conditioners of the medium. A comprehensive review of publications dealing with the occurrence of organic materials in lakes and oceans has been furnished by Vallentyne (1957).

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The presence of dissolved carbohydrates in water from salt marshes was reported by Collier, *et al.* (1950, 1953). They measured uncharacterized carbohydrates by the N-ethyl carbazole technique of Erdman and Little (1950) and correlated the amount of carbohydrate present in the marsh waters with the pumping rates of oysters supplied with this water. The authors concluded that carbohydrates, or substances associated with carbohydrates, influenced the pumping rates, hence the feeding rates, of the oysters. They gave no indication of the mode of action of the carbohydrates. Since neither filtration nor centrifugation reduced the concentration of carbohydrates significantly, they assumed that a great part of the carbohydrate material was present in true solution.

Using the same technique, Wangersky (1952) determined the concentration of carbohydrates in samples taken from the Gulf of Mexico. High concentrations were found in some inshore waters and much smaller amounts in the open Gulf. Lewis and Rakestraw (1955) found values ranging from 0.1 to 0.4 mg/l in filtered seawater samples and from 0.3 to 8.0 mg/l in coastal lagoons. They, too, found little difference between filtered and unfiltered samples and concluded that most of the carbohydrate material was present in true solution.

The present investigation, which followed the changes in concentration of dissolved and total carbohydrate in a selected part of the Sound through a complete yearly plankton cycle, reports the relationship between the blooms of diatoms and dinoflagellates and the occurrence of free carbohydrates. Samples were taken at several depths at Sts. 1, 3, and 5 A of the Long Island Sound Project (see Riley's fig. 1 in this volume) at approximately monthly intervals. Chlorophyll, phosphate, nitrate, dissolved oxygen, and salinity determinations, as well as plankton tows made at these stations, are being reported by other members of the Project.

METHODS

The carbohydrates, determined by the N-ethyl carbazole method of Erdman and Little (1950) as modified by Guillard and Wangersky (1958), were determined in both filtered and unfiltered samples. A Millipore HA filter was used in the filtration. The filters as received from the manufacturer contained small particles of cellulose which could be washed into the samples during filtration; the filters were therefore washed with one liter of distilled water before use.

DISCUSSION

Results of the analyses are presented in Table I. In general, the values are quite low. For much of the year the filtered samples contained no carbohydrate; the highest values found in these samples were of the order of 2.0 mg/l expressed as glucose. The unfiltered samples contained higher carbohydrate concentra-

TABLE I. CARBOHYDRATE VALUES.

Date	St. 1			St. 3			St. 5A		
	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.
XII/4/56	1	–	1.5	1	–	0	0.5	–	0
	4	–	0.4	5	–	1.2	2.5	–	0.3
	7.5	–	0.1	10	–	0.4	5	–	0.4
	–	–	–	25	–	2.5	10	–	2.1
	–	–	–	–	–	–	20	–	2.2
	–	–	–	–	–	–	34	–	0.3
I/8/57	1	0	–	1	0	0.4	1	0	0
	4	0	0	5	0	0.4	2.5	0	0
	9	–	0	10	0	0	5	0	0
	–	–	–	25.5	0	0.4	10	0	0
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	33	0	0
I/25/57	1	0	0	1	0	0	–	–	–
	4	0	0	5	0	0	–	–	–
	8	0	0	10	0	0	–	–	–
	–	–	–	25	0	0	–	–	–
II/5/57π	1	0	0	1	0	0	0.5	0	0
	4	0	0	5	0	0	2.5	0	0
	7.5	0	0	10	0	0	5	0	0
	–	–	–	25	0	0	10	0	0
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	35	0	0
II/12/57	1	0	0	1	0	0	–	–	–
	4	0	0	2.5	0	0	–	–	–
	8	0	0	5	0	0	–	–	–
	–	–	–	10	0	0	–	–	–
	–	–	–	30	0	0	–	–	–
II/26/57†	1	0	0.7	1	0	0	1	0	0
	4	0	0.7	5	0	0	2.5	0	0.5
	8.5	0	0.4	10	0	0	5	0	0
	–	–	–	25	0	0	10	0	0
	–	–	–	–	–	–	20	0	1.0
	–	–	–	–	–	–	35	0	0
III/23/57††	1	0	0.9	1	0	0	0.5	0	0
	4	0	0	5	0	0	2.5	0	0
	7.5	0	0	10	0	0	5	0	0
	–	–	–	26	0	0	10	0	0
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	39	0	0
IV/11/57	1	0	0.5	1	0	0	0.5	0	0
	4	0	0.4	5	0	0	2.5	0	0
	8	0	0	10	0	0	5	0	0
	–	–	–	26	0	0	10	0	0
	–	–	–	–	–	–	20	0	0.4
	–	–	–	–	–	–	35.5*	0	5.0

(cont.)

TABLE I. CARBOHYDRATE VALUES. (cont.)

Date	St. 1			St. 3			St. 5A		
	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.
IV/29/57	1	0	0	1	0	0	–	–	–
V/27/57α	1	0.6	1.3	1	0	2.2	0.5	0	1.8
	5	0	0.6	5	0	0.3	2.5	0	1.3
	10	0	0.9	10	0	0	5	0.2	0.9
	–	–	–	26	0	1.1	10	0	0.7
	–	–	–	–	–	–	20	0	0.2
	–	–	–	–	–	–	30	0	0
VI/15/57	1	0	0.8	1	0	0	–	–	–
VI/20/57	1	0	0.9	1	0	1.2	0.5	1.6	1.7
	4	1.1	1.1	5	0	0.5	2.5	0.4	0.8
	8	0	0.8	10	0.5	0.6	5	0.4	0.7
	–	–	–	26	0	0	10	0.5	0.8
	–	–	–	–	–	–	20	0	0.8
	–	–	–	–	–	–	33	0.4	0.7
VII/10/57	1	0.5	0.9	1	0	0	0.5	–	0
	5	1.2	1.3	5	0	1.1	2.5	0	0.8
	10	0.7	1.0	10	0	1.2	5	0	1.1
	–	–	–	29	0.4	0.6	10	0	0
	–	–	–	–	–	–	20	1.1	1.5
	–	–	–	–	–	–	35	0.9	2.1
VII/23/57⊿	1	0	0.9	1	0	2.1	–	–	–
	5	0	2.3	5	0	2.0	–	–	–
	8.5	2.5	5.9	10	0	8.6	–	–	–
	–	–	–	27	0	1.7	–	–	–
VIII/20/57	1	0	0	1	0	0	0.5	0	0
	4	0	0.5	5	0	0	2.5	0.4	0.9
	8	0	0.5	10	0	0	5	0	0.9
	–	–	–	25	0	0.6	10	0	0
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	34	0	0
IX/25/57β	1	0	0.5	1	0	1.0	0.5	0	0
	5	0	0.5	5	0	0	2.5	0	0
	9	0	1.0	10	0	0	5	0	0.7
	–	–	–	26	0	0	10	0	0
	–	–	–	–	–	–	20	0.1	1.7
	–	–	–	–	–	–	35.5	–	0
X/31/57	1	0	0	1	2.3	2.3	0.5	0	0
	4	0.8	0.8	5	0	0	2.5	0	0
	7	0.8	0.8	10	0	0	5	0	0
	–	–	–	27	0	0	10	0	0.9
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	38	0	0
I/29/58	1	0.2	0.2	1	0.1	0.2	0.5	0	0
	5	0.5	1.4	5	0	0	2.5	0	0.5
	9.5	0.3	2.2	10	0	0	5	0	0.7

(cont.)

TABLE I. Carbohydrate values. (cont.)

Date	St. 1			St. 3			St. 5A		
	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.	Depth (m)	Filt.	Un-filt.
	–	–	–	28	0.2	0.4	10	0	0
	–	–	–	–	–	–	20	0	1.1
	–	–	–	–	–	–	40	0.1	0.2
III/5/58Φ	1	0	1.1	1	–	0.6	0.5	–	0.4
	3	0.1	0.5	5	0	0.6	2.5	0	0
	5	0	0.4	10	0	0.3	5	0	0
	–	–	–	30.5	0	0	10	0	0
	–	–	–	–	–	–	20	0	0.8
	–	–	–	–	–	–	43	0.8	1.8
IV/17/58††	1	0	0	1	0	–	0.5	0	0
	5	0	0	5	0	0	2.5	0	0
	8.5	0	0	10	0	0	5	0	0
	–	–	–	26	0	0	10	0.1	0.7
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	42	0	0
V/20/58	1	0	0	1	0	0	0.5	0	0
	5	0	0	5	0	0	2.5	0	0
	10	0	0	10	0	0	5	0	0
	–	–	–	28	0	0	10	0	0
	–	–	–	–	–	–	20	0	0
	–	–	–	–	–	–	40	0	0

π – Diatom bloom in progress.
† – Peak of bloom probably past.
†† – Bloom definitely over.
α – Small flowering.
Δ – Chlorophyll values do not indicate bloom.
β – Slight flowering.
Φ – Near peak of diatom bloom.
* – Bottle probably hit bottom.

tions than did the filtered samples, but even these did not exceed 5.0 mg/l. In contrast to the results of Collier, *et al.* (1950) and of Lewis and Rakestraw (1955), the unfiltered samples often contained significantly higher quantities of carbohydrate than did the filtered samples. There is apparently a higher concentration of particulate organic material in Long Island Sound than in either the Gulf of Mexico or in the coastal regions of the Pacific Ocean.

While the pattern of occurrence of dissolved carbohydrates seems random in space, perhaps because of the discontinuous distribution of the masses of plankton, the distribution in time agrees with data from pure culture experiments. During the winter and through the spring diatom bloom no dissolved carbohydrate was found in these samples; particulate carbohydrate appeared spottily and in concentrations of less than 1.0 mg/l. Guillard and Wangersky (1958) found 1.0–2.0 mg/l of dissolved carbohydrate in the medium during the period of rapid growth of bacteria-free pure cultures of green algae. As the diatom cultures became senescent the dissolved carbohydrate content of the medium rose to 5.0–10.0 mg/l. At no time did the amounts of soluble carbohydrates released by the diatoms approach the 25–120 mg/l found in aging dinoflagellate cultures.

Lewin (1956), on the other hand, found the concentration of soluble carbohydrates in his diatom cultures to be a function of the species and of the number of cells in the culture. However, most of the algae studied by Lewin produced mucilaginous capsules, and the dissolved carbohydrates in these cultures were probably derived largely from disintegration products of the sheaths. On the other hand, the three nonmucilaginous species studied by him produced considerably less soluble carbohydrate.

No free carbohydrate appeared in the Sound during the period of rapid growth of dinoflagellates. The first appreciable concentrations of dissolved carbohydrates, from 0.5–1.5 mg/l, appeared on 21 July 1957, after the peak of the mixed diatom and dinoflagellate bloom had passed. The high concentrations of carbohydrate were restricted in area.

In pure cultures of dinoflagellates, Guillard and Wangersky (1958) observed large amounts of carbohydrate in solution only as the cultures became senescent. The quantity of free carbohydrate in the medium could be increased by a factor of five by rough treatment of the fragile cells. It is probable that in nature most of the dissolved carbohydrate present during dinoflagellate blooms is the result of disintegration of dead cells. This method of release of organic materials was postulated by Proctor (1957) for a substance from dead *Chlamydomonas* cells that inhibited growth of *Haematococcus*. While the material, probably a long-chain fatty acid, was concentrated in the live cells, it was released to the medium only upon death and disintegration of the cells.

Three types of soluble carbohydrate production may be listed: (1) in organisms with profuse mucilaginous capsules, the amount of soluble carbohydrate produced is a function of population size; (2) in many of the planktonic species little soluble carbohydrate is evident until the population is senescent, and only small amounts are released by dying organisms; (3) some dinoflagellates and perhaps other algae release large quantities of soluble carbohydrates during injury and death. The soluble carbohydrates released by the first group of organisms should consist of complex structural polysaccharides while those released by the second and third groups should be comparatively simple reserve carbohydrates.

CONCLUSIONS

The role of dissolved carbohydrates in the plankton cycle is still far from clear. Since the amounts found in even the last phases of a dinoflagellate bloom are an order of magnitude less than the amounts produced by the same organisms in bacteria-free culture, it is probable that the material is being utilized almost as fast as it is released. Collier (1958) suggested that carbohydrates and other organic substances released by plankton blooms may serve as a substrate for marine bacteria, which in turn supply the dinoflagellates with growth requirements, such as vitamin B_{12}. The diatoms, which can be grown for the most part on entirely inorganic media, lose rags and tatters of their outer coating to the medium, rather than their reserve carbohydrates.

It cannot be concluded from the small amounts found in Long Island Sound that soluble carbohydrates play only a minor role in the maintainance of the plankton cycle. The dominant diatoms of the Sound, like the nonmucilaginous diatoms studied by Lewin (1956) and Guillard and Wangersky (1958), probably liberate little if any soluble carbohydrate. The dinoflagellates are known to produce large amounts of soluble carbohydrate in the late stages of their growth cycle when present in bacteria-free culture. The small "standing crop" of carbohydrates present in the equivalent stages of the Sound's dinoflagellate bloom may be an indication of rapid utilization rather than of small production. Elucidation of the relationships between dinoflagellates and marine bacteria is primarily a task for pure culture techniques in the laboratory.

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Петр Вангерский

Растворенные углеводы в проливе Лонг Исланд Соунд 1956–1958.

Краткий обзор

Пробы воды пролива были анализированы на содержание в них углеводов в продолжение целого планктоннаго цикла. Во время расцвета диатомей весною никаких углеводов в воде не было найдено. Заметные количества растворенных углеводов были получены только в конце расцвета динофлагеллатов. Эти количества от 0.5 до 1.5 мг/l меньше тех которые были найдены в культурах тех же организмов в среде очищенной от бактерий.

Pelagic Fish Eggs and Larvae of Long Island Sound

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ABSTRACT

Pelagic fish eggs and larvae of 22 species were taken throughout Long Island Sound in 1954–1955. Comparison of data for these years with those for 1952–53 shows that the seasonal cycles of eggs and larvae were similar, gradually increasing in numbers and variety in spring to a peak of abundance in summer followed by a decline in autumn. In winter no eggs were taken, and the larvae of only one species (*A. americanus*) occurred in abundance. Comparison also showed that for the most part eggs and larvae of the same species were found each year. As expected, variations in total numbers of eggs and larvae occurred, these undoubtedly being caused by a combination of many factors such as changes in the adult population, environmental conditions, predators, etc. Fluctuations of annual totals were influenced to a great degree by variations in the abundance of eggs and larvae of the more common species, particularly *A. m. mitchilli.*

A greater abundance and variety of species spawned throughout the year in the western half of the Sound than in the central and eastern regions, except during the fall of 1955 when hurricane damage was presumably responsible for the scarcity of eggs and larvae. Comparison of data from St. 1 (the most consistently sampled location from 1952 through 1955) with the averaged data for the Sound as a whole showed parallel fluctuations in abundance of total species of eggs and larvae; however, there were significant differences in the abundance for single species, e.g. *E. cimbrius.*

Although the eggs spawned by some species decreased in size throughout the spawning season, the total volume of eggs spawned increased in direct proportion as the number of eggs increased. It is postulated that, for a summer spawning species, large larvae from large eggs do not have an advantage over small larvae from small eggs, since the latter hatch at a time of greater food supply (see *A. m. mitchilli*).

Species ranging primarily south of Cape Cod (whether migratory or residential) which produce small pelagic eggs and larvae spawn in the warm half of the year while both temperature and availability of zooplankton are increasing. Species ranging primarily north and east of Cape Cod, usually with large pelagic and demersal eggs and large larvae, spawn during the cold half of the year.

INTRODUCTION

The data recorded in this paper are a continuation of those reported by Wheatland (1956) for 1952–53 from L.I.S. As in the first two years there were regional and seasonal differences in abundance and variety of eggs and larvae, and most of the discussion concerns such differences. Also, some annual fluctuations of individual species in the Sound as a whole and at St. 1 in particular are compared: 1952–53 with 1954–55, and 1954 with 1955. Comparisons used here are valid when dates and localities of the tows and of the spawning season of each species are similar. Total spawning and species survival cannot be estimated because intervals in both space and time between tows are so great that such estimates are unreliable. Trends which are indicated may be compared with environmental changes, thus increasing our knowledge of L.I.S. as a whole. An annotated list of species as well as a discussion of species which spawn in southern New England waters has been included.

METHODS OF COLLECTING

Eggs and larvae were sorted from a total of 129 zooplankton samples obtained during 35 two-day cruises from 30 March 1954 to 9 November 1955. Collections were made with a Clarke-Bumpus sampler, using both No. 2 and No. 10 nets. The cruise pattern is described elsewhere in this volume by Riley. Occasional irregularities in the sampling pattern occurred; in summer few tows were taken during the spawning peak due to limited boat time; in winter inclement weather often interfered. The amount of water sampled during each cruise depended upon the number of tows, the nets used, and the amount of phytoplankton and detritus present. Obviously some samples filtered smaller amounts of water than others, but all were included in the totals for each cruise; see Table I.

TABLE I. DATE AND LOCALITY OF THE SAMPLES AND TOTAL ABUNDANCE OF PELAGIC EGGS AND LARVAE IN LONG ISLAND SOUND FROM 30 MARCH 1954 THROUGH 9 NOVEMBER 1955.

Date	Cruise Number	Region Sampled	Water Sampled (m3)	Number of Samples	Number of Species	Total Eggs/m3	Total Larvae/m3
1954							
III/30–IV/1	400 A	E	74.0	5	4	0.14	0.23
IV/12–13	400 B	W	37.8	5	4	0.90	0.76
IV/26–27	500 A	E	71.0	5	4	0.68	0.11
V/10–11	500 B	W	62.0	6	6	2.37	0.03
VI/1–2	600 A	E	34.0	5	7	1.97	0.00
VII/1–2	600 B	W	62.9	9*	11	21.64	1.20
VII/22	700 A	St. 3	Qual.	2	7	–	–
VIII/13	700 B	W	16.9	2	6	23.64	4.04
IX/9	800 A	E	11.0	2	3	0.45	0.09
IX/30–X/1	800 B	W	36.6	4	3	1.56	0.03
X/14–15	900 A	E	14.8	2	2	0.27	0.41
X/28	900 B	W	17.5	3	2	0.29	0.74
XI/18–19	1000 A	E	21.9	3	1	0.00	0.13
XII/2–3	1000 B	W	29.6	5	2	0.00	0.10
XII/27–28	1100 A	E	13.3	3	0	0.00	0.00
1955							
I/13	1100 B	St. 1	0.6	1	0	0.00	0.00
I/21	1100 B	W	43.9	3	1	0.00	4.60
I/31	1200 A	St. 4	5.3	1	0	0.00	0.00
II/17–18	1200 B	E	41.9	3	3	0.02	0.12
III/3–4	1300 A	W	21.9	3	2	1.78	0.46
III/24–25	1300 B	E	22.3	4	2	0.00	0.22
IV/5–6	1400 A	W	54.2	5	4	6.06	0.46
IV/21–22	1400 B	E	31.9	6†	4	0.44	0.63
V/5–6	1500 A	W	48.6	5†	3	3.56	0.10
V/26–27	1500 B	E	20.0	3	4	2.20	0.05
VI/7	1600 A	W	34.8	3	8	2.88	0.00
VI/23, 24	1600 B	E	20.8	4	10	25.49	0.70
VII/12	1700 A	W	42.1	3	12	21.15	0.70
VII/28, 29	1700 B	E	27.2	3	10	21.53	2.68
VIII/9	1800 A	W	10.3	2	7	19.31	9.42
IX/1, 2	1800 B	E	20.1	4	4	0.10	0.45
IX/21, 22	1900 A	W	22.8	4	1	0.05	0.00
X/12, 13	1900 B	E	41.9	5	3	0.67	0.31
X/27, 28	2000 A	W	44.8	5	1	0.00	0.02
XI/8, 9	2000 B	E	25.3	3	1	0.08	0.00

E = eastern end.
W = western end.
* = 1 station with four day and night tows.
† = 1 station with a qualitative tow.

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HORIZONTAL DISTRIBUTION OF ALL SPECIES

For a discussion of the horizontal distribution of spawning products, the Sound has been divided into three longitudinal sections (Fig. 1): eastern (72° 00′–72° 25′), central (72° 25′–73° 15′), and western (73° 15′–73° 45′); each of these sections was further subdivided into a series of ten minute longitudinal widths, three in the eastern, five in the central, and three in the western section. In some cases it is desirable to discuss horizontal distribution in terms of these ten-minute areas, but in general the stations were neither numerous nor consistent enough in sampling from cruise to cruise to warrant small-scale comparison. For the most part, then, discussion will hinge on averages for the three large sections.

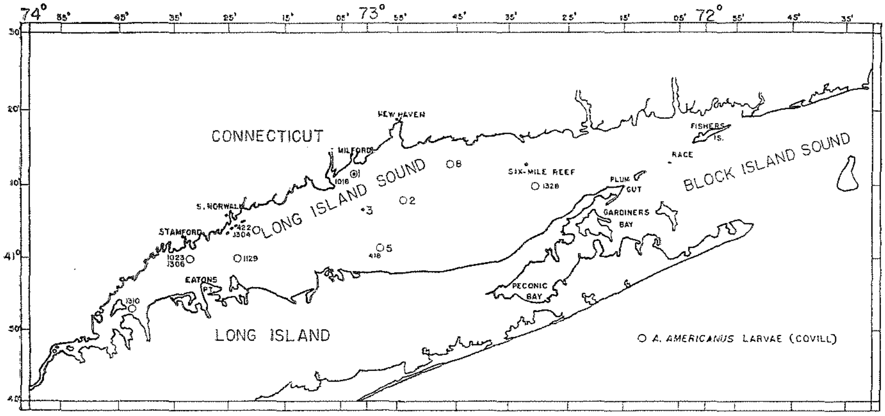

Figure 1. Chart of Long Island Sound, divided into ten-minute longitudinal intervals, and adjacent areas.

In the eastern section, from which we have the least data, the easternmost ten-minute area was represented by samples at only one station (the Race), where tidal currents are so swift that large fluctuations in abundance would be expected. A few eggs were collected here in summer, and some larvae (mostly *M. octodecimspinosus*) were taken during spring. Data were inadequate for analysis.

In the other two areas of the eastern section (72° 05–15′ and 72° 15–25′) eggs, mostly those of *B. tyrannus*, *T. onitis*, and *L. aquosa*, were present only during summer and fall while larvae of *B. tyrannus*, *M. octodecimspinosus*, and *L. aquosa* were taken throughout spring, summer and fall; no *A. m. mitchilli* and *E. cimbrius* eggs or *A. americanus* larvae were taken. The number of eggs and larvae in autumn 1955 was slightly less than in autumn 1954.

The central section was the most frequently sampled of the Sound[1]. Although eggs and larvae appeared to be more abundant in the western part of this central section, existence of a marked east-west gradient cannot be determined with certainty because of the irregular collecting schedule. The seasonal spawning pattern in the four ten-minute areas sampled[2] in the central section was similar. This pattern is particularly evident in the data from one of these areas (72° 55′ –73° 05′) where most of the samples were obtained in 1952–53. Most annual differences here were due to a genuine increase in spawning products, particularly of *A. m. mitchilli*; these eggs were always so abundant that their numbers dominated the total abundance in this area. However, in another area of this section (72° 25–35′), where anchovy eggs were entirely absent, there was a great increase in spawning products due to a large quantity of *S. chrysops* eggs (at St. 1626).

The western section, which was sampled more regularly than the eastern section because of its smaller size and greater land protection, revealed a seasonal pattern of abundance similar to that in the central region; here, however, there was an increase in the numbers of *E. cimbrius* eggs and *A. americanus* larvae. Although there was little or no apparent east-west gradient in this region, there was a north-south gradient on a line west of S. Norwalk (73° 25′) where the northern part contained more eggs than the southern part; it also contained more than the far western end of this section. This large abundance of eggs and larvae along the north shore may have resulted from a combination of many factors, such as a richer plankton supply which attracted more spawning fish, winds, currents, etc. Apparently the wind was not an effective factor, for vector analysis of direction and force during summer showed that there were inadequate southerly components before each cruise to cause such distribution. According to Riley (1956), a weak current flows westward along the north shore while a stronger one flows eastward along the south shore; thus eggs spawned along the northern shore may drift westward more slowly and remain more concentrated for a longer period than along the southern shore.

Within most of these three western areas, more eggs were taken during spring than in eastern regions, due primarily to the presence of *E. cimbrius* which spawned only in the western half of the Sound. During each summer from 1952 through 1955 there has been an enormous increase annually in the abundance of all species, this being followed by a great decrease in the fall; in

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[1] This is the only area which encompasses the regularly sampled stations of 1952–53.

[2] One ten-minute area (72° 35–45′) was not sampled.

the fall of 1955, this decrease was even more precipitous than in 1954. In winter *A. americanus* larvae were common, being taken occasionally in large quantity, *e.g.*, at St. 1129 on 17 January 1955.

Regional comparison (Table II) shows that in 1954 the eastern section was apparently much less productive than the western section and that the central section was only half as productive as the western section; in 1955, however, the conditions were reversed with the western section being only half as productive as the central section.

TABLE II. COMPARISON OF ABUNDANCE OF EGGS AND LARVAE IN EACH REGION OF L.I.S. IN 1954–55, WITH AND WITHOUT ANCHOVY EGGS.

Region	1954		1955	
	Eggs/m3	Larvae/m3	Eggs/m3	Larvae/m3
Eastern section				
with anchovy eggs.........	0.14	0.15	0.30	0.23
without anchovy eggs......	0.14	–	0.30	–
Central section				
with anchovy eggs.........	3.66	0.55	7.66	0.60
without anchovy eggs......	2.19	–	3.26	–
Western section				
with anchovy eggs.........	7.78	0.85	3.97	1.72
without anchovy eggs......	4.86	–	3.26	–

This decrease in 1955 was probably due to abnormal meteorological conditions. During late summer and fall of 1955 there was an easterly wind component which was almost entirely lacking in 1954; furthermore, two hurricanes with resultant flooding in the early fall of 1955 caused an abnormal amount of freshwater drainage into the Sound, thus producing a layer of surface water of much lower salinity than is usually present. That this decrease was due largely to meteorological conditions is further strengthened by the fact that these abnormal weather conditions culminated in a plankton bloom which was enhanced by the presence of a relatively stable water column, factors which might be beneficial to eggs and larvae. It seems likely that physical damage rather than lack of available food quantitavely reduced these normally abundant species.

The Sound exhibits east-west gradients in environmental conditions, with maximum salinities in the eastern section and maximum nutrients, phytoplankton and zooplankton in the western end, particularly along the northern side. In general, these environmental conditions were fairly closely correlated with the sectional abundance of eggs and larvae, a much larger quantity being taken in the western than in the eastern end.

In spite of the fact that there are some indications that annual variations in egg and larval gradients were effected by changes in the same environmental factors, there were many cases in which similar correlations did not obtain. Some of those noted are as follows. In winter, as expected, gradients were minimal throughout the Sound, yet *A. americanus* larvae were found almost exclusively in the central and western sections. During spring, gradients naturally strengthened, yet *Myoxocephalus* and *P. americanus* larvae (both from demersal eggs) were widely distributed while the pelagic eggs of *E. cimbrius* and *L. aquosa* appeared almost exclusively in the central and western sections. In summer there was a strong salinity gradient, with zooplankton generally found in abundance everywhere, yet fish eggs and larvae were more abundant in the western end than elsewhere. In autumn, the temperature gradient decreased and the salinity gradient increased throughout the Sound while regeneration of nutrients increased more strongly in the western end, yet the east-west gradient in egg and larval abundance became noticeably inconsistent.

Vertical distribution of eggs and larvae was not studied during this survey.

STATION 1, 1952–1955

St. 1 was sampled more consistently than any other station in L.I.S.: 28 collections in 1952, 27 in 1953, 15 in 1954, and 14 in 1955. The decreasing number of collections each successive year was not satisfactory, but there was at least one collection each month during those four years at this station. From November 1955 through November 1956, samples were taken fortnightly.

To determine whether differences resulted from fortnightly tows as compared with weekly tows, data from alternating weekly tows at St. 1 for 1952–53 were combined into two separate groups which were then treated as fortnightly tows. Analysis of all of these data shows that *total annual abundance* based on combined tows differed little from that based on weekly tows. However, variations in numbers were greater between fortnightly tows than between weekly tows, particularly at the time of maximum spawning. (Differences at times of light spawning are small.) As maximum spawning is approached, data from weekly tows portray more accurately than fortnightly tows the variations in numbers, for with weekly tows it is more probable that wide fluctuations in numbers of eggs and larvae will be sampled. For optimal accuracy, then, the sampling should be more intense in early and late summer than at any other time of year. However, seasonal or large monthly variations in spawning products as revealed in the data are manifestations of actual variations in abundance rather than of an artifact resulting from reduction to fortnightly sampling.

Qualitatively the spawning population at St. 1 as well as in L.I.S. generally has been rather stable, most of the species being well represented during the

TABLE III. Comparison of species taken at St. 1 and elsewhere in L.I.S., 1952–55.

Species	St. 1				Elsewhere in L.I.S.			
	'52	'53	'54	'55	'52	'53	'54	'55
*C. harengus**	–	–	–	–	–	+	–	–
B. tyrannus	+	+	+	+	+	+	+	+
A. m. mitchilli	+	+	+	+	+	+	+	+
E. cimbrius	+	+	+	+	+	+	+	+
*G. morrhua**	–	–	–	–	–	–	–	+
*P. virens**	+	–	–	–	–	–	–	–
*M. m. notata**	–	–	–	+	+	–	–	+
*S. peckianus**	–	–	–	–	+	–	–	–
*A. rostrata**	–	–	–	–	–	+	–	–
B. chrysura (?)*	–	–	–	–	–	–	–	+
C. regalis	+	+	+	–	+	+	+	+
M. saxatilis	+	+	–	+	+	+	–	+
S. chrysops	+	+	+	+	+	+	+	+
T. adspersus	+	+	+	+	+	+	+	+
T. onitis	+	+	+	+	+	+	+	+
*A. americanus**	+	+	+	+	+	+	+	+
Unknown larva–1 (?)*	–	–	–	–	–	–	–	+
S. scombrus	+	–	–	–	+	+	–	–
P. triacanthus	+	–	+	–	+	+	+	+
P. carolinus	+	+	+	+	+	+	+	+
P. evolans	+	+	+	–	+	+	+	+
Myoxocephalus sp.*	–	–	–	–	+	+	+	+
P. oblongus (?)	+	–	+	+	–	–	+	+
L. ferruginea†	–	–	–	–	–	+	–	–
L. aquosa	+	+	+	+	+	+	+	+
*P. americanus**	+	+	–	+	+	+	+	+
*S. maculatus**	–	–	–	–	+	–	+	–
Unknown larva–2*	–	–	–	–	–	–	–	+

* Only larvae taken.

† Larvae listed from St. 1 in Wheatland (1956) have been found to be *P. virens*.

four years. Certainly more than half of the spawning species have turned up in the Sound every year, and the majority were taken at St. 1. Stray species, which come mainly from inshore, occasionally appeared at deep stations.

Although the spawning population is not and was not expected to be quantitatively stable, fluctuations at St. 1, though similar to those for the Sound as a whole, were somewhat sharper, due no doubt to more concentrated and consistent sampling of one area. For example, the peaks for 1952–53 and 1955 which resulted from an increase in the abundance of anchovy eggs and from both anchovy and sand eel larvae, were greater at St. 1 (see Table IV) than in the Sound generally.

TABLE IV. ABUNDANCE OF EGGS AND LARVAE AT ST. 1 COMPARED WITH THOSE IN L.I.S. AS A WHOLE, 1952–55.

Year	Months	Station 1		L.I.S.	
		Eggs/m3	Larvae/m3	Eggs/m3	Larvae/m3
1952–53.....	Mar.–Mar.	11.81	0.50	7.42	0.73
1953–54.....	Mar.–Mar.	1.40	0.22	2.30	0.36
1954–55.....	Mar.–Mar.	5.35	0.42	2.44	0.39
1955........	Mar.–Nov.	14.86	1.00	6.16	0.63

TABLE V. SEASONAL ABUNDANCE AND VARIETY OF EGGS AND LARVAE AT ST. 1, 1952–55.

Season	Water sampled (m3)	No. Species eggs	Eggs/m3	No. Species Larvae	Larvae/m3
1952–1955					
winter......	172.2	0	0.00	2	0.11
spring......	266.8	5	1.57	3	0.16
summer	223.1	14	27.47	10	1.15
autumn	175.4	4	0.18	4	0.95
1952					
winter*.....	–	–	–	–	–
spring......	145.2	5	1.45	2	0.23
summer	82.9	11	47.36	5	1.45
autumn	50.7	4	0.59	3	2.46
1953					
winter......	75.4	0	0.00	1	0.07
spring......	63.2	4	1.01	2	0.06
summer	69.4	8	3.66	3	0.20
autumn	65.2	0	0.00	1	0.48
1954					
winter......	68.1	0	0.00	2	0.24
spring......	45.0	4	1.38	1	0.04
summer	25.1	10 or 11	18.25	10	1.32
autumn	26.5	0	0.00	1	0.24
1955					
winter......	10.8	0	0.00	1	0.19
spring......	30.0	2	1.67	2	0.17
summer	29.4	6 or 7	48.50	8	3.06
autumn	37.0	1	0.03	2	0.14

* No tows taken in the winter of 1952.

At St. 1, when the number of spawning species is compared with the abundance of eggs and larvae, it is obvious that times of greatest variety coincided with the greatest annual abundance (see Table V). Between May and August for all years the peaks were sharply defined, particularly in 1952 and 1955. Smaller peaks, produced by few species, were apparent in the spring.

In the first part of Table V, the total data for St. 1 from 1952 through 1955 are grouped into four seasonal categories to show seasonal abundance and variety of eggs and larvae: winter (December through February), spring (March through May), summer (June through August), and autumn (September through November). In winter there were no pelagic eggs here, but there were larvae of two species, *B. tyrannus* and *A. americanus*. (Actually the menhaden continued over from fall and perhaps should be included in that category). In the spring there were five species which produced a few eggs, the greatest number appearing toward the end of May; larvae of three species were taken in small numbers. During summer 14 species produced many eggs, the majority being those of *A. m. mitchilli*, *T. adspersus*, *T. onitis*, and *C. regalis*; larvae of ten species were taken, and of these only anchovy occurred consistently in July and August. In the fall, eggs and larvae were taken in small quantity; anchovy and cunner larvae were found often in early fall while eggs and larvae of menhaden and windowpane flounder occurred as late as November-December. Evidently this general pattern occurred each year at St. 1 with minor variations.

The remainder of Table V shows the annual data for St. 1 divided into seasonal groupings.

During winter, no pelagic eggs were taken in any year, but larvae were taken each year. In 1953 and 1955 only *A. americanus* larvae were taken whereas in 1954 *B. tyrannus* was also taken. However, these larvae had little influence on the total. The highest figure (0.24) resulted from an unusual number of sand eels in December 1954, possibly due to a higher than usual water temperature that year.

During spring the total number of eggs produced and the number of species represented at St. 1 were reasonably uniform each year from 1952 through 1954; in 1955, however, about the same number of eggs was produced by only half as many species, the numbers this year being maintained largely by the abundant production of *E. cimbrius* eggs throughout the western half of the Sound. *T. adspersus* and *T. onitis* eggs, usually found at this time, were not recorded at St. 1 in 1955, probably because of lack of sampling in the western end (including St. 1) between 5 May and 7 June.

In summer there were sharp annual differences in the abundance of eggs and larvae due to variations in the abundant and consistently collected species rather than to differences in the number of species or to increased spawning by one or more migratory strays. In Table VI it is seen that anchovy eggs contributed the major portion of the totals for St. 1 in each year. The large annual fluctuations appear to be correlated to some extent with the lesser variations of other species.

A precipitous decline in actual numbers of all eggs and a decline in the percentage of anchovies is evident for 1952–53 at St. 1. In 1954 there was an increase in the total number of eggs as well as an increase in the percentage of anchovy eggs, but in 1955, when the total number of eggs increased also, there was little increase in the percentage of anchovy eggs. The data suggest that there is a common factor which is responsible for the decrease in eggs in 1953 and for the increase during each summer of 1954 and 1955. Such a factor might be explained by the abundance of spring zooplankton. Most of the species concerned are zooplankton feeders or are indirectly effected by the amount of zooplankton available, and it seems reasonable to assume that the amount of spawning might be affected by the amount of food available during the time of gonad maturation.

TABLE VI. ABUNDANCE OF EGGS/M3 IN SUMMER AT ST. 1, WITH AND WITHOUT ANCHOVY EGGS, AND SPRING VOLUMES OF ZOOPLANKTON TAKEN WITH BOTH NO. 2 AND NO. 10 NETS.

	1952	1953	1954	1955
Total species:				
with anchovy	47.36	3.66	18.25	48.50
without anchovy	4.23	1.62	5.30	12.82
Total anchovy	43.13	2.04	12.95	35.68
% anchovy	91	55	71	74
spring zooplankton volumes				
No. 2 net	0.61	0.01	0.27	1.15
No. 10 net	1.21	0.38	0.94	3.25

In Table VI it is seen that the volume of spring zooplankton at St. 1 decreased from 1952 to 1953 and increased in the following two years. In general this pattern was similar to the fluctuations in egg abundance.

In summer the fluctuations in both number and variety of larvae were not proportional to egg abundance or to the amount of water sampled. In 1954 and 1955, approximately twice as many species showed an increase in the abundance of larvae as in 1952–53 (Table V).

In 1952, when larvae of only five species were collected at St. 1, 97% were anchovy, but in 1955, when there were 8 species, 50% were anchovy. While 1955 showed only 50% anchovy, this percentage contributed to a much larger total than the 97% in 1952. The difference in variety depended somewhat upon sampling of recently hatched individuals. For instance, on 1 July 1954 recently hatched larvae of eight species were taken, this being the largest number of species taken in any one tow. Differences in abundance as well as variety may be effected by net escapement when the larvae have developed adequate swimming ability, and this in turn might influence the reliability of the samples.

During the fall a pronounced decrease in the number of spawning species took place at St. 1, not more than four being recorded in any one of the four years; this maximal figure of four in 1952 resulted from the presence of anchovy and cunner eggs during the first two weeks of September. (Actually anchovy and cunner eggs should be included only with summer data.) In some years, eggs and larvae of menhaden and windowpane flounder and larvae of anchovy occurred sporadically as late as November and December.

SPECIES COMPOSITION[1] IN LONG ISLAND SOUND
1954–1955

Brevoortia tyrannus. Eggs and larvae.

DISTRIBUTION. The locations and abundance of menhaden eggs and larvae varied not only between 1954 and 1955 but also between spring and fall of each year.

While most of the eggs taken in 1954 were collected in the western end of the Sound, menhaden spawned in early summer and autumn in such widely spaced localities as Plum Gut region in the eastern end and west of Stamford in the western end. Between these two areas, eggs were taken sporadically east of the central section in June, July, and September and more abundantly west of it in May, June, and October.

The larvae which appeared in the western area in early summer and fall were not always taken in the same area as the eggs. For instance, recently hatched larvae were collected in October in the central region where no eggs had been collected previously. This is understandable if one considers that the samples were taken at intervals of two weeks and that incubation occupied 48 hours at 22°C (Kuntz and Radcliffe, 1917); spawning, hatching and early development of the larvae could easily have transpired between successive sampling periods.

In both spring and fall of 1955 less eggs and larvae were taken than in those seasons of 1954. No eggs appeared as early as May and none remained after mid-October. Particularly noticeable was the difference in the quantity of eggs and larvae taken in these two years at the western end. In 1954 most of the eggs and larvae taken were collected in the western end whereas in 1955 only three eggs and no larvae were found west of St. 1, none of these having been taken in the fall. This paucity in 1955 could be due to insufficient sampling, absence of spawners west of St. 1, hurricanes (and accompanying abnormalities) or a combination of these and possibly other factors. Sampling

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[1] Listed in the order of Berg (1940), as in Wheatland (1956).

was admittedly scanty, yet it was probably sufficient to pick up the eggs had they been there. Data on landings for New York City (Fish and Wildlife Service, 1954–55) show that menhaden were caught from Peconic-Gardiner's Bay in 1955 in greater quantity and over a longer summer period than in the remaining areas of L.I.S.; this suggests that they remained in that area and did not move out into the Sound. Hurricane damage is probably the most likely explanation for the absence of fall eggs, since there was a decrease in the quantity of all spawning products taken in the western end following the two storms.

GENERAL REMARKS. Wheatland (1956) stated that "presumably these fish spawn when the temperature is above 16°C". In 1955 the water was barely above 13°C when the eggs initially appeared, and in 1954 they were collected when the surface water was only 10.01°C. Apparently, then, menhaden spawn when the temperature is as low as 10°C.

Variations in the rate of egg development in different regions and seasons may be an important factor when considering the size of the resultant year-

TABLE VII. PERTINENT DATA OF FISH EGGS AND LARVAE OF L.I.S., 1954–1955.

	1954					
	Eggs			Larvae		
Species	Date	Actual No.	Size range (mm)	Date	Actual No.	Size range (mm)
B. tyrannus	V/10–VII/2	47	1.51–1.95	VII/1–VII/22	23	3.5–10.9
	VIII/13–X/28	31	1.35–1.68	IX/1–XII/2	23	4.1–10.6
A. m. mitchilli	VII/1–VIII/13	854	0.71–1.01	VII/1–IX/9	104	1.9–8.4
*G. morrhua**	–	0	–	–	0	–
E. cimbrius	II/10–V/11	148	0.72–1.02	V/10	1	3.6
M. m. notata	–	0	–	–	0	–
*B. chrysura**	–	0	–	–	0	–
C. regalis	VI/2–VIII/13	141	0.76–0.94	VII/1–VII/22	29	2.1–5.3
M. saxatilis	–	0	–	–	0	–
S. chrysops	VI/2–VII/1	12	0.86–0.98	VI/15–VII/1	7	2.2–3.4
T. adspersus	V/10–IX/30	566	0.73–0.96	VII/1–VIII/13	15	1.4–5.0
T. onitis	V/10–VIII/13	150	0.85–1.15	VII/1–VII/22	9	2.5–3.4
*A. americanus**†	–	0	–	III/30–IV/27	19	10.6–23.1
Unknown larva-1*	–	0	–	–	0	–
P. triacanthus	VII/1,2	9	0.61–0.76	VII/1	1	2.6
P. carolinus	VI/1–VIII/13	35	0.96–1.10	VII/1–VII/22	7	2.4–4.6
P. evolans	VI/2–VIII/13	11	1.00–1.06			
M. octo & aeneus†	–	0	–	IV/1–IV/13	4	5.3–8.4
P. oblongus?	VII/1–VIII/13	13	0.86–0.99	VIII/13	1	3.2
L. aquosa	IV/26–VII/2	107	0.96–1.24	VII/1	1	2.8
	VIII/13–X/28	30	1.00–1.11	X/15	1	2.8
P. americanus	–	0	–	III/30–V/10	32	2.9–7.2
S. maculatus	–	0	–	VII/22	2	3.2, 3.5
Unknown larva-2*	–	0	–	–	0	–

(cont.)

TABLE VII. (cont.)

	1955					
	Eggs			Larvae		
Species	Date	Actual No.	Size range (mm)	Date	Actual No.	Size range (mm)
B. tyrannus	VI/1–VII/7	10	1.54–1.79	VI/23–VII/12	10	3.7–7.3
	X/12,13	24	1.45–1.65	X/12,13	12	4.0–6.5
A. m. mitchilli	VI/7–VIII/9	1377	0.73–1.02	VI/23–IX/2	185	3.1–8.0
*G. morrhua**	–	0	–	V/27	1	10.4
E. cimbrius	II/18–V/26	495	0.75–1.05	–	0	–
M. m. notata	–	0	–	VII/12	3	4.4–5.1
*B. chrysura**	–	0	–	IX/1	1	4.3
C. regalis	VI/7–VIII/9	27	0.76–0.90	VIII/9	1	1.9
M. saxatilis	VII/12	12	0.79–0.84	–	0	–
S. chrysops	VI/24–VII/12	162	0.86–1.03	VI/23–VII/28	4	2.4–3.5
T. adspersus	VI/7–VIII/9	411	0.71–0.94	VII/28	10	1.9–4.7
T. onitis	V/26–VIII/9	169	0.89–1.14	VI/23	1	+3.0
A. americanus	–	0	–	XII/2–IV/22	253	4.3–37.0
Unknown larva-1*	–	0	–	X/12	1	9.4
P. triacanthus? ...	VI/24–VII/12	19	0.70–0.81	–	0	–
P. carolinus	VI/7–VIII/9	27	1.00–1.11	VII/28–VIII/13	3	+1.6–4.0
P. evolans	VI/7	1	–			
M. octo & aeneus .	–	0	–	II/17–IV/22	7	5.9–7.5
P. oblongus?	VI/24–VIII/9	6	0.90–0.98	–	0	–
L. aquosa	V/25–VII/29	107	0.96–1.26	VI/23, VII/29	5	1.7–3.5
	IX/1–XI/9	8	1.02–1.12	X/27	1	2.7
P. americanus	–	0	–	IV/5–V/6	14	3.9–6.0
S. maculatus	–	0	–	–	0	–
Unknown larva-2*	–	0	–	VII/28	1	2.1

* Represented by one specimen.
? Tentatively identified.
† Collected before this survey started..

class. Although an accurate appraisal of the relationship of an east-west surface temperature gradient with development rates would require extensive experimental work as well as numerous simultaneous collections within different regions of the Sound at different seasons, it appears from present data that fall eggs of *B. tyrannus* develop more rapidly than spring eggs.

Anchoa mitchilli mitchilli. Eggs and larvae.

Distribution. West of 72°45′ eggs were found at almost all depths throughout the Sound and were most abundant in the central region from June to August. East of this longitude it spawned almost exclusively in shallow inshore areas. Eggs were never taken in the easternmost region, although four to six-day old larvae were found near the Race; these may have drifted there from spawning grounds north of Fisher's Island.

Since a continuous and more rigorous sampling schedule could not be carried out, the exact dates of the beginning, peak, and end of the anchovy spawning season could not be ascertained. However, according to our data, the eggs first appeared simultaneously in mid-June 1954 and in early June 1955 at all stations and depths of the central and western areas. Not since 1952 had there been many eggs in June. During both 1954 and 1955 the peaks occurred in late July or early August, with spawning completed by September. Larvae first appeared in our collections two weeks after the eggs, during early July 1954 and mid-June 1955, but the great majority was taken in late July and August; a few were caught as late as early September.

Noticeable differences in abundance between various central and western areas occurred during both summers. The greatest concentration of eggs was found between 72°55′ and 73°05′; from 73°05′ to 73°15′ they were less abundant; and from 73°15′ towards the extreme western end the eggs were collected in progressively greater abundance. In 1954 there were almost as many eggs taken here as in the central region whereas in 1955 noticeably fewer eggs were found in the western than in the central area, probably owing to inadequate sampling in the western end during summer.

Depth appears to be an important factor in limiting the location of spawning of *A. m. mitchilli.* Within the central region the eggs in all years were usually far more abundant near shore, or in water less than 20 m deep, than in deeper water. In the western region, where both depths and distances are less than elsewhere in the Sound, spawning areas may extend further out from shore, in which case a greater number of eggs will be more widely scattered. Attempts to determine the amount of drift from the age of the eggs failed. For both shallow and deep water, examination only showed that the eggs are either spawned at night or that eggs spawned in the shallows are carried into deep water on a single tidal excursion.

Occasionally larvae turned up in collections from the far eastern end. In the central and western regions their pattern of distribution was similar to that of the eggs. The whole central region and that west of 73°15′ provided a great abundance of larvae. In both of these regions they were similarly concentrated as to depth and there was no apparent age difference regardless of whether they were taken from shallow or deep water. Few recently hatched larvae were taken, the majority being approximately two to five days old. The larger postlarvae are probably able to escape the plankton net, but they may be taken by the hundreds in a bottom trawl (*e.g.*, in 1955, and in the fall of 1956 at St. 1).

GENERAL REMARKS. Although the size of individual eggs decreased from June through August, the total volume of eggs increased in direct proportion to the number per cubic meter. The figures in Table VIII are based on diameter measurements taken from the long axis of the egg. The measured volume per egg then is larger than the true value, but since the shape of the egg does not change significantly throughout the summer (Wheatland, 1956), the figures for the groups as used here are valid for comparative purposes. The total volumes in this report, based on the catch only, are obviously far below the actual egg volume of the entire spawning population.

The total energy expended by spawning fish undoubtedly increases to a peak in July in direct proportion to the total volume of eggs produced, despite the size of the eggs. If large larvae develop from large eggs that are spawned in the early part of the season, their chances of survival may be greater (Svärdson, 1949) than the chances of small larvae from small eggs spawned later. But since the amount of zooplankton in L.I.S. increases throughout the summer, small larvae probably have as good a chance of survival, from the point of view of available food supply, as large larvae. If there is little difference in the survival rate between large and small larvae, then there would seem to be little advantage for an increasing number of spawning fish to continue to lay large eggs. Obviously some fish still spawn early, since large larvae from large eggs apparently survive. Most fish, however, do spawn in the latter part of the spawning period when a greater food supply enhances survival and when a greater volume of egg material may be produced with relatively less increase in energy; presumably this pattern results in a greater survival of late spawners, as compared to early spawners.

TABLE VIII. VOLUME OF ANCHOVY EGGS TAKEN DURING EACH CRUISE IN THE SUMMERS OF 1954 AND 1955 AS DERIVED FROM THE FORMULA GIVEN BELOW.

Date	Cruise	Volume (mm3)	n/m3	Av. Diam. (mm)
VI-1-54	600A	–	–	–
VII-1	600B	2.0×10^{-3}	0.51	0.88
VII-22	700A	–	–	–
VIII-13	700B	9.0×10^{-1}	3.02	0.83
IX-9	800A	–	–	–
VI-7-55	1600A	1.3×10^{-1}	0.29	0.95
VI-23	1600B	4.0×1	10.55	0.90
VII-12	1700A	4.2×1	12.62	0.86
VII-28	1700B	5.1×1	17.09	0.83
VIII-9	1800A	4.4×1	15.53	0.82
IX-1	1800B	–	–	–

$\overline{D}_n/m^3\ (\frac{1}{6}\,\pi\,\overline{D}^3 n/m^3) \times n/m^3$, where $\overline{D}$ is the mean diameter and n/m^3 is the number per cubic meter.

The above data from plankton samples are not adequate. In order to demonstrate the possible advantage of decreasing egg size, we must know when they spawn, the number of fish spawning throughout the season, the number and volume of eggs per fish, the exact size of hatching larvae, and the survival rates. This, then, is an extremely complex problem requiring extensive data and study.

Gadus morrhua. No eggs, one larva.

On 27 May 1955 one larva (10.4 mm) at least two weeks old and maybe older (Bigelow and Schroeder, 1953) was taken at St. 1529 near Six-mile Reef, 18 km west of the Race. The size corresponded to those taken on 27 May 1945 near the bottom in Block Island Sound (Merriman & Sclar, 1952), possibly the location from which our specimen came.

Pollachius virens. No eggs, one larva; formerly reported erroneously as *Limanda ferruginea.*

A 13.8-mm larva that was caught on 9 April 1952 was erroneously listed as *Limanda ferruginea.* Attention to this mistake was brought about by the appearance of pollack larvae in the ring and bottom trawls at St. 1 in the spring of 1956. Therefore table XXVII (Wheatland, 1956: 300) should be corrected: insert an × instead of the dash in the third column opposite *P. virens* and change the total from 23 to 24.

Enchelyopus cimbrius. Eggs and larvae.

DISTRIBUTION. The four-bearded rockling spawned mainly in the western half of L.I.S. Except for a few taken at Six-mile Reef (72°27′) on 26 April 1954 and one at the Race in April 1955, no eggs were found east of 72°55′. It was taken in numbers at Sts. 1, 2, and 4 and in less quantity around Middleground (73°05′). From there the eggs steadily increased in abundance westward. The high percentage of heavy blue mud clay (a preferred bottom habitat of the rockling) in the western region may account for this gradient. Since development is slow, they may drift considerable distances from the original spawning grounds. However, the length of drift was not ascertained from the age of the eggs, for development is of such long duration that eggs at similar stages might have been of different ages.

Spawning occurred over the same period throughout the Sound. In 1954 the eggs first appeared on 10 February and were last collected on 11 May; in 1955 eggs occurred between 18 February through 26 May, in greater numbers than in 1954. The increased abundance in 1955 was evident not only throughout the entire western half of the Sound but also at St. 1, where, since 1952 at least, they have not been indicative of abundance in the remainder of the Sound (see Table IX) since they apparently drift there from other spawning areas.

Oddly enough larvae were taken only in 1954 when the eggs were least abundant. All specimens (2.6–5.0 mm) were taken in the western region during the 500–B cruise in May (2.6–5.0 mm).

TABLE IX. Abundance of Rockling Eggs per Cubic Meter at St. 1 Compared with Totals for all other Stations in L.I.S.

Date	Station 1	L.I.S.*
1952	1.09	0.69
1953	0.68	0.78
1954	0.89	0.61
1955	1.12	2.06

* Based on other stations.

General Remarks. The average temperature of the water column when these eggs first appeared was 1.2° in 1954 and 1.4°C in 1955; during the peak of abundance it was 8–11.5° in 1954 and 4–9° in 1955. Apparently the rockling spawned for four years in L.I.S. in temperatures which Battle (1929) found were too cold for successful development in Passamaquoddy Bay.

The average diameter of the eggs decreased during the spawning season from 1.02 to 0.80 mm in 1954 and from 0.97 to 0.82 mm in 1955.

Adults were taken rather commonly in 1956 from the bottom at 15 m depth three miles south of St. 1. Only one occurred in tows from the hard sand-shell bottom of St. 1.

Menidia menidia notata. No eggs, three larvae.

No larvae were taken in 1954, but on 12 July 1955 three (5.1, 4.9, 4.4 mm) were caught at St. 1. Although they are uncommon at St. 1, larvae by the hundreds are observed every summer near the U.S. Fish and Wildlife Service dock in Milford Harbor, Conn.

Bairdiella chrysura (?). Only one larva (?).

No specimens of silver perch were taken in L.I.S. in 1952–54. One 4.3 mm larva was taken on 1 September 1955 in the eastern end of the Sound near Plum Gut; presumably it drifted there from the shallow and warm area of Peconic Bay.

Cynoscion regalis. Eggs and larvae.

Distribution. Weakfish eggs and larvae occurred at scattered locations during summer, primarily in the western half. Although eastern sampling was spotty, the eggs appeared once east of 72° 45′ whereas larvae never occurred east of 73° 00′.

In 1954 eggs were taken from 9 June until 13 August, the majority being collected in the area just west of the regular mid-Sound stations. Twenty-nine larvae, 2.1–5.3 mm, were collected at 73° 00′–15′ on 1 and 22 July. In 1955 a few eggs from various western areas and one larva (1.9 mm) were found between 7 June and 9 August; during this year, for the first time no eggs or larvae were collected at St. 1.

GENERAL REMARKS. Weakfish eggs showed no pronounced trend of decreasing diameter such as that of anchovy or rockling. The eggs, ranging in size from 0.75 to 0.94 mm, are difficult to distinguish with complete accuracy from butterfish eggs.

Menticirrhus saxatilis. Eggs but no larvae.

No kingfish eggs or larvae were taken in 1954. In 1955 12 eggs were collected on 12 July from the area of the regular stations, the majority being taken at St. 1.

Stenotomus chrysops. Eggs and larvae.

Evidently scup spawned only in the eastern half, since no eggs or larvae were taken west of 73° 05′. About 50 °/o of all eggs occurred in the central region where all of the larvae were taken.

A few well developed eggs were collected between 2 June and 1 July 1954; seven larvae (2.2–3.4 mm) were found in that year: two at St. 3 (VI–7) and five at St. 1 (VII-1). In 1955, between 24 June and 12 July, many more eggs in all developmental stages appeared, the majority from the far eastern end near Plum Gut. These eggs probably came from Peconic Bay. Some miles farther west, St. 1626 at Six-mile Reef provided 81 eggs/m3. Possibly these eggs also drifted from Peconic Bay, but more probably scup find the area of the Reef a good spawning ground. Four larvae (2.4–3.5 mm) were taken at St. 1: one on 23 June, two on 12 July, and one on 28 July.

Tautogolabrus adspersus. Eggs and larvae.

DISTRIBUTION. Although cunners spawned simultaneously throughout L.I.S. in summer, most of the eggs were taken from the western half in 1954–55. The apparent heterogeneous distribution may have resulted from a lack of sampling, particularly in the shallow areas of the eastern end, although within the western region the eggs were most abundant towards the center of the channel rather than along the northern shore. Larvae occurred exclusively in the western half, particularly in the environs of 73° 10′.

In 1954 eggs were taken between 10 May and 30 September; and 48 larvae (1.3–5.0 mm) were collected, 33 throughout July and 15 on 13 August. In 1955 the number of eggs was similar to that in the 1954 collections; they were present from 7 June until 9 August, the majority in the central region. Apparently the delayed appearance was not due to temperature but to the timing of the sampling in the western half. The 1500–B cruise on 26 May took place at the eastern end where the cunner was less prolific. Only ten larvae (1.9–4.7 mm) were taken, one on 28 July and nine on 9 August.

General Remarks. The average egg diameter decreased 0.11 mm through the summer of 1954, but by September the size had increased slightly. Since no eggs were taken in May 1955, the total decrease in diameter hardly could be measured accurately. No significant difference in sizes was noted in eggs from various localities.

Tautoga onitis. Eggs and larvae.

Distribution. Although blackfish eggs were collected more frequently than cunner in the deep regions of the eastern half of the Sound, the greatest abundance still occurred in the western half. In 1954 a few eggs were taken at the Race, but the rest were evenly distributed between 72° 55′ and 73° 35′. A similar distribution was noted in 1955, although the greatest abundance was in the central area. Since no eggs were taken anywhere in the eastern end except at the Race, and then during flood tide or immediately following it, the few eggs found may have originated from Block Island Sound. Due to a net easterly transport of surface water here, such eggs would not be expected to add significantly to the total abundance in L.I.S.

In 1954 eggs appeared between 10 May and 13 August and in 1955 a slightly larger number occurred between 26 May and 9 August. Nine larvae (2.5–3.4 mm) were taken during July 1954 and one (over 3 mm) in late June of 1955.

General Remarks. The average diameter of the eggs decreased erratically in 1954 but progressively in 1955. In 1954 the range decreased from 1.06–1.12 mm in May to 0.85–1.09 mm in August, whereas in 1955 the range in May was 1.01–1.14 mm and declined to 0.91–0.99 mm in August.

Ammodytes americanus. No eggs, many larvae.

Distribution. The 1954 sand eel spawning season was well underway before the fortnightly cruises began. Larvae totalling 112 (4.0–15.2 mm), the first of which appeared on 9 December (1953), were collected before March at the regular stations throughout the winter. Beginning in March, only two larvae (17.9 and 19.1 mm) were taken east of 72° 50′, and during April 1954 there were no areas of marked abundance, presumably because the larvae had already drifted away from the spawning areas.

In January 1955 many more larvae were taken at 73° 15–25′ than in any other area, the greatest number being found off Eaton's Point on the south shore; the February sampling was incomplete; by March and April the larvae were again well scattered throughout the western half.

General Remarks. In the 1954 season larvae (4.0–20.4 mm) were found between 9 December (1953) and 27 April. Of the total number, 41 % were taken by 3 March and 84 % by 30 March. In the 1955 season a great number (4.3–37.0 mm) were taken between 2 December (1954) and 22 April, 82 %

before 3 March, and 86% by 25 March. Variations in spawning, survival, rate of development, availability of food, or the possibility of two successive spawning groups of fish perhaps accounted for these fluctuations in abundance at different times. Covill (in this volume) examined the feeding habits of the larvae and the possible effect of the size of the plankton bloom on the annual abundance of larvae; he concluded that some factor other than availability of food caused the decrease in abundance.

Poronotus triacanthus (?). Eggs and larvae.

DISTRIBUTION. Identification of butterfish eggs is not at all satisfactory, but a few eggs from offshore stations were classified as butterfish according to the best available evidence. The eggs appeared in the central and eastern regions in 1954 on 17 June, 1 and 2 July, and in 1955 on 24 June, 12 and 29 July. The peak of abundance undoubtedly occurred during the week in June when no samples were obtained.

One larva, 2.6 mm, probably that of butterfish, was taken at St. 3 on 17 June 1954.

GENERAL REMARKS. The egg diameter ranged from 0.61 to 0.81 mm and the usually-single oil globules ranged from 0.16 to 0.21 mm. Although the size and appearance of the embryos differed somewhat from those of weakfish, positive separation is impossible.

Prionotus carolinus. Eggs and larvae, the latter included as *Prionotus* sp.

DISTRIBUTION. The common sea robin spawned throughout the entire Sound. The eggs, seldom taken in large quantity at any one location, were consistently found in small quantities at nearly all locations. They were most abundant in the east-central region and least abundant in the far western end. All larvae were taken west of 73° 20′.

In 1954 eggs first appeared on 1 June and thereafter in half of the samples until 13 August. In 1955 they occurred in more widely spaced localities in half of the samples from 7 June until 9 August. Ten larvae were taken: seven (2.4–4.6 mm) in 1954 from the central region and three in 1955 (1.6 mm with broken tail–4.0 mm) from west of the central region, at St. 1 and at the Race.

GENERAL REMARKS. A slight decrease in average egg diameter was noted during both seasons; 1.14 to 1.02 mm in 1954, 1.07 to 1.03 mm in 1955.

Prionotus evolans. Eggs and larvae, the latter included under *Prionotus* sp. and listed under *P. carolinus*.

A few eggs of the striped sea robin were concentrated in the western half of the Sound. In 1954 there were 11 eggs in four samples between 2 June and 13 August, but in 1955 only one egg was found, that on 7 June. The basis for identification has been described by Wheatland (1956).

Myoxocephalus octodecimspinosus and *aeneus* (?). Only larvae.

Sculpin larvae taken in the spring (April 1954, February–April 1955) were frequently found at both ends of the Sound. Early in the season the larvae in the eastern half tended to be larger than those at the western end.

TABLE X. List of Sculpin Larvae from L.I.S., Tentatively Identified to Species.

Date	St.	Area	Length of Larvae	Tentative Identification
IV–1–54*..........	411	eastern	8.4	*octodecimspinosus*
IV–1..............	418	central	6.0	*aeneus*
IV–13.............	426	western	5.3	*aeneus*
IV–13.............	429	western	5.9	*aeneus*
II–17–55	1216	eastern	7.5, 7.2	*octodecimspinosus*
III–24	1324	eastern	7.2	*octodecimspinosus*
III–25	1325	eastern	6.3, 7.2	*octodecimspinosus*
IV–6..............	1410	western	6.1	*aeneus*
IV–22.............	1427	eastern	5.9	*aeneus*

* No samples at the eastern end before 1 April.

The large eastern larvae may have developed from eggs spawned from December through January (Morrow, 1951), the smaller western larvae from a later spawning. No differences other than size were noted between these groups of larvae. Newly ripe *M. aeneus* adults were caught by trawl at St. 1 in February and ripening *M. octodecimspinosus* were found there in November and December 1956.

Paralichthys oblongus (?). Eggs (?) and larvae.

Identification of four-spot eggs and larvae awaits clarification. Some eggs occurred in both years well scattered throughout the Sound; these resembled but were smaller than those of *L. aquosa*. They also resembled half developed four-spot eggs which had been kept in the laboratory but which died before hatching.

Thirteen eggs were obtained from five locations between 1 July and 13 August 1954, and six were taken from six different locations between 24 June and 9 August 1955.

One larva (3.2 mm), probably a four-spot, was caught on 13 August 1954 at the western end.

Lophopsetta aquosa. Eggs and larvae.

Distribution. With the exception of *P. americanus*, the windowpane spawned in a greater percentage of all localities in L.I.S. than any other species; the extreme western end of the Sound was the only sampled area where the eggs and larvae were not collected. The spring eggs were distributed from 72° 25′ to 73° 35′, with the greatest abundance in the western third. The less abundant summer and fall eggs were distributed in a more homogeneous fashion; in no area were they particularly abundant except at 73° 25–35′ in October 1954. Presumably because of differences in sampling times, more eggs were found in the eastern half in 1955 than in 1954. During 1954 eggs were taken from 26 April through 2 July and from 13 August through 28 October; the five-week interval in midsummer was inadequately sampled; the majority of these eggs occurred in the western half within which the spring locality of abundance was slightly eastward of that in the fall. In 1955 few eggs were collected between 5 May and 9 September; the majority between 5 May and 29 July was taken from two areas, 72° 05′–73° 05′ and 73° 35′; the others, taken only during the first week of September, were scattered throughout the eastern half in small quantities.

Few larvae were collected in either year, these from the central and eastern sectors only. Only two larvae (2.8 mm) were collected in 1954, one from St. 1 on 1 July and one from near the Race on 15 October. Six (1.7–3.5 mm) were found in 1955 on 23 and 24 June, 29 July, and 27 October, all between St. 1 and just west of the Race. None was found west of Sts. 1 and 3.

GENERAL REMARKS. Egg diameters ranged from 0.96 to 1.26 mm, but those below 1.00 mm, taken in summer, were difficult to separate from eggs of *P. oblongus*. The average diameter decreased during spring and summer. Although they were smaller in the fall, the measurements fluctuated by virtue of the small numbers available.

The fact that there are higher water temperatures in fall than in spring probably increases the speed of egg development which in turn might result in less total egg predation during fall. However, such a situation apparently has no selective advantage, since most of the eggs were taken every spring.

Pseudopleuronectes americanus. Only larvae.

So far as we know, the winter flounder, one of the common species of the area, remains within the confines of L.I.S. or its estuaries during the spawning season. In the past four years larvae have been found in nearly every locality within the Sound, but in surprisingly small numbers. This suggests that the majority of the spawning probably occurred in shallow areas that were not sampled.

In 1954 32 larvae (2.9–7.2 mm) were collected with the 12.3-cm net between 30 March and 10 May in all parts of the Sound. The majority was taken from the western part in April. In 1955 only 14 (3.2–6.0 mm) were collected between 5 April and 6 May, mostly from the eastern and central regions. The larvae in 1954–55 were not taken as late in the season as in 1952–53. The reason for this remains unknown. The dissimilarity in total numbers and the distribution of adults and larvae have little significance since it is apparent that in neither year were the important centers of larvae sampled.

Sphaeroides maculatus. Only larvae.

Two larvae (3.2, 3.5 mm) were collected at St. 3 on 22 July 1954. Evidently the puffer spawned in quantity in some place other than those sampled, because hundreds of juveniles appeared in the trawl at St. 1 in September-October.

Unknowns. Eggs and larvae.

Three eggs taken in 1955 were not identified. Two from the far western end taken on 6 June were the size of scup but came from too far west; they resembled windowpane but were too small; and they were taken too early to be those of the four-spot. One other, 0.64 mm, taken on 9 August was one of the smallest eggs ever collected in the survey and seemed too late in the season to have been butterfish.

One larva (9.4 mm) taken on 12 October 1955 near Plum Gut is illustrated in Fig. 2. The possibility that this larva is one of the blennies cannot be overlooked, but more material is necessary before positive identification can be made.

Another larva (2.1 mm) taken at the Race on 28 July 1955 is illustrated in Fig. 2 also. Since yellow pigment fades upon preservation, only black pigment is illustrated.

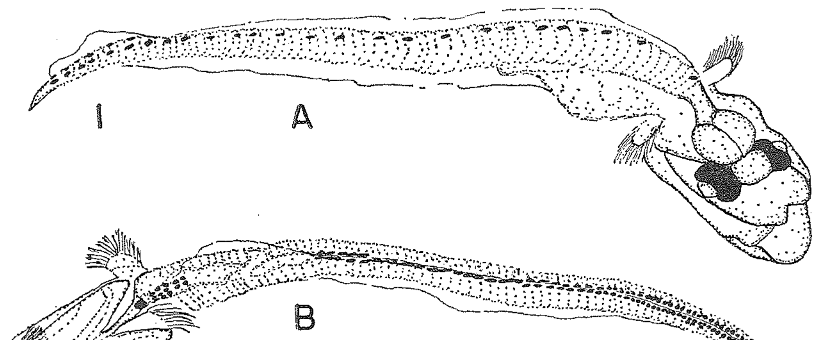

Figure 2. Two unknown larvae: 1 (A–C), dorsal, ventral and lateral views of 9.4 mm specimen taken near Plum Gut on 12 October 1955; 2, lateral view of 2.1 mm larva taken at the Race on 28 July 1955.

SUMMARY OF SPECIES COMPOSITION

Twenty-two species of eggs and larvae are represented in this survey, 15 taken in 1954 and 20 in 1955. The diversity of sampled localities during these years did not increase the number of species above that which was recorded for 1952–53. Five species which were collected during the first two years were not found in 1954–55, but three additional species (five, including both unknowns) were represented by single larvae in 1954–55. Three of the five which occurred only in 1952–53 recurred during the spring of 1956.

Fig. 3 shows the catch distribution by year of the 12 common species taken in the samples of 1954 and 1955. It is apparent from Fig. 3 that in 1954 the

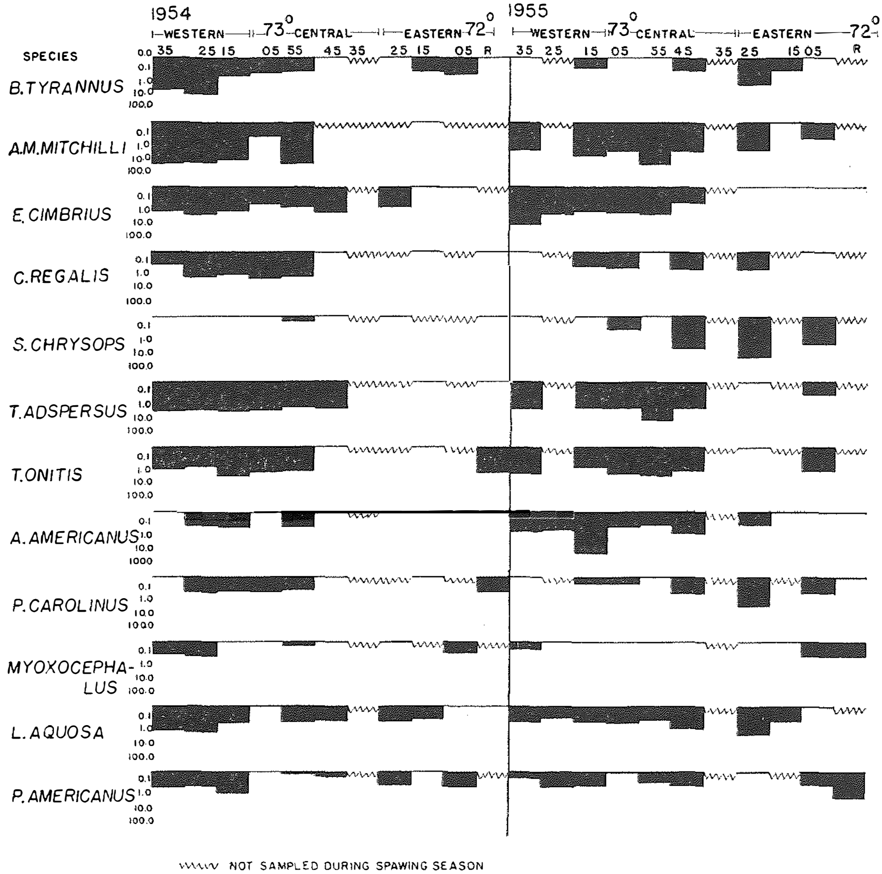

Figure 3. Eggs and larvae per cubic meter of 12 common species which spawned in Long Island Sound in 1954 and 1955 in the western, central and eastern regions.

majority of these common species (*B. tyrannus*, *A. m. mitchilli*, *E. cimbrius*, *C. regalis*, *T. adspersus*, *T. onitis*, *A. americanus*, and *P. carolinus*) spawned most heavily in the western end of the Sound. Of the remaining species, the spawning activity of three (*Myoxocephalus*, *L. aquosa*, and *P. americanus*) was widely scattered; *S. chrysops*, during this year, was taken in only small quantity. In 1955 only four species (*E. cimbrius*, *T. adspersus*, *T. onitis*, *A. americanus*) more or less limited their spawning to the western end, the remaining species scattering their spawning widely. Note that *S. chrysops* during this year was much more abundant than in 1954.

Sampling differences account for some variations in the data. For instance in the eastern end of the Sound, when anchovy were spawning, five areas were not sampled in 1954 whereas in 1955 only two areas remained unsampled. Regarding weakfish, essentially the same number of areas was sampled, but in this case the time of sampling varied; in 1954 the eastern end was sampled in June before the weakfish spawned whereas in 1955 it was sampled in June after they commenced to spawn.

In spite of the sampling differences a few species (*T. adspersus*, *T. onitis*, *S. chrysops*, and *P. americanus*) appeared to be more widely distributed throughout the Sound in 1955 than in 1954. Apparently these differences are not normally explainable on the basis of pronounced variations in environmental conditions. Although *B. tyrannus* and *L. aquosa* normally spawn in both spring and fall, they did not spawn much during the fall of 1955 in the western end; this may have resulted from abnormal meteorological conditions such as those which accompanied the hurricanes that occurred as the spawning seasons of most of the species here considered were coming to a close.

Apparently some species, such as *L. aquosa* and *P. americanus*, find L.I.S. sufficiently homogeneous so that spawning extends throughout the whole area while others, notably *E. cimbrius* and *A. americanus*, definitely limit their spawning to the western half.

SPAWNING BEHAVIOR AND TYPE OF EGGS IN SOUTHERN NEW ENGLAND WATERS

The literature reveals that the average annual cycle in abundance of fish eggs and larvae is roughly similar in all southern New England waters. Throughout spring there is a gradual increase in number and variety of pelagic eggs to a summer peak of abundance which is followed by a decrease in the fall. Excepting *A. americanus*, the larvae follow the same cycle as the eggs with minor variations. Observations indicate that in southern New England waters as a whole more of the recorded species spawn during the warm period (May through October) than during the cold period (November through April). Of the warm weather spawners 79 % are pelagic egg layers, 68 % of which migrate from the south;

TABLE XI. SPAWNING BEHAVIOR, TYPE AND SIZE OF EGGS, AND SIZE OF HATCHING LARVAE OF SPECIES SPAWNING IN SOUTHERN NEW ENGLAND WATERS AND LONG ISLAND SOUND.

	Resident				*Migratory*			
	Northern		Southern		Eastern		Southern	
	No. species	Size (mm)	No. species	Size (mm)	No. species	Size (mm)	No. species	Size (mm)
NOVEMBER THROUGH APRIL								
Southern New England								
Demersal	4		0		2		0	
eggs		1.0 –1.5		–		1.1 –2.6		–
larvae		1.0 –3.1		–		4.0 –7.4		–
Pelagic	1		0		3		0	
eggs		0.87–0.94		–		1.1 –1.8		–
larvae		–		–		2.8 –3.6		–
Long Island Sound								
Demersal	3		0		1		0	
eggs		0.74– ?		–		1.1 –1.4		–
larvae		2.8 –3.7		–		5.0 –6.0		–
Pelagic	0		0		1		0	
eggs		–				0.85–		–
larvae		–				–		–
MAY THROUGH OCTOBER								
Southern New England								
Demersal	1		3		0		1	
eggs		1.1 –1.2		1.2 –2.0		–		0.90
larvae		3.8 –5.0		2.0 –7.7		–		1.8
Pelagic	4		2		3		10	
eggs		0.76–1.25		0.70–1.0		0.72–1.8		0.70–1.6
larvae		2.0 –2.8		1.6		2.0 –4.5		1.7 –3.1
Long Island Sound								
Demersal	1		0		0		1	
eggs		1.1 –1.2		–		–		0.90
larvae		5.0		–		–		1.8
Pelagic	4		2		0		7	
eggs		0.90–1.35		0.70–1.0		–		0.70–1.6
larvae		1.8 –2.2		1.6		–		2.4 –3.1

Note. This table does not include the Syngnathidae or Anguillidae or species of which little is known. The L.I.S. group does not include species which rarely enter, such as *G. morrhua.*

the other 21 °/₀ lay demersal eggs and are primarily residents, only *S. maculatus* being a migrant from the south. Of the cold weather spawners 60 °/₀ lay demersal eggs, 66 °/₀ of these being northerly residents; the winter pelagic spawners are few in number and all are migrants from eastern or northern areas. With the exception of the puffer, the demersal eggs and hatching larvae of the warm period are on the whole larger than those of the pelagic spawning species, whereas eggs of cold weather demersal spawners are not appreciably larger than the eggs of winter pelagic spawners. Cold weather pelagic eggs are a little larger than the summer pelagic eggs, and the hatching larvae are longer.

In L.I.S. the same general pattern obtains. Although the number of species that are definitely known to spawn within its boundaries is small, residents producing demersal eggs spawn in winter and spring and migratory species with pelagic eggs spawn in summer, the latter being present in greater variety and numbers. While anchovy eggs form a large increment of the increased summer abundance, it is apparent that there is an increase in the other species also. Pelagic eggs and larvae of winter spawners such as *Gadus morrhua* are seldom taken in L.I.S., but such species do migrate into Block Island Sound from the east.

Species laying pelagic eggs in summer are almost equally divided between residents and migrants. Most residents commence to spawn early in the warm season when the temperature is still low for southern migrants, but nevertheless the size of their slowly developing eggs and hatching larvae is only slightly greater than the size of the products of summer migrants. Possibly the slightly smaller larvae of summer spawning migrants and of residents have a more rapid metabolism and a more limited power of swimming than the larger resident species, and possibly smaller larvae can use the increasing supply of zooplankton rather efficiently. For example, anchovies 3.1 mm long, with no fin development, are able to catch and devour the abundant copepod nauplii.

From observation in L.I.S. it appears that the reduced rate of metabolism and a presumed greater swimming ability of the larger larvae produced in cold weather may provide them with a feeding advantage at a time when minimum amounts of zooplankton are present (October–February). *A. americanus* and *P. americanus*, on the basis of present data, provide conflicting yet interesting speculation concerning this idea. The larvae of *A. americanus*, which hatch from demersal eggs laid in cold weather, feed on phytoplankton in winter while in the size range of 3–5 mm, and subsequently they subsist almost entirely on zooplankton. In studies of the stomach contents, Covill (in this volume) found in 200 specimens a low percentage of empty stomachs. On the contrary, it was found that the larvae of 66 *P. americanus*, which also hatch from demersal eggs laid mostly in cold weather, had a high percentage of empty stomachs, suggesting that these larvae feed less efficiently on zooplankton than do the larvae of *A. americanus*. The fact that they appear after the spring flowering when zooplankton is on the increase should give them a feeding advantage even though they hatch at less than 3 mm, a smaller size than *A. americanus*. However, as noted previously, few *P. americanus* larvae have been taken in deep waters, which suggests that they normally inhabit inshore areas which are not regularly sampled. Further, one might reasonably expect, in the case of the flounder, that an increase in swimming ability would coincide with metamorphosis. These factors suggest then that the larvae of *P. americanus* may well find a more suitable source of food inshore and that they are not adequately equipped for competition with open water species until after metamorphosis.

In summary, it appears that in temperate regions the larvae from small eggs may survive best in summer while the large larvae from demersal eggs or large pelagic eggs may survive well in winter. Since the northern species are as limited by temperatures as those from the south, spawning of the former takes place in winter and of the latter in summer. The type and size of egg appears to be adapted for the seasonal conditions under which the larvae have to develop.

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Сара В. Ричардс

Яйца и личинки пелагических рыб пролива Лонг Исланд Соунд

Краткий обзор

Яйца и личинки 22 видов пелагических рыб были собраны на всем протяжении пролива в 1954–1955 г. Сравнение данных этих лет с данными 1952–1953 г. показало что сезонные циклы яиц и личинок те же, весною с постепенным возрастанием количества и разнообразия, достижением максимума летом и уменьшением осенью. Зимою яиц не было, а из личинок попадался только один вид в изобилии *(A. americanus)*. Было так же установлено что в каждом году были собраны яйца и личинки тех же видов рыб. Колебания в количестве яиц и личинок несомненно зависило от многообразных причин, от колебаний во взрослых населениях, в состоянии окружающей среды, в числе хищников и т.д. Колебания в годовых количествах зависели от колебаний в количестве яиц и личинок более обычных вилов, в особенности *A. m. mitchilli.*

Большинство видов рыб метали икру в продолжении всего года больше в западной половине пролива, чем в его центральной и восточной части, за исключением осени 1955 г., когда беднота яиц и личинок была вероятно последствием урагана. Сравнение данных станции Но. 1, где большинство сборов были сделаны в 1952–1955 г. с общими данными всего пролива показало соответственные колебания в количестве яиц и личинок всех видов рыб. Но в отдельных случаях значительные колебания были найдеы только в одном виде – *E. cimbrius.*

Хотя яйца некоторых видов рыб к концу икрометания были меньшаго размера чем в начале, общий обьем отложенных яиц возрастал пропорционально с их возрастающим числом. Это приводит к выводу что у видов мечущих икру летом большия личинки из больших яиц не имеют никакого преимущества над маленькими личинками из маленьких яиц так как выклев последних приурочен к сезону наибольшаго богатства пищи *(vide A.m. mitchilli)*.

Местные и проходные виды рыб распространенных преимущественно на юг от мыса Кэп Код с маленькими яйцами и личинками мечут икру в теплой половине года когда и температура и зоопланктон возрастают. Виды живущие главным образом на север и на восток от мыса с большими пелагичесеними и придонными яйцами и с большими личинками мечут икру в холодной половине года.

Food and Feeding Habits of Larvae and Postlarvae of Ammodytes americanus,

1952-1955

R. Wade Covill

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TABLE OF CONTENTS

ABSTRACT

The stomachs of 200 *Ammodytes americanus* larvae, 3.2–23.1 mm, were observed for food content and composition. Diurnal, seasonal, and annual variations, as well as effects of size and location of capture, were studied. Several aspects of the nutrition of larvae were also considered.

Comparison with data from other investigations showed a much lower incidence of empty stomachs in the L.I.S. specimens. Particulate material, especially copepods and their nauplii, was apparently more important than dissolved food material in the nutrition of these larvae;

phytoplankton was also an important item, especially in young larvae. Major variations in stomach contents were due to size. Minor annual and monthly variations were also noted. Obviously larvae must ingest a considerably greater quantity of food per day for growth than that indicated by an analysis of this nature.

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INTRODUCTION

For a number of years the staff of the Bingham Laboratory has been engaged in a study of the ecology of Long Island Sound (L.I.S. hereafter), and bit by bit more information has been added to the fund of knowledge which is essential to a more thorough understanding of the complex relationships of the components that make up the ecosystem. Many gaps in our basic knowledge still remain, among them an estimate of the extent to which fish larvae participate in the over-all picture and how they contribute to the efficiency of energy transfer between trophic levels.

For the New England area there are but few systematic studies of the food relationships of fish larvae and of the effects of environmental variables on either the quality or quantity of food ingested. Over the years a substantial volume of data on the diets of some larvae has been accumulated, but most of the basic problems of ecology remain unanswered. The present study, which examines in detail the economy of a single species, the American sand eel (*Ammodytes americanus*), has been undertaken in the hope of contributing, in small part at least, basic information toward a more comprehensive understanding of the entire productivity of the Sound.

A. americanus, a schooling fish, is common over sandy shoal areas and beaches from Labrador to Cape Hatteras. Adults reach a size of four to six inches and are an important constituent in the diet of many commercial food fish such as cod, haddock, mackerel, and striped bass (Bigelow and Schroeder, 1953). Little has been published on the American sand eel except for occasional references to it in faunal studies.

In L.I.S., adults have not been commonly taken along the Connecticut shore; however, in summer they may be collected in quantity along the shore of Long Island. From December through April 1956–57 adults were taken by otter trawl from depths of 12 to 35 feet in waters off Milford and New Haven, Connecticut (Richards, unpubl.).

The sand eel larvae, second in abundance in L.I.S., commonly occur in the western half. Since the adults spawn in late fall, probably November (Wheatland, 1956), the eggs hatch in winter when one might expect conditions to be unfavorable for survival, *i.e.*, when there is a minimum of plankton. Larvae have been collected in L.I.S. from December through the following April, a comparatively long larval period which affords study of the feeding habits of a single species over a very wide range of environmental changes.

MATERIALS AND METHODS

The material used in this study was taken in routine oblique plankton tows by means of a 12.5 cm net, with No. 2 or No. 10 mesh, attached to a Clarke-Bumpus plankton sampler. During March and April 1952, 15-minute tows were made at weekly intervals at Sts. 1, 2, 5, and 8 (see Richards, fig. 1 in this issue). Such tows were continued at Sts. 1 and 2 through April 1954 while biweekly tows were made at Sts. 5 and 8. Special night tows were made with a closing net at two different depths in March 1954 (St. 418). The 1955 material was taken from a series of stations designated 1018, 1023, 1129, 1304, 1306, 1310, and 1328. All material was preserved immediately in a 10 % solution of neutralized formalin and sea water.

Each specimen used for stomach analysis was measured and placed in a watch glass containing distilled water, after which the gut was dissected away from the body by means of fine wire teasing needles under a low power dissection microscope. Before analysis, the gut was measured and transferred intact to a clean watch crystal containing distilled water. The gut, a straight tube of uniform diameter extending from esophagus to anus, was cut under high power magnification into thin doughnut-shaped segments which were then laid over so that the lumen could be adequately examined for food remains. In this way virtually none of the gut content escaped detection.

The contents were identified and counts were made of all recognizable organisms. In addition to a qualitative analysis, the relative degree of stomach fullness was estimated for each gut and classified according to four general categories: empty, trace to 25 % full, 25 to 50 % full, and more than 50 % full. In such cases where a gut was broken prior to dissection, the data were recorded but not used in the final analysis.

Of the 744 specimens of *A. americanus* taken in plankton samples from March 1952 to March 1955 (3.2 to 37.0 mm), 200 were selected for analysis according to the sampling plan presented in Table I. This plan enabled an analysis of the

TABLE I. Number of *A. americanus* Larvae Stomachs Analyzed by Size Categories (in mm) During Each Month of the Spawning Season in L.I.S. from 1952–1955, Showing Offshore and Inshore Distribution* and the Time of Capture.

Length groups, mm	3.2-4.9	5.0-9.2	9.3-13.0	13.1-16.0	16.1-19.5	19.6-23.1	Totals
1952 Spawning season							
Mar.	6	5	5	5	2	2	25
Apr.	0	15	12	14	5	1	47
							72
Offshore	6	14	15	14	6	2	57
Inshore	–	5	2	5	1	1	14
							71
Time of capture							
0900–1130	0	14	14	11	4	3	46
1130–1400	0	1	0	3	1	0	5
1400–1630	6	4	3	5	2	0	20
night	0	0	0	0	0	0	0
							71
1952–1953 Spawning season							
Dec.	0	2	0	0	0	0	2
Jan.	0	6	2	0	0	0	8
Feb.	0	0	3	1	0	0	4
Mar.	0	0	4	4	2	0	10
Apr.	0	0	0	1	2	0	3
							27
Offshore	–	6	7	5	3	–	21
Inshore	–	2	2	1	1	–	6
							27
Time of capture							
0900–1130	0	4	8	5	2	0	19
1130–1400	0	4	0	1	2	0	7
1400–1630	0	0	1	0	0	0	1
night	0	0	0	0	0	0	0
							27
1953–1954 Spawning season							
Dec.	6	5	0	0	0	0	11
Jan.	1	2	4	0	0	0	7
Feb.	0	3	2	3	0	0	8
Mar.	0	1	0	2	2	2	7
Apr.	0	0	2	0	2	1	5
							38
Offshore	5	9	7	4	4	3	32
Inshore	2	2	–	1	–	–	5
							37

(cont.)

TABLE I. (cont.)

Length groups. mm	3.2-4.9	5.0-9.2	9.3-13.0	13.1-16.0	16.1-19.5	19.6-23.1	Totals
Time of capture							
0900–1130	6	7	6	3	0	0	22
1130–1400	1	2	1	0	1	1	6
1400–1630	0	2	0	1	0	0	3
night	0	0	0	1	3	2	6
							37
1954–1955 Spawning season							
Dec.	1	1	0	0	0	0	2
Jan.	7	19	23	1	0	0	50
Mar.	0	2	6	1	2	0	11
							63
Offshore	–	–	–	–	–	–	–
Inshore	–	–	–	–	–	–	–
Time of capture							
0900–1130	1	0	0	0	0	0	1
1130–1400	8	21	29	2	2	0	62
1400–1630	0	0	0	0	0	0	0
night	0	0	0	0	0	0	0
							63
Totals	21	61	63	32	17	6	200
Percent	11.5	30.5	31.5	16.0	8.5	3.0	100.

* Numbers here used represent only the data actually employed in the study of offshore-inshore distribution (see page 141).

nature and amount of food ingested and of the effect of the variables discussed under FOOD AND FEEDING HABITS: for March and April 1952, 72 specimens were observed; for December 1952 through April 1953, 27 specimens; for December 1953 through April 1954, 38 specimens; for December 1953 through March 1955, 63 specimens. These quantities were considered adequate for this study.

Since *A. americanus* larvae are commonly found in L.I.S. for as long as five consecutive months, the specimens were selected so as to represent each month as equally as possible. Larvae were measured and placed in size length categories as listed in Table 1. Each length category was selected according to observed "natural" length groups in the sample.

Wheatland (1956) noted that *A. americanus* larvae in L.I.S. were taken more frequently at offshore than at inshore stations. Accordingly, specimens were selected so as to sample both areas adequately to ascertain whether or not feeding was a factor in determining such distribution. Specimens were selected, within the framework of the other variables, to represent morning, mid-day, afternoon, and night periods.

FOOD AND FEEDING HABITS

Food of Larvae. Between 1918 and 1921 Lebour (1918, 1919, 1920, 1921) analyzed the stomach contents of 246 larvae of *A. tobianus* and *A. lanceolatus*, two European species closely related to *A. americanus*. She found that the majority of the guts were empty or contained traces of unidentified materials which she conveniently termed "green food remains". Few larvae less than five mm contained any food whatsoever and only larvae greater than 10 mm contained copepods or gastropod larvae.

TABLE II. Seasonal Variations in the Quantity of Food Remains in *A. americanus* Stomachs, L.I.S., 1952–1955.

	Dec.	Jan.	Feb.	Mar.	Apr.	Total No. and °/₀
No. and °/₀ of specimens	2	5	0	2	4	13
with empty stomachs	13.3	7.7	0.0	3.8	7.3	6.5
No. and °/₀ of specimens	8	19	7	17	24	75
with trace to 25 °/₀ fullness ..	53.5	29.2	58.3	32.1	43.6	37.5
No. and °/₀ of specimens	3	22	4	26	14	69
with 25 to 50 °/₀ fullness	20.0	33.8	33.3	49.1	25.5	34.5
No. and °/₀ of specimens....	2	19	1	8	13	43
with more than 50 °/₀ fullness	13.3	29.2	8.4	15.1	23.6	21.5
Total no. of specimens	15	65	12	53	55	200
Percent of specimens	7.5	32.5	6.0	26.5	27.5	100.0

In the present study only 6.5 °/₀ of the stomachs were devoid of food remains. The remaining 93.5 °/₀ contained quantities of food varying from trace amounts to quantities occupying 75 °/₀ of the gut. Table II shows the percentages of stomachs in each month's sample in each of the categories of fullness.

Table III summarizes the eight kinds of food remains recorded from stomachs; it also gives the percentages of each according to size.

One to 29 copepod nauplii were found in 59.0 °/₀ of the guts examined. One postlarva (29.4 mm), which has not been included in Table III because of its size, contained 237 copepod nauplii in addition to several late-stage copepods; this serves to illustrate the maximum extent of feeding. The majority of feeding larvae contained from one to 12 nauplii, depending on its size (see Table III). The average number of nauplii in a single larva was 6.2, approximately 5 °/₀ of these being *Temora longicornis*. Those not identified were presumed to be nauplii of some of the other copepod species which are dominant in L.I.S. (see Deevey, 1956).

Copepods, including copepodid stages, were encountered in 39.5 °/₀ of the guts examined, and identification of at least one copepod was possible in almost

TABLE III. PART A, NUMBER AND PERCENT OF LARVAE IN WHICH THE DIFFERENT FOOD ORGANISMS WERE POUND. PART B, VARIATIONS IN STOMACH FULLNESS.

Length groups, mm	3.2–4.9	5.0–9.2	9.3–13.0	13.1–16.0	16.1–19.5	19.6–23.1	Total No. and °/₀
No. larvae examined	21	61	63	32	17	6	200
PART A – STOMACH CONTENTS							
Copepods, adults (total)...	0	7	26	25	16	5	79
Percent of larvae with:	0.0	11.5	41.3	78.1	94.1	83.3	39.5
Av. no./gut	0	1.1	1.7	3.1	4.2	5.2	2.8
No. of specimens ident.							
Acartia sp.	–	–	3	4	6	3	16
Temora longicornis ..	–	1	4	7	4	2	18
Pseudocalanus minutus	–	–	–	1	1	–	2
Oithona sp.	–	–	–	2	–	–	2
Paracalanus sp.	–	–	–	–	1	–	1
Copepods, nauplii (total)..	4	31	47	24	11	1	118
Percent of larvae with:	19.0	50.8	74.6	75.0	64.7	16.7	59.0
Av. no./gut............	1.0	3.0	4.8	12.0	11.2	2.0	6.2
No. of specimens ident.							
T. longicornis	–	5	10	4	4	–	23
Invertebrate eggs	3	7	10	12	7	0	39
Percent of larvae with:	14.3	11.5	15.9	37.5	41.2	0.0	19.5
Av. no./gut............	3.0	3.3	2.2	5.1	3.0	0	3.5
Cladocerans	0	0	0	1	0	0	1
Percent of larvae with:	0.0	0.0	0.0	3.2	0.0	0.0	0.5
Phytoplankton, unident...	17	31	39	2	1	1	91
Percent of larvae with:	81.0	50.8	61.9	6.3	5.9	16.7	45.5
Coscinodiscus sp.	1	5	8	1	1	0	17
Percent of larvae with:	4.8	11.5	12.7	6.3	5.9	0.0	8.5
Diatoms, unident.	1	1	0	0	0	0	2
Percent of larvae with:	4.8	1.6	0.0	0.0	0.0	0.0	1.0
Peridinium sp.	3	2	0	0	0	0	5
Percent of larvae with:	14.3	3.3	0.0	0.0	0.0	0.0	2.5
Av. no./gut............	2.7	3.0	0	0	0	0	2.8
PART B – DEGREE OF FULLNESS							
No. and °/₀ of specimens with:							
empty stomachs	4 19.0	7 11.5	1 1.6	0 0.0	1 5.9	1 16.7	13 6.5
trace to 25 °/₀ fullness..	4 19.0	32 52.5	24 38.1	9 28.1	2 11.8	3 50.1	74 37.0

(cont.)

TABLE III. (cont.)

Length groups, mm	3.2–4.9	5.0–9.2	9.3–13.0	13.1–16.0	16.1–19.5	19.6–23.1	Total No. and %
25 to 50 % fullness....	7	14	27	13	7	2	70
	33.3	23.0	42.9	40.6	41.2	33.4	35.0
more than 50 % fullness	6	8	11	10	7	0	43
	28.7	13.1	17.5	31.3	41.2	0.0	21.5
Total number............	21	61	63	32	17	6	200
Total percent............	10.5	30.5	31.5	16.0	8.5	3.0	100.0

50 % of the specimens. Further identification was complicated by partial digestion and by the high incidence of copepodid stages that were not easily identified. Among the identified, *Temora longicornis* and *Acartia clausii* were about equal in importance, whereas species of *Pseudocalanus*, *Oithona*, and *Paracalanus* were represented by only one or two individuals. It is probable that many of the unidentified copepods were of these genera.

Three types of invertebrate eggs which were tentatively identified as copepod were found in 19.5 % of the stomachs examined: 1) A spherical egg, 50 μ in diameter, with a clear hyaline layer surrounding the embryo; 2) a darkly colored spherical egg, 75–80 μ in diameter; 3) a light brown or tan elliptical egg 60 by 90 μ in diameter.

No significant correlation was found between the presence of copepods and invertebrate eggs in individual stomachs when an attempt was made to determine if the eggs, assumed to be those of copepods, were ingested separately or accidently along with gravid copepods. It is problematical whether eggs were taken separately, collectively in egg sacs, or with gravid females. In the case of small larvae (3.2–9.2 mm), it is probable that eggs were ingested independently, since these larvae did not feed on mature egg-bearing copepods. It is also quite possible that one or more of the eggs described may belong to some other common invertebrate. Although only 19.5 % of the stomachs contained invertebrate eggs, it is worthy of note that larvae which feed on eggs have generally ingested several, between two and five on an average. This may indicate either the ingestion of a group of eggs in an egg sac or a selective feeding behavior. Unfortunately eggs pass freely through the meshes of the net so that no comparison can be made with plankton tows to determine if copepod eggs were particularly abundant at specified times.

Unidentifiable material of plant origin, no doubt similar to that described by Lebour (1918), Wiborg (1948), and others working with fish larvae, was found in 45.5 % of the guts. In general the unidentified matter taken from specimens collected in January and February was greenish in color and was probably phytoplankton remains, or what Lebour calls "green food remains".

The siliceous skeletal remains of diatoms of the genus *Coscinodiscus*, commonly imbedded in large masses of this material, were found in 8.5 % of the stomachs examined; in only a few isolated instances were *Coscinodiscus* and other diatoms found exclusive of unidentifiable plant material.

Peridinians were encountered in only 2.5 % of the stomachs examined; in all cases they were observed in larvae of less than nine mm which were taken in January or February. It is interesting to note that in the few stomachs which contained peridinians, the average number per gut was 2.8, indicating an apparent importance of this food to the individual organism at the time. To the larvae collectively, peridinians were of negligible importance.

Annual Variations. Marked variations in abundance of *A. americanus* larvae were noted in L.I.S. during 1952–55, the numbers in 1953 being clearly lower than those taken in any of the other years (Wheatland, 1956). The limitations of the sampling in L.I.S. are obvious, but the estimates are at least indicative of the magnitude of the annual variations although they cannot be used as figures of absolute abundance.

Note in Table IV that a decrease in the quantity of stomach contents accompanied the 1953 decrease in numbers of larvae. Twice as many empty guts were encountered in 1953 as in any other year, and of the remaining stomachs almost 60 % were less than 25 % full. Only 25.9 % of the stomachs in 1953 were more than 25 % full as compared with figures of 52.6–68.3 % for the other three years. Comparison of comparable data for 1952, 1954, and 1955 showed no significant differences in the relative quantities of larvae or in the amount of food present. The larvae found in March and April 1952 were more abundant but smaller than those in the corresponding period in 1953, but these differences obviously were not the primary factors effecting the relative amounts of food in the stomachs.

Analysis of annual qualitative data for stomach contents showed considerable annual variation, but much of this was due to differences in the seasonal distribution of larvae between the years; *e.g.*, the high percentage of stomachs containing phytoplankton remains in the 1955 spawning season (87.3 %) was due primarily to the large sample (50 specimens) taken at St. 1129 in January. The only other major difference was the high percentage of stomachs containing invertebrate eggs in March and April 1952, also attributable to unequal seasonal distribution. The copepods and their nauplii, which constituted the bulk of the sand eel's diet, were found about as commonly in 1953 as in the other years. Therefore it appears extremely unlikely from this evidence that the composition of the diet seriously effected the decreased abundance of larvae in 1953.

On the theory that a poor food supply may have influenced the survival of young fish and may have been responsible for the small quantity of larvae in 1953, further analysis was made to determine whether the food supply in winter

TABLE IV. PART A, STOMACH CONTENTS OF *A. americanus* LARVAE IN L.I.S., 1952–1955. PART B, ANNUAL VARIATIONS IN THE DEGREE OF STOMACH FULLNESS.

	Mar.-Apr. 1952	Dec.1952 -Apr.1953	Dec.1953 -Apr.1954	Dec.1954 -Mar.1955	Total No. and %
Average number of larvae/m3	1.25	0.13	0.46	1.02	0.71
No. larvae examined	72	27	38	63	200
PART A – STOMACH CONTENTS					
Copepods, adults (total)...	34	11	15	19	79
Percent of larvae with:	47.2	40.7	39.5	30.2	39.5
No. of specimens ident.					
Temora longicornis...	8	4	2	4	18
Acartia sp.	9	3	3	1	16
Pseudocalanus minutus	–	2	–	–	2
Oithona sp.	–	–	–	2	2
Paracalanus sp......	–	–	1	–	1
Copepods, nauplii (total)..	53	17	18	30	118
Percent of larvae with:	73.6	63.0	47.4	47.6	59.0
No. of specimens ident.					
Temora nauplii	8	2	5	5	23
Invertebrate eggs.........	31	3	2	3	39
Percent of larvae with:	43.1	11.1	5.3	4.8	19.5
Cladocerans	1	0	0	0	1
Percent of larvae with:	1.4	0	0	0	0.5
Phytoplankton, unident...	15	5	18	55	91
Percent of larvae with:	20.8	18.5	47.4	87.3	45.5
Coscinodiscus sp.	0	4	1	12	17
Percent of larvae with:	0	14.8	2.6	14.3	8.5
Diatoms, unident.	1	0	1	0	2
Percent of larvae with:	1.4	0	2.6	0	1.0
Peridinium sp............	0	0	2	3	5
Percent of larvae with:	0	0	5.3	4.8	2.5
PART B – DEGREE OF FULLNESS					
No. and % of specimens with:					
empty stomachs	4	4	3	2	13
	5.6	14.8	7.9	3.2	6.5
trace to 25% fullness..	25	16	15	18	74
	34.7	59.3	39.5	28.6	37.0
25 to 50% fullness....	27	5	13	25	70
	37.5	18.5	34.2	39.7	35.0
more than 50% fullness	16	2	7	18	43
	22.2	7.4	18.4	28.6	21.5
Total no.	72	27	38	63	200
Total %.................	36.0	13.5	19.0	31.5	100.0

and spring of 1953 was significantly lower than that of other years. There were no differences in the amount of winter and spring plankton available to the 1953 larvae, nor were there any significant differences in the composition of winter plankton between 1953 and the other years studied (Deevey, 1956; Conover, 1956). Therefore, the low number of larvae was probably not associated directly with the quantity or kinds of food available to the sand eel. It is possible that low populations of *A. americanus* larvae in 1953 resulted from factors quite apart from the food supply, such as poor spawning conditions or high egg mortality. No plausible explanation for the occurrence of small stomach content at a time of poor year class is apparent. But it may indicate some as yet unknown obscure factor of importance in determining the relative size of year classes.

Seasonal Variations. During winter and early spring the absolute and relative abundance of various phytoplankton and zooplankton organisms in L.I.S. undergo marked fluctuations. Deevey (1956) reported that numbers of zooplankton organisms were usually minimal in December and January, not becoming abundant before late spring or early summer. The phytoplankton, on the other hand, began to bloom early in February (Conover, 1956). Measurements of phytoplankton chlorophyll and zooplankton displacement volumes have shown a great increase in the over-all plankton through winter and spring as well as a "lag" in the zooplankton cycle.

In order to determine what effect these variations in quantity and composition of the plankton might have on the diet of fish larvae, the data were divided into two seasonal periods. Table V shows the types of food found in the stomachs of 92 larvae taken in December, January, and February and of 108 larvae taken in March and April 1952–55; the percentage of guts in each size category containing the food item is listed in the left-hand column. Comparison must be made according to each size category, since the average size increased with time during the whole season; an unsatisfactory picture might otherwise result due to the use of food selection as a function of size.

Phytoplankton was of great importance in the early period. In fact, more than three times as many larvae in the 5.0–16.0 mm size categories fed on green foods in the earlier period as compared to the later period. Peridinians were found in small numbers in larvae of 3.2–9.2 mm only in January and February.

Invertebrate eggs (probably copepod) were found almost entirely in larvae taken in late spring. Due to their small size relative to other food items, it is doubtful whether these eggs were ever important in the sand eel's diet.

Of the animal remains, copepod nauplii were found in 20 % fewer guts during winter (December–February) than during spring, whereas adult copepods appeared to be equally important food items in the three size categories (5.0–16.0 mm) during both winter and spring. According to Deevey (1956), her No. 10 net collections showed that only about a third of the January

TABLE V. Stomach contents of *A. americanus* Larvae in L.I.S., 1952–1955, from Winter (Dec.–Feb.) and Spring (Mar.–Apr.) periods. Number and Percent of Larvae in which the different Organisms were found.

Length groups in mm	3.2–4.9		5.0–9.2		9.3–13.0		13.1–16.0		16.1–19.5		19.6–23.1		Total	
	(D–F)	(M–A)	(D–F)	(M–A)	(D–F)	(M–A)	(D–F)	(M–A)	(D–F)	(M–A)	(D–F)	(M–A)	(D–F)	(M–A)
No. larvae examined....	15	6	38	23	34	29	5	27	0	17	0	6	92	108
Copepods, adults (total)	0	0	2	5	14	12	4	21	–	16	–	5	20	59
Percent of larvae with:	0.0	0.0	5.3	21.7	41.2	41.4	80.0	77.8	–	94.1	–	83.3	21.7	54.6
No. of specimens ident.														
Acartia sp.	–	–	–	–	2	1	1	3	–	6	–	3	3	13
Temora longicornis	–	–	–	1	1	3	1	6	–	4	–	2	2	16
Pseudocalanus minutus.	–	–	–	–	–	–	–	1	–	1	–	–	–	2
Oithona sp.	–	–	–	–	1	1	–	–	–	–	–	–	1	1
Paracalanus sp.	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Copepods, nauplii (total)	1	3	16	15	22	25	3	21	–	11	–	1	42	76
Percent of larvae with:	6.7	50.0	42.1	65.2	64.7	86.2	60.0	77.8	–	64.7	–	16.7	45.7	70.4
No. of specimens ident.														
T. longicornis	–	–	1	4	4	6	–	4	–	4	–	–	5	18
Invertebrate eggs.......	0	3	1	6	2	8	0	12	–	7	–	0	3	36
Percent of larvae with:	0.0	50.0	2.6	26.1	5.9	27.6	0.0	44.4	–	41.2	–	0.0	3.3	33.3
Cladocerans, unident....	0	0	0	0	0	0	0	1	–	0	–	0	0	1
Percent of larvae with:	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	–	0.0	–	0.0	0.0	0.9
Phytoplankton, unident.	13	4	26	5	31	8	1	1	–	1	–	1	71	20
Percent of larvae with:	86.7	66.6	68.4	21.7	91.2	27.6	20.0	3.7	–	5.9	–	16.7	77.2	18.5
Coscinodiscus sp.	1	0	5	0	7	1	0	2	–	1	–	0	13	4
Percent of larvae with:	6.7	0.0	13.2	0.0	20.6	3.4	0.0	7.4	–	5.9	–	0.0	14.1	3.7
Diatoms, unident.	0	1	1	0	0	0	0	0	–	0	–	0	1	1
Percent of larvae with:	0.0	16.7	2.6	0.0	0.0	0.0	0.0	0.0	–	0.0	–	0.0	1.1	0.9
Peridinium sp.	3	0	2	0	0	0	0	0	–	0	–	0	5	0
Percent of larvae with:	20.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	–	0.0	–	0.0	5.4	0.0
Empty stomachs........	3	1	4	2	0	1	0	0	–	1	–	1	7	6
Percent of larvae with:	20.0	16.7	10.5	8.7	0.0	3.4	0.0	0.0	–	5.9	–	16.7	7.6	5.6

population consisted of nauplius forms whereas in March about two thirds were nauplii.

Although utilization of phytoplankton and invertebrate eggs may have been associated with seasonal factors, mature copepods, which comprised the vast bulk of the diet, were eaten at all times to approximately the same degree, particularly by the large larvae.

The data, also analyzed to determine whether stomachs contained abundant food in months of abundant plankton, provide no evidence to indicate significant differences in the degree of stomach fullness between larvae taken from relatively rich and poor plankton.

Variations with Size. Analyses were carried out to determine what percent of larvae in each of the six size groups fed on a given food organism, how many of such organisms comprised the average stomach content, and what differences existed in relative degrees of stomach fullness between size groups.

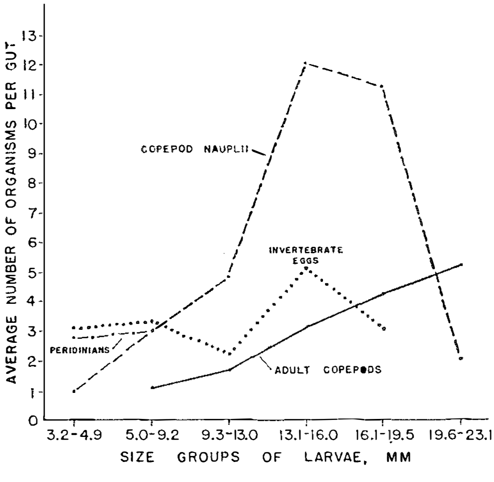

Figure 1. Average numbers of organisms found in guts of different size groups of *A. americanus* larvae in L.I.S., 1952–1955.

In the smallest of the size groups listed, 3.2–4.9 mm (see Table III), there was no food in 19.0% of the 21 guts examined, this being the highest percentage of empty stomachs encountered in this study. Varying amounts of phytoplankton occurred in the remaining 81.0%. *Coscinodiscus* and several unidentified diatoms were commonly found imbedded in the mass of phytoplankton; 14.3% stomachs contained peridinians, with an average of 2.7 per stomach (Fig. 1); also, 14.3% showed an average of three invertebrate eggs; 19.0% contained one copepod nauplius. None contained copepodids or copepods, a fact that is probably explained by the small size of the larvae; mature copepods of the genera *Acartia* and *Temora* measure approximately one and two mm respectively, a size not suitable for ingestion by a three or four mm larva. It is significant that these small sand eel larvae had already begun to feed on the naupliar stages of copepods, which measure approximately 0.1–0.3 mm.

In the second size category, 5.0–9.2 mm, 61 larvae were studied, and a noticeable change was found in the feeding of this group. Phytoplankton was found in only 50.8 % as compared with 81.0 % in the 3.7–4.9 mm category. *Coscinodiscus* and a few stray cells of other diatoms were also encountered. Peridinians, present in 14.3 % of the first group, were found in only 3.3 % of this group and were not found at all in the stomachs of larger groups. The frequency of invertebrate eggs was approximately the same as that in the first group. On the other hand, copepod nauplii increased in frequency from 19.0 to 50.8 % in this size category and each larva contained an average of three instead of one nauplius. In addition, this group fed to some extent on adult copepods, 11.5 % containing an average of 1.1 copepods. *T. longicornis* was identified in both the nauplius and adult stages.

In the 9.3–13.0 mm size range, 63 larvae were examined. Phytoplankton remains, while commonly found in these stomachs, were present in smaller quantities on the average than in the two preceeding groups. Copepod nauplii constituted the dominant food item; an average of 4.8 nauplii were found in 74.6 % of the stomachs, a notable increase in numbers over the two previous size groups. Copepodids and copepods were also common, 41.3 % of the sample containing mature copepods or copepodids, with an average of 1.7 per gut.

All of the 32 larvae of the 13.1–16.0 mm size contained some food remains. Phytoplankton was relatively unimportant in this and larger groups. In these larvae, invertebrate eggs were more abundant than in the previous three groups, being found in 37.5 % of the larvae; possibly this is related to the fact that large larvae were generally collected in the latter part of the spring when copepod spawning had increased. Copepods and copepod nauplii were found in approximately the same percentages of stomachs analyzed, 78.1 % and 75.0 % respectively, with an average of 3.1 copepods and 12.0 nauplii per stomach.

In the 17 larvae of the 16.1–19.5 mm size range, copepods were the important food, an average of 4.2 being found in 94.1 % of the guts. Copepod nauplii, next in importance, were found in 64.7 % of the guts examined, but the average number per gut (11.2) was slightly lower than that in the 13.1–16.0 mm larvae in spite of the increase in size.

Only six larvae were examined in the 19.6–23.1 mm size range. Although this group was so small that it could not be subjected to statistical analysis, it illustrates a continuing tendency of larvae to feed on large items. In this group mature copepods far outranked nauplii in frequency of occurrence. The average number of copepods per gut increased to 5.2 as compared with 4.2 in the 16.1–19.5 mm group while the average number of nauplii per gut decreased from 12.0 to 2.0. It seems likely then that larvae, as they increase in size, tend to select progressively larger food items.

Since the change in diet with size may be correlated with seasonal changes in the food supply, the plankton samples from St. 1129 (see Richard's fig. 1 in this issue), which were taken on 21 January 1955 and which contained a large number of larvae of the four selected size categories (3.2–16. mm), were subjected to special analysis. Fifty specimens were analyzed and the data are presented in Table VI. Comparison of data from St. 1129 with those of the various size groups from the Sound as a whole shows two outstanding differences: a high frequency of phytoplankton and an almost complete absence of invertebrate eggs in the stomachs of the sample from St. 1129; otherwise the results were similar (see Table III). Copepods occurred as commonly in the stomach contents in January as at other times during the season, in spite of the decrease in zooplankton during winter. Also, the average number of adult copepods per stomach was essentially the same in January as during the season as a whole. Evidently seasonal changes in food supply did not greatly influence the feeding habits of the larvae.

TABLE VI. NUMBER AND PERCENTAGE OF *A. americanus* LARVAE, TAKEN IN L.I.S. AT ST. 1129, 21 JANUARY, 1955, IN WHICH THE DIFFERENT FOOD ORGANISMS WERE FOUND.

Length groups, mm	3.2-4.9	5.0-9.2	9.3-13.0	13.1-16.0	16.1-19.5	19.6-23.1	Totals
No. larvae examined	7	19	23	1	0	0	50
Copepods, adults (total)..	0	1	11	1	–	–	13
Percent of larvae with:	0.0	5.3	47.8	100.0	–	–	26.0
No. of specimens ident.							
Acartia sp.	–	–	1	–	–	–	1
T. longicornis.......	–	–	1	–	–	–	1
Oithona sp.	–	–	1	–	–	–	1
Copepods, nauplii (total) .	–	7	16	1	–	–	24
Percent of larvae with:	0.0	36.8	69.6	100.0	–	–	48.0
No. of specimens ident. ..							
T. longicornis.......	–	1	3	–	–	–	4
Invertebrate eggs........	0	0	1	0	–	–	1
Percent of larvae with:	0.0	0.0	4.3	0.0	–	–	2.0
Phytoplankton, unident...	7	19	23	0	–	–	49
Percent of larvae with:	100.0	100.0	100.0	0.0	–	–	98.0
Coscinodiscus............	0	4	7	0	–	–	11
Percent of larvae with:	0.0	21.1	30.4	0.0	–	–	22.0
Peridinium sp.	2	1	0	0	–	–	3
Percent of larvae with:	28.5	5.3	0.0	0.0	–	–	6.0
Empty stomachs	0	0	0	0	–	–	0
Percent of larvae with:	0.0	0.0	0.0	0.0	–	–	0.0

In order to determine the degree to which size played a role in the relative quantity of food consumed by larvae, individuals from each length category discussed previously were grouped according to degree of stomach fullness (see Table III, Fig. 2), excepting the 19.6–23.1 mm group which, because of the small number, was not statistically reliable. Data from the five length categories indicate that the relative quantity of stomach contents increased as a function of size, with the exception of larvae in the 3.2–4.9 mm group. Since no significant seasonal variation in quantity was found, the variation was clearly due to size alone.

The small larvae fed on phytoplankton even before the yolk sac was completely resorbed at about 3.0–3.3 mm. From 4 mm on, the young larvae ingested invertebrate eggs and copepod nauplii as well, continuing to take larger and larger forms as they grew until their diet included mature copepods. The large larvae ate more mature copepods, fewer nauplii, and less phytoplankton. The relationship between the average number of food organisms of various sizes and the corresponding size of the predators are presented in Fig. 1.

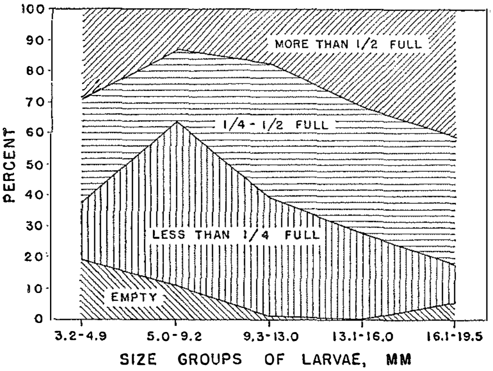

Figure 2. Relative percentages of different length groups of *A. americanus* larvae in different degrees of fullness categories.

Lebour (1918–1920), Wiborg (1948), and Lindström (1955) have discussed the importance of food size in relation to fish size. Although the poor condition of the food remains in the stomach did not permit a precise correlative analysis of this relationship, it is nevertheless evident that size factors influenced the larva's feeding. It is particularly notable that the 18.0–23.1 mm specimens had consumed adult copepods (0.75–2.0 mm) to the near exclusion of nauplii (0.1–0.3 mm). There is little indication that the observed results were due to seasonal changes in the kinds of food available. Hence it seems reasonable to conclude that large larvae select large food organisms.

Local Variations. The majority of *A. americanus* larvae were taken in the central portion of L.I.S. at offshore stations where the water depth was greater than 15 m (Wheatland, 1956), but some samples were obtained inshore at depths shallower than 15 m. The data from 135 gut analyses were employed to obtain a qualitative and quantitative comparison of stomach contents from inshore and offshore larvae in order to ascertain whether or not food factors influenced offshore distribution.

Of these 135, 110 were taken at Sts. 2 and 5 (offshore) and 25 from Sts. 1 and 8 (inshore). An analysis of variance showed no significant differences in size between the two groups. The data in Table VII show that there were slightly more empty guts among larvae from inshore than from offshore stations, but no significant difference in quantity of food was noted between inshore and offshore larvae.

TABLE VII. LOCAL VARIATIONS IN THE RELATIVE DEGREE OF STOMACH FULLNESS OF *A. americanus* LARVAE IN L.I.S., 1952–1955.

Degree of	Inshore Stations			Offshore Stations		
Stomach Fullness	No. 1	No. 8	Total	No. 2	No. 5	Total
No. and °/₀ of:						
empty stomachs	1	2	3	3	5	8
	6.3	22.2	12.0	5.3	9.3	7.3
trace to 25 °/₀ fullness	9	1	10	21	23	44
	56.3	11.1	40.0	37.8	42.6	40.0
25 to 50 °/₀ fullness...	3	4	7	21	17	38
	18.8	44.4	28.0	37.8	31.5	34.5
more than 50 °/₀ fullness	3	2	5	11	9	20
	18.8	22.2	20.0	19.4	16.7	18.2
Total number	16	9	25	56	54	110

A qualitative comparison of the diets of the two groups also failed to indicate any differences between the food of inshore and offshore larvae. From available evidence it seems likely that the general offshore-inshore distribution of larvae is related either to spawning behavior or current patterns rather than food factors.

Diurnal Feeding Activity. In obtaining an appraisal of the hours when larvae feed, the day was divided into three major periods: morning 0900–1130, mid-day 1130–1400, and afternoon 1400–1630. A few larvae, taken between nightfall and midnight, are included in a separate category.

Table VIII shows the relative quantities of stomach contents for the major periods of the day. Comparison of these time groups shows that the quantity of stomach contents was minimal in the morning but increased rapidly into

TABLE VIII. DIURNAL VARIATIONS IN THE QUANTITY OF FOOD REMAINS IN STOMACHS OF *A. americanus* LARVAE IN L.I.S., 1952–1955.

Time period	0900–1130	1130–1400	1400–1630	Night	Total
No. hrs. after sunrise	2–5	4–8	8–9	12, 18	
No. and °/₀ of:	4	7	2	0	13
empty stomachs........	4.5	9.6	8.3	0.0	6.5
trace to 25 °/₀ fullness..	42	24	6	2	74
	47.7	30.0	25.0	33.3	37.0
25 to 50 °/₀ fullness....	28	28	10	2	68
	31.8	35.0	41.7	33.3	34.0
more than 50 °/₀ fullness	14	21	6	2	43
	15.9	26.3	25.0	33.3	21.5
Total number............	88	80	24	6	198*
Total percent............	44.4	40.4	12.1	3.1	100.0

* Time not recorded for sample in which two specimens were taken.

mid-day and then diminished slowly into late afternoon. It is not known how rapidly the food digested, consequently no actual rate of food consumption can be calculated. The small quantities of food in larvae taken in night tows together with the fact that the food remains in these specimens were almost completely digested probably indicate a nocturnal cessation or diminution of feeding activity. However, the night sample was too small to merit an unqualified conclusion. Further conclusions concerning diurnal variations in feeding activity depend upon a better knowledge of digestive rate and food requirements than is yet available.

GENERAL DISCUSSION

Copepods and copepod nauplii, found in 80 °/₀ of the guts examined, undoubtedly are the main constituent of the diet of larvae and postlarvae of the sand eel. So far as the small larvae are concerned, phytoplankton also generally occurred in amounts that appeared to be nutritionally significant. Lebour (1918–1920) commonly found "green food remains" in stomachs of *A. tobianus* and *A. lanceolatus*, but her attempts to keep the larvae alive for study in aquaria were unsuccessful. Although the feeding habits have never been studied experimentally and although it has not been shown that young larvae will subsist solely on phytoplankton, it seems reasonable to assume that any regularly ingested food probably plays a role in an organism's nutrition.

Copepod eggs probably play a minor part in nutrition in spite of the high percentage of guts containing them. The small egg size (only 50–80 μ in diameter) and quantity preclude the possibility of their constituting a significant volume of the diet, at least on the basis of the present study. Likewise *Coscinodiscus* and peridinians were of insufficient mass to contribute appreciably to the sand eel's economy.

Lebour (1918–1920) observed that "each species selects its own favorite food to which it keeps, indiscriminate feeding seldom or never taking place, and one can usually assign to each fish its own particular food". Shelbourne (1953), in a study of the feeding habits of plaice postlarvae in the Southern Bight (North Sea), showed that young postlarvae usually utilized *Oikopleura,* a small tunicate, as their principal food, even though it was a minor constituent of the plankton. However, when *Oikopleura* was not available, an alternative diet composed of more abundant plankton organisms was utilized. He concluded that the vulnerability of the prey is in all probability a determining factor in so-called "food selection".

Evidence from the present study indicates that *A. americanus* larvae do not show extensive discrimination in the selection of food organisms. Although the vast majority of food was copepods, this is not surprising in light of the fact that they and their nauplii commonly constitute 95 °/o or more of the midwinter and early spring zooplankton in L.I.S. It is noteworthy that all of the dominant species of copepods were represented in the stomach contents and that the plankton was dominated by *Acartia* sp. and *T. longicornis,* the species most often identified among the food remains. It is concluded, therefore, that *A. americanus* larvae take suitable food organisms more or less randomly and that the several pelagic copepods probably are about equally vulnerable to predation by the larvae. The absence of harpacticoids and other benthic organisms strenghtens the observation that these larvae are pelagic feeders.

The quantity of food necessary to supply a larva with sufficient energy for growth and respiration has not been determined, but such information is essential in order to ascertain the efficiency of energy transfer between trophic levels and to understand predation effects and other interspecific interactions. Some rough estimates at least may prove interesting.

Table IX shows the length-weight relationships for preserved *A. americanus* larvae over the course of a season. The average weight of an adult *Acartia* copepod is taken as 0.004 mg wet weight (preserved), and it is assumed here to be the average weight of an adult copepod; most of those found in the guts were approximately of that size. This weight was multiplied by the average number of copepods per stomach in each size category to get the average weight of ingested copepods per larva. The weight of mature copepods found in the stomachs is at most 0.3–0.4 °/o of the larva's body weight, a quantity wholly inadequate in light of the fact that a larva increased in weight approximately 0.1 mg or 1.0 °/o of its body weight per day. Since the combined weight of all other food constituents per gut averaged considerably less than the weight of adult copepods per gut, the maximum percentage of weight of food to weight of body would in no case exceed twice the figure for adult copepods alone. Hence, the weight of food found in a gut at any one time is, as would be expected, less than the daily increase in weight due to growth. It is probable, moreover, that weights of food somewhere on the order of four or five percent of the body weight would have to be ingested daily to assure normal growth and activity.

TABLE IX. SOME APPROXIMATE PERCENTAGES OF STOMACH CONTENT WEIGHT TO BODY WEIGHT IN *A. americanus* LARVAE, L.I.S., 1952–1955.

Length of larvae, mm	3.2–4.9	5.0–9.2	9.3–13.0	13.1–16.0	16.1–19.5	19.6–23.1
Average weight, mg...	0.09	0.40	1.22	3.37	6.01	7.80
Av. no. adult copepods per gut............	0	1.1	1.7	3.1	4.2	5.2
Percent body weight ..	0.0	0.4	0.4	0.3	0.3	0.3

If we use these rough approximations, 10 to 16 times the weight of food actually found in the average stomach must be ingested daily to supply the larva with the requisite energy for growth and maintenance; this implies a much higher rate of assimilation than has commonly been thought probable. Rapid digestion and elimination, in combination with factors of diurnal variation, may explain the high incidence of empty stomachs noted by other workers[1].

It is reasonable to assume that food is being continually ingested, at least during daylight, and that we see at any one time only a small part of the food consumed in a day. This is supported further by anatomical evidence. *A. americanus* larvae have long straight guts with no gastric enlargements of functioning valves. Consequently, ingested material cannot be held but must be digested while passing along the digestive tract.

Assuming a much greater food consumption than that indicated by the stomach contents of a deceased individual, the problem of food supply arises, particularly in midwinter when zooplankton is at a minimum. Little is known of true productivity rates in plankton, but their abundance and availability can be calculated approximately from plankton tows. The data for zooplankton abundance in L.I.S. for the years 1952 and 1953 show a minimal copepod population of approximately 2000 individuals per m^3. Thus an average of eight copepods will be found within 10 cm of any given locus. Assuming a larval population of 20 per m^3 (actually more than has been encountered), there would be approximately 100 copepods available to each

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[1] A paper by Bhattacharyya (1957) has recently been brought to my attention. He suggests that the digestion of copepods by herring is rapid whereas copepod eggs, lamellibranch larvae and *Limacina retroversa* larvae are digested more slowly than copepods.

larva. It appears from these estimates that food is available in sufficient quantities at most if not all times of the season to support populations of larvae feeding at the estimated rates.

At present there is some controversy as to the precise means by which fish larvae receive nourishment. It has been logically assumed that larvae derive their energy from the ingestion of organisms selected from the plankton, and indeed most of the evidence supports this line of reasoning. It has been argued, however, that the high incidence of empty stomachs found in most analyses indicates some other means of nutrition. Morris (1955) has suggested that marine larvae feed largely on dissolved organic matter trapped on a mucous membrane in the buccal cavity. In studies of quantities of food which such a membrane would be exposed to, he obtained a value of approximately one percent of body weight per day for a larva weighing 0.9 mg. It seems unlikely that dissolved organic matter, even if it were completely absorbed from the water by such a mechanism, would be adequate for the sand eel's nutritional requirements. During the past year, Wangersky (in this volume), in carbohydrate analyses of millipore-filtered water, has found that the Sound waters contain only negligible quantities of dissolved carbohydrates during winter months. It is obvious that a high percentage of the basic nutrients must be invested in particulate matter at this season, hence they are probably not available in dissolved form.

Histological evidence also supports the contention that dissolved organic matter does not play an important nutritional role. *A. americanus* larvae 5–9 mm long, subjected to histological study, reveal no mucous secreting cells in the epithelia of the throat and buccal cavity. It is concluded that a mucous trapping mechanism does not function in sand eel larvae, at least in larvae larger than five mm.

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Р. Ваде Ковилл

Пища и пищевые нравы личинок и молоди пескороя, *Ammodytes americanus*, 1952–1955.

Краткий обзор

Желудки 200 личинок американскаго пескороя от 3.2 до 23.1 мм были вскрыты для изучения их содержания и состава пищи. Были изследованы не только суточные, сезонные и годовые вариации, но и влияние места сбора и его размера. Разныя фазы питания личинок тоже были приняты во внимание.

Сравнение с данными других изследований показыло значительно мкньшее число пустых желудков у пескороев пойманных в проливе Лонг Исланд Соунд. Очевидно для питания личинок пескороев частицы в особенности копеподов и их науплиусов более важны чем пищевые вещества растворенные в воде. Фитопланктон тоже играет важную роль в питании особенно молодых личинок. Крупныя вариации содержания желудков зависят от их величины. Большия годовыя и месячныя вариации тоже были найдены. Ясно что для поддержания роста личинки едят значительно больше пищи чем может быть учтено анализом содержания их желуков.

Guide for Preparing Figures[1]

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INTRODUCTION

Most of the illustrations submitted for publication in the Journal of Marine Research and in the Bulletin of the Bingham Oceanographic Collection have been satisfactory. However, some illustrations are still received which are not as well prepared as they should be, and occasionally some must be rejected. When this happens, time of both author and editor is consumed in explanations, correspondence, redrawing, etc. Hence, it is to the advantage of all concerned if an illustration is well prepared in the first place.

While an illustration usually augments the text, often it is at least as important as the text itself, since it gives the reader a visual interpretation of the author's findings with a minimum of effort and time, an important consideration in these days of innumerable publications. It is reasonable, then, for both author and editor to consider an illustration as equal in importance to the text. Although the conception and design of an illustration are of great importance, this phase of preparation is primarily the responsibility of the author and will not be con-

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[1] Reprints of this article are available on request. This guide supersedes "Editorial note on the preparation of figures for publication" by Parr and Pitcher, J. Mar. Res., 3 (1), 1940: 89–91.

sidered here. The main purpose of this note is to give an author or illustrator some helpful guides in the techniques of executing the design, that is, drawing it with the proper size of letter and line so that it will be an attractive illustration and also one which will achieve the maximum of legibility and interpretation in reduction.

Experience has shown that the major difficulty in preparing an illustration lies in determining the proper size and weight of letter and line for a given reduction. Special emphasis will therefore be given to this problem. The following criteria will form the basis on which an illustration will be judged acceptable for publication. To avoid stereotyped illustrations, authors are given considerable latitude in executing their drawings.

TECHNIQUES

The basic tools of a draftsman are not difficult to use. Authors who are not familiar with problems of illustrating are urged to take the time necessary to become reasonably proficient in the use of the following: drawing board, T-square, triangles, splines and irregular curves, ruling pen, compass, mechanical lettering guides and pens, and a reducing glass. Directions for the use of these and other instruments that might be required may be found in any text of mechanical drawing.

MATERIALS

All drawings and graphs must be executed in India ink on a good grade of white drawing paper, of *blue-lined* cross-section paper, or of tracing cloth or paper. Use only the best grades of paper and ink. Cheap paper will not usually stand erasure without leaving marks that necessitate redrawing. Therefore, good rag content paper that will stand erasing is recommended and will prove to be a good investment. Many cheap India inks are not truly black and do not take reproduction well.

Since a photographic process which filters out blue is generally used in making line cuts, cross-section paper, if used, should be of blue lines if the guides are not to be reproduced. All lines that are to show in the final cut must be drawn with *black* India ink.

LINES

1. Draw all lines with a *ruling pen*; avoid the use of lettering pens for drawing lines.

2. Draw noncircular curved lines with ruling pen, using irregular curves or splines as guides. Few authors are skilful enough to produce good free hand curves. Draw circles with a compass pen.

3. Heavy borders around a graph only distract the eye from the essential data in the body of the illustration. If borders are used, draw them slightly heavier than the heaviest line of the graph.

4. Lines in graphs must be heavy enough to stand out and attract the eye of the reader, yet light enough to produce a clean-cut appearance. Avoid extremely heavy lines; when in doubt, test by examining the drawing through a reducing glass.

5. Broken lines appear heavier than solid lines of the same weight; therefore draw broken lines somewhat lighter than solid lines.

6. Draw a broken line with adequate spacing so that the dashes are clearly separated. Test with a reducing glass when in doubt.

7. For a line composed of long and short dashes, the long dash should be about four times the length of the short one.

8. Bar graphs and histograms should first be outlined with the ruling pen. Be sure that corners of bars and columns are square and sharp. After outlining, the bars may be cross-hatched, filled in, or left open. Large solid masses of black do not enhance the appearance of a printed page and should be avoided.

SYMBOLS

1. Where only one or two symbols are essential, circles should be used, *drawn with a compass pen.* Use only *open* or *completely solid* circles.

2. Where more than two symbols are needed, use squares and triangles in addition to circles; again, use only open or completely solid symbols. Squares are best drawn with a template. Triangles may be made from the capital V of the lettering template.

4. Avoid such symbols as crosses, X's, or partly filled in symbols.

5. The size of symbol is best governed by the size of letters used. In general, the diameter of a symbol should be about equal to the height of the medium-sized letters.

LETTERS

1. All lettering must be done with a good lettering set, *e.g.*, the Leroy or Wrico.

2. Space the letters to equalize the *area* rather than the distance between them. Thus, LT would be spaced closer than would HM.

3. Use capital letters only. If mixed capital and lower case letters are absolutely essential, they must be at least one size larger than those used for capitals alone, to preserve legibility.

4. Lettering may be done with either Roman (upright) or Italic (slant) letters. Italics appear larger than Roman letters of the same size, and this factor should be taken into consideration.

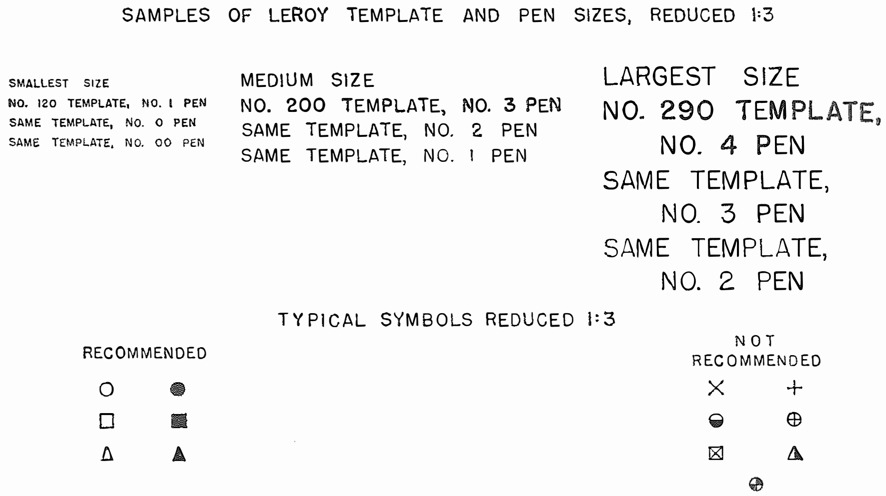

Figure 1. Letters and symbols, drawn at various sizes and with various weights of line, reduced 1 : 3, to show appearance in reduction.

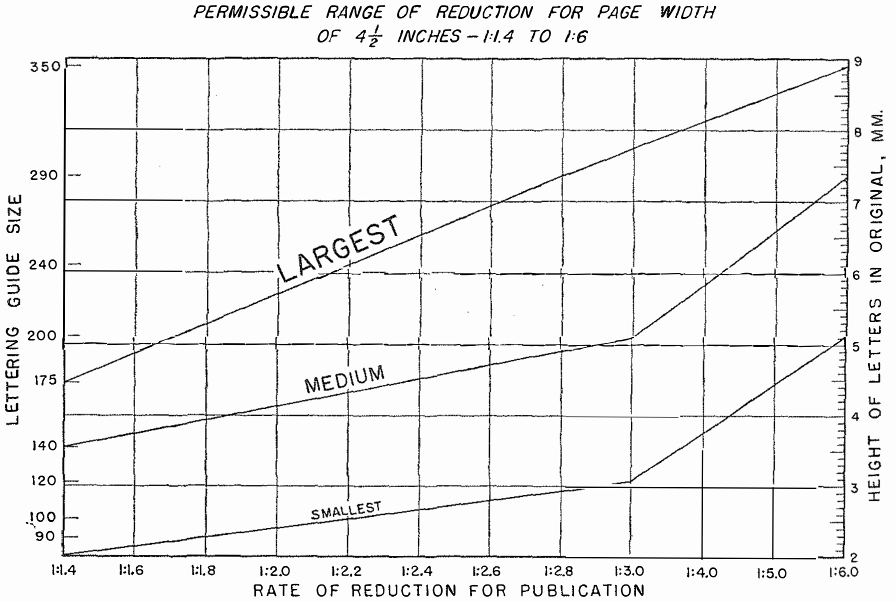

Figure 2. The recommended sizes of letters for various degrees of reduction. Find the desired rate of reduction at the base of the figure; then move up the graph to the lines labelled "smallest", "medium", or "largest", as desired; then move to the right or left side of the graph to find the proper size of letter and template to be used. For example, if a reduction of 1 : 3 with medium size letters is desired, then the height of the letters to be used in the original illustration should be 5.1 mm (Leroy template 200); if a reduction of 1 : 2.6, with small letters, is desired, then the height of letter would be 2.8 mm; in this case template 120, somewhat larger than the size indicated by the graph, would be used.

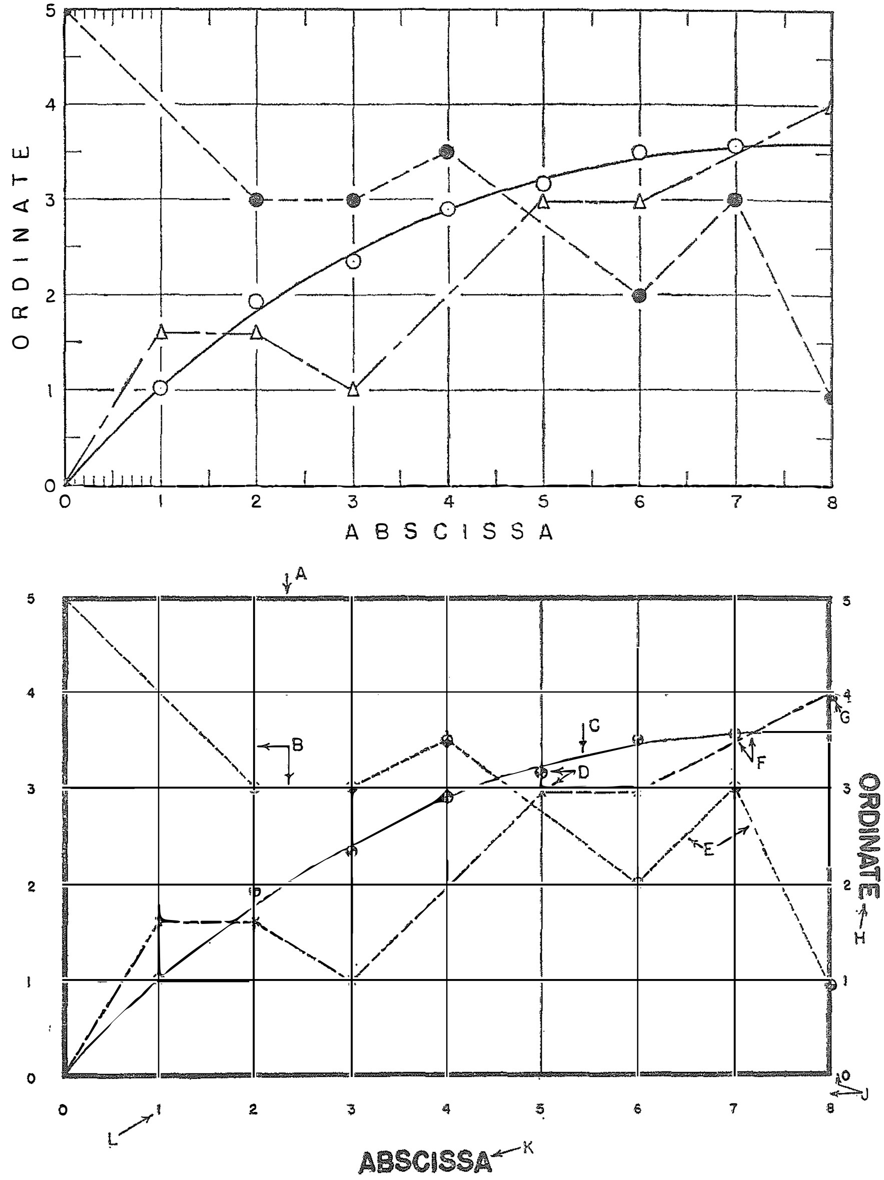

Figure 3. A well drawn graph (above) compared with a poorly executed graph (below). In the upper figure, note especially the clarity of lettering, line, and symbols. In the lower figure, note the following undesirable features: *A* Border too heavy; distracts eye from main body of graph. *B* Guide lines too heavy; obscure data. *C* Free hand curves not smooth. *D* Symbols too small, not easily legible after reduction. *E* Broken line too heavy, dashes too close together and unevenly spaced. *F* Long and short dashes hardly distinguishable; line too heavy. *G* Blots resulting from attempts to hurry. *H* Ordinate lettering reads from wrong side of page and is much too heavy. *J* Numbers poorly spaced. *K* Abscissa lettering too heavy, poorly centered and too far from body of graph. *L* Numerals too small and too heavy.

5. Superior reproduction of lettering is obtained by spacing the letters a little wider than is indicated on the templates and by using a slightly lighter than normal weight of line. As a general rule, use a pen one size smaller than that recommended for the lettering template.

6. Lettering size on the original illustration must be prepared according to the reduction to be used. See Fig. 1. If in doubt, use a larger letter.

7. Illustrations must be lettered to read from the bottom and from the right side (see Fig. 2).

GENERAL COMMENTS

In Fig. 3, the upper illustration shows features that are desirable in a good figure, the bottom one, features that contribute to an undesirable figure. Please note the comments in the figure caption regarding undesirable features.

It is seldom necessary to prepare an illustration in poster size. As a general rule, the size of the illustration need not be more than two or three times that of the printed figure. It is therefore recommended that illustrations be drawn for reductions of 1 : 3 or less.

Be sure to allow for the figure caption if the illustration is to occupy a full page.

Note in Fig. 3 that the illustrations were prepared without adequate allowance for the caption so that the figure and caption occupy more than seven inches.

It is desirable to reproduce complicated illustrations at full page width, but simple drawings containing only a line or two and a few symbols should be prepared for reduction to $2^1/_2$ or 3 inches. A simple illustration not so prepared may be returned to the author for redrawing, thus delaying publication.

The author's name and the figure number should be written in the lower right-hand corner of each illustration. Particularly if borders are not used, the "top" of an illustration should be indicated.

Avoid stippling so densely that the dots fuse or merge in reduction, and if possible do not draw lines so close together that they will merge. Test your shading with a reducing glass.

Pasting tabs on illustrations should be avoided, as they tend to fall off. Tabs are sometimes used to correct errors on poor quality paper, and some authors use printed numerals and letters. This journal will accept satisfactory illustrations with pasted tabs, but it *will not be responsible* if tabs fall off in handling. If a new cut has to be made because a tab has fallen off, the author will be charged for the extra cut. Illustrations with pasted tabs should never be rolled, but should be mailed flat.

Photographs of illustrations may accompany a manuscript submitted for consideration. When the paper is accepted, however, the original illustrations will be required.

THE FIGURES IN THIS ISSUE

Since examples are always helpful in explaining poor features as well as good, comments on the figures printed in this issue of the Bulletin are given below. The figures were not prepared according to the above *Guide*, hence our comments are in no sense a reflection on the authors who prepared them. In fact, several figures on which we comment adversely were drawn by the second author of this article. The figures in this isssue are used in lieu of other illustrations only because they are convenient and readily available to the reader of this *Guide*.

In our opinion, the figures on pp. 12 and 140 stand out as being excellent in every respect. On p. 12, the figure was reduced to page width because of the closeness of the lines in some places; had it been reduced further the lines might not have remained clearly defined. On p. 140, the cross-hatching is done lightly and neatly, the hatched areas are clearly defined with light lines, and the lettering is sufficiently large and well spaced for easy reading.

Many of the other figures in this issue of the Bulletin are quite satisfactory, but it is felt that the small letters or numerals in many of these figures should have been slightly larger to make them more easily readable. The simplicity of these figures permitted reduction to $2^1/_2''$ and $3''$; their reduction to page width would have occupied more space than is necessary and would have increased the cost of publication. Such figures are seen on pp. 13, 14, 16, 17, 18, 21, 36, 39, 41, 49, 80, 84, and 137.

Note that in some figures the subscripts and superscripts are barely readable and should have been drawn considerably larger (pp. 37, 39, 41, 72, 74).

While the symbols in some figures are quite clear and satisfactory, as on pp. 36, 39, and 49, some or all of those in figures on pp. 41, 72, 74, and 80 could stand improvement. Note on pp. 41, 72, 74, and 80 the use of the symbol ×, which is not recommended. On pp. 72 and 74 the △ and × are too small, and on p. 80 the dots are too small.

On pp. 11, 33, 98, and 119 the figures were given minimal reduction, to page width, because of their cemplexity, yet in all cases much of the lettering is too small for ease of reading. For example, on p. 11 the numbers of the stations, 1, 3, and 5 A, Gardiners Bay, New Haven, and the names of the rivers could easily have been drawn larger, since there is adequate space for larger letters; in the case of Gardiners Bay, this could have been drawn to the right of the present lettering with an arrow indicating its exact location. Note also that most of the numbers for latitude and longitude are smaller than necessary. Similar comments apply to the figures on pp. 33, 98, and 119, especially the last two, in which the lettering is almost unreadable in part. Note also the undesirable crowding at the top of the figure on p. 119 and the uneven line-up of *Western*, *Central* and *Eastern*.