BULLETIN OF THE BINGHAM OCEANOGRAPHIC COLLECTION

Yale PEABODY MUSEUM OF NATURAL HISTORY

P.O. Box 208118 | New Haven CT 06520-8118 USA | peabody.yale.edu

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

VOLUME XIII, ARTICLE 3

HYDROGRAPHIC AND BIOLOGICAL STUDIES OF BLOCK ISLAND SOUND

BY

GORDON A. RILEY
GEORGIANA B. DEEVEY
DANIEL MERRIMAN AND RUTH SCLAR
HOWARD L. SANDERS

Issued July, 1952
New Haven, Conn., U. S. A.

HYDROGRAPHIC AND BIOLOGICAL STUDIES OF BLOCK ISLAND SOUND

By

Gordon A. Riley
Georgiana B. Deevey
Daniel Merriman and Ruth Sclar
Howard L. Sanders

Volume XIIII, Article 3

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

Issued July, 1952
New Haven, Conn., U. S. A.

CONTENTS

Vol. XIII, Art. 3.

HYDROGRAPHY OF THE LONG ISLAND AND BLOCK ISLAND SOUNDS

By Gordon A. Riley

Woods Hole Oceanographic Institution[1]
and
Bingham Oceanographic Laboratory

TABLE OF CONTENTS

---

[1] Contribution No. 578 from the Woods Hole Oceanographic Institution. This work was supported by contract No. N6onr-277 with the Office of Naval Research.

ABSTRACT

Nine cruises in the Long Island and Block Island Sounds[2] in 1946 provide a basis for the description of temperature and salinity distribution in these waters. Data on tides, currents, and freshwater drainage are summarized, and all available information is combined into an analysis and discussion of the physical oceanographic processes that produce the observed distribution of temperature and salinity.

There is a slow southwesterly drift in the coastal waters off southern New England. Part of this water moves into the Sounds, particularly along the bottom, where it is gradually mixed with the products of river drainage; thus the salinity decreases from the open coastal waters toward the innermost ends of the sounds and bays. From these inner waters a compensating surface current moves seaward and joins the general coastwise drift.

L. I. S., being a semi-enclosed body of water, is particularly favorable for quantitative investigation of currents, mixing processes, and the total exchange with adjacent waters. The circulation is mainly controlled by river drainage. Addition of fresh water into the shore zone tends to produce a counterclockwise circulation; however, tidal mixing in areas of little river outflow breaks up the coastal density gradient. The net result appears to be a series of three main eddies—counterclockwise in the east and west ends of L. I. S., with a clockwise eddy between.

The net transport of water from L. I. S. must equal the freshwater drainage, which amounted to 35% of the volume of this body of water in 1946. Observed surface currents indicate a much larger surface transport from L. I. S. into B. I. S., and this is part of the evidence favoring the existence of a two-layered transport system, with water flowing out at the surface and in at the bottom. To maintain the observed salinity in L. I. S., it was necessary for B. I. S. water to be brought in at a mean rate of 7500 m^3/sec, totalling 3.8 times the volume of L. I. S. during 1946. These figures represent the combined effects of lateral eddy diffusion and mass transport.

Although there is a slight seasonal variation in salinity in L. I. S., the salinity distribution tends to be self-regulating. With an increase in river drainage and a decrease in average salinity, there is an increase in the amount of exchange between the two Sounds, so that more B. I. S. water is brought in to counteract the freshening effect. It is suggested that a decrease in salinity increases the slope of the free surface between L. I. S. and the open sea and accelerates both the surface velocity and the compensating bottom current. Quantitative aspects of the theory are briefly examined.

Problems of turbulence are discussed from time to time, and coefficients of lateral eddy diffusivity and vertical eddy conductivity are evaluated. In B. I. S. the eddy coefficients and the observed salinity distribution are used to estimate current velocities.

ACKNOWLEDGMENTS

This survey was made possible by a grant from the Office of Naval Research, to whom grateful acknowledgment is made at this time.

---

[2] Hereafter Long Island Sound will be referred to as L. I. S. and Block Island Sound as B. I. S.

A large part of the field work and processing of the data was done by the physical oceanographic staff of the Woods Hole Oceanographic Institution. The writer is particularly indebted to Dean F. Bumpus, Frederick C. Fuglister, Carl Hayes, Garry Metcalf, and to the dozen or more technicians who participated in various aspects of the survey, as well as to the officers and men of the Woods Hole vessels PHYSALIA and ANTON DOHRN.

At various stages in the analysis of data and preparation of the manuscript the work has been discussed with the men listed above and with Columbus O'D. Iselin, Alfred C. Redfield, Henry Stommel, Daniel Merriman, E. F. Thompson, and others. To all of them the writer is grateful for their advice and suggestions.

INTRODUCTION

The following report is based primarily on nine cruises from Woods Hole, Massachusetts to L. I. S. during the period from January 22, 1946 to January 5, 1947. Fig. 1 is a chart of the area covered, with place names that will be referred to and with depth contours taken from U. S. Coast and Geodetic Survey charts. The latter were also used to prepare estimates of the area and volume of L. I. S. and certain subdivisions thereof for use in quantitative analyses to be presented later. Results of these measurements are shown in Table I.

During each cruise, surface bucket temperatures and salinity samples were obtained every 15 minutes en route, together with bathythermograph measurements of the vertical temperature structure. At less frequent intervals, hydrographic stations were occupied, these consisting of temperature and salinity readings at about five depths between surface and bottom. Figs. 2 to 5 show the surface temperature and salinity distribution observed during four of the cruises, and they also serve to illustrate the general cruise pattern. Other cruises, which are not figured but which will be used in later analyses of temperature and salinity distribution, were made on the following dates: Cruise 2, March 17 to 25, 1946; 3, April 29 to May 4; 5, July 11 to 13; 7, October 7 to 13; 9, December 31, 1946 to January 5, 1947.

Also included in the report is a series of bathythermograms and salinity measurements obtained in B. I. S. in 1949. The area covered in the later survey was small, and the observations are therefore of limited interest from a physical oceanographic standpoint. They are included mainly to provide a basis for the physical aspects of the

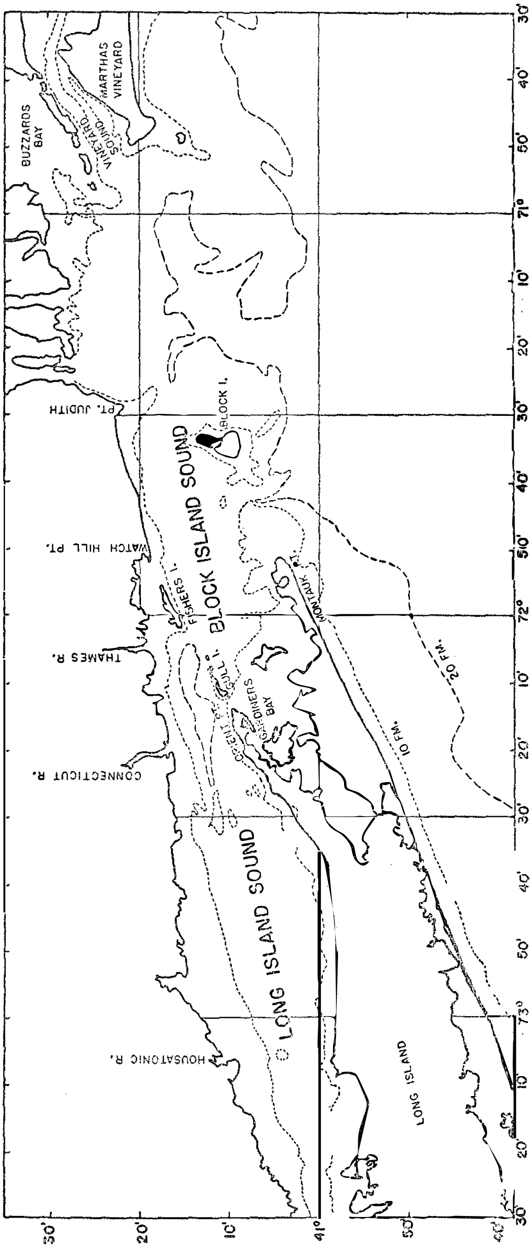


Figure 1. Chart of area covered by the survey, showing place names and bathymetric contours.

TABLE I. AREA AND VOLUME OF L. I. S. THE SOUND WAS SUBDIVIDED BY DRAWING NORTH-SOUTH LINES ACROSS THE U. S. COAST AND GEODETIC SURVEY CHARTS OF THE SOUND AT INTERVALS OF 10 MINUTES OF LONGITUDE. THE AREAS AT MEAN LOW WATER AND AT SUCCESSIVE DEPTH INTERVALS WERE MEASURED PLANIMETRICALLY. THE DEPTH INTERVALS, LISTED IN FEET, WERE LARGELY TAKEN FROM CONTOURS PRINTED ON THE CHARTS, BUT A FEW ADDITIONAL CONTOURS WERE DRAWN WITH THE AID OF THE SOUNDINGS. THE AREAS LISTED HERE INCLUDE FISHERS ISLAND SOUND BUT NOT THE WATERS SOUTH AND EAST OF FISHERS ISLAND, GULL ISLANDS, ETC.

	Area M. L. W.	*Volume in m³ x 10⁷ between successive depth contours*										
	Naut. sq. mi.	*0–20*	*20–30*	*30–45*	*45–60*	*60–75*	*75–100*	*100–125*	*125–150*	*150–175*	*175+*	*Total vol.*
71° 50′–72° 00′	15.8	25	6	3	—	—	—	—	—	—	—	34
72° 00′–72° 10′	38.0	76	34	41	33	28	38	35	30	24	47	386
72° 10′–72° 20′	59.0	115	52	72	67	63	89	62	32	9	—	561
72° 20′–72° 30′	80.5	158	71	96	82	66	72	39	21	5	—	610
72° 30′–72° 40′	116.7	234	109	148	132	102	72	6	1	—	—	804
72° 40′–72° 50′	128.8	257	119	159	142	128	118	18	1	—	—	942
72° 50′–73° 00′	130.0	256	114	151	124	98	101	37	8	—	—	889
73° 00′–73° 10′	99.6	195	85	108	88	67	74	37	11	—	—	665
73° 10′–73° 20′	98.0	194	87	116	92	57	49	16	—	—	—	611
73° 20′–73° 30′	70.7	127	49	59	45	32	28	9	2	—	—	351
73° 30′–73° 40′	54.2	97	38	46	26	10	6	1	—	—	—	224
73° 40′–73° 50′	37.4	59	18	18	12	—	—	—	—	—	—	107
Total	928.7	1793	782	1017	843	651	647	260	106	38	47	6184

interpretation of biological and chemical observations that were made at the same time and which will be described in subsequent papers.

It is not the purpose of the writer to present a detailed account of the mass of accumulated information, which is likely to be of interest only to local investigators. Instead, small samples of data and condensed summaries have been prepared in an attempt to evaluate principles of temperature and salinity distribution that will be of more general interest.

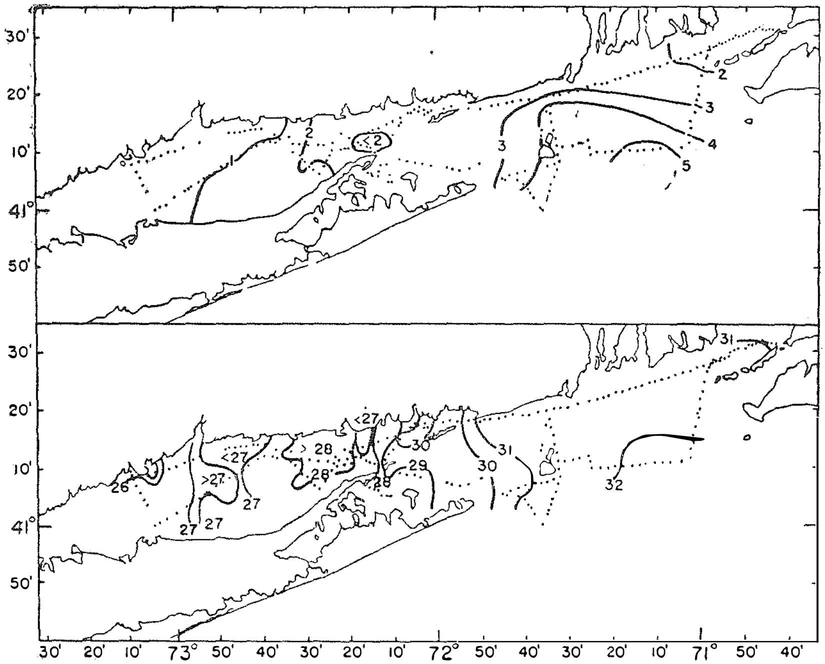


Figure 2. Distribution of surface temperature in °C (top) and salinity in °/₀₀ (bottom) during Cruise 1, January 22 to February 8, 1946.

SALINITY AND TEMPERATURE DISTRIBUTION

Various earlier studies have demonstrated the existence of a slow southwesterly drift of water along the continental shelf off southern New England. Part of this water is diverted into the sounds, where it is gradually freshened by admixture with coastal drainage. The product of admixture is gradually removed from the sounds, and Figs. 2 to 5 indicate that the major outflow occurs between Montauk Point and Block Island. Generally this drainage is revealed only by a bending of the isohalines around Montauk Point and a general increase in salinity toward the east and north, but occasionally, as in Fig. 3, there appears to be a discrete mass of low-salinity water traversing the area.

In the semi-enclosed basins of L. I. S. and Gardiners Bay, and to a lesser extent in Vineyard Sound and Buzzards Bay, the salinity decreases from the entrances toward the inner portions as a result of progressive dilution by river drainage. The charts show examples of various stages in the mixing process between river water and the main body of coastal water, including pockets of very fresh water at the immediate mouths of the rivers as well as larger and more diffuse eddies that have been carried away by the tide. Occasionally, more detailed observations have been obtained by towing an automatically recording conductivity cell. A highly irregular distribution of salinity was found within the freshwater patches, often consisting of

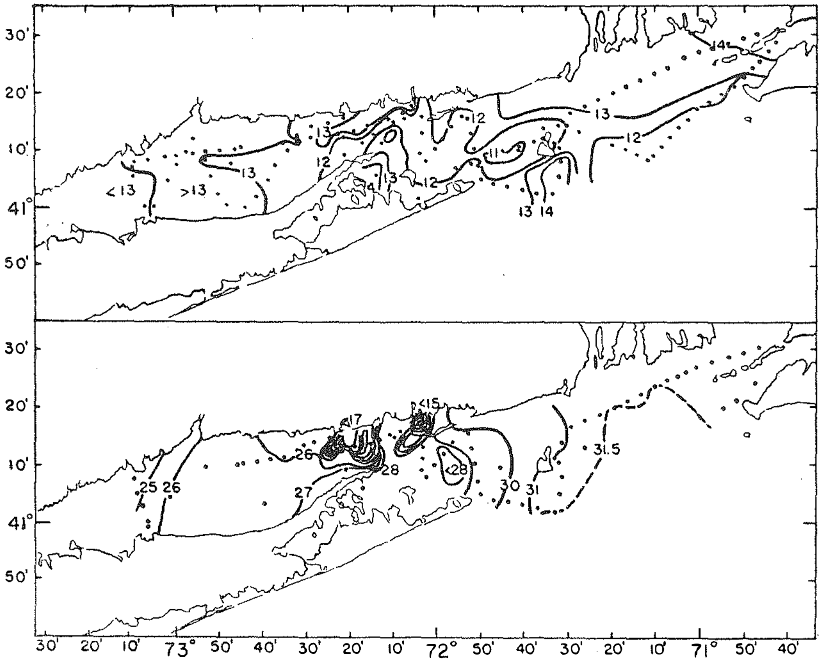


Figure 3. Surface temperature and salinity during Cruise 4, May 31 to June 7, 1946.

alternating streaks of high and low salinity which were demarked by rips on the surface as well as by a change in turbidity. Such structures moved and changed continually with the tide and appeared to be largely dissipated within a few hours. Thus the charts are compounded of large-scale features that changed little between the outbound and homeward passages of the vessel and small-scale structures that probably changed significantly while they were being traversed.

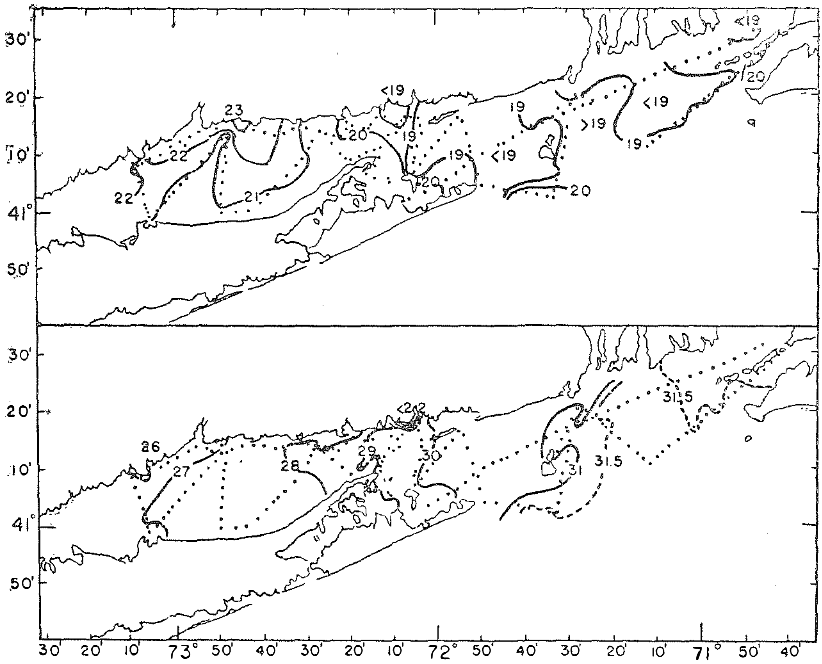


Figure 4. Surface temperature and salinity during Cruise 6, August 20 to 25, 1946.

Galtsoff and Loosanoff (1939) recorded the surface and bottom temperatures and salinities at numerous stations in L. I. S. during three cruises in May–June, August–September, and December, 1935. They reported a seasonal variation in salinity that is confirmed in the present survey. The largest seasonal range is found in the western part of L. I. S., where it reaches a magnitude of two or three parts per mille, the minimum salinity occurring in spring, the maximum in autumn, corresponding to the seasonal variation in river drainage. In the relatively open waters between Block Island and Marthas

Vineyard, the charts show a smaller but otherwise similar variation of 1°/₀₀.

Subsurface salinity measurements revealed small vertical salinity gradients throughout most of the area. The increase between surface and bottom was seldom more than 1°/₀₀ except in the vicinity of river mouths.

The midwinter surface temperature was 4–5° C off Block Island and decreased toward the freezing point in inshore waters. Conversely, summer temperatures near the coast were generally a few degrees higher than those in the outer part of the area. The total seasonal range was of the order of 15° off Block Island and 20° in much of the coastal zone. According to data published by Prytherch (1929) and Riley (1941), the shallow waters of harbors and inlets have an annual range of about 25°.

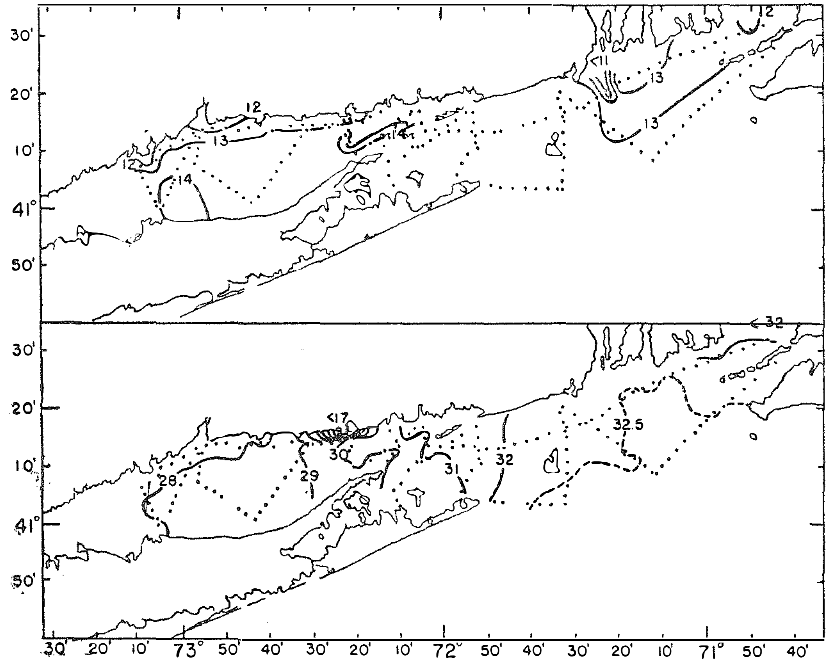


Figure 5. Surface temperature and salinity during Cruise 8, November 13 to 17.

Strong thermal stability was found only in the outer waters off Block Island, where in midsummer there was a sharp thermocline with a temperature decrease of about 10°, centered at a depth of 15–20 m. In the remainder of the region there was usually a temperature decrease of 1–2° between surface and bottom during the spring and summer. Occasionally the gradient was as much as 5°. In winter, positive gradients were common, and increases of as much as 1° between surface and bottom were recorded.

The charts show that localized patches of low-salinity water sometimes had distinctive temperature characteristics. In winter they tended to be colder than the surrounding water of higher salinity, and in summer warmer. To some extent this may have been due to the fact that the seasonal temperature cycle of the rivers is marked. However, it is regarded as more important that the eddies had strong vertical stability, as indicated by salinity gradients, so that the effects of surface heat exchange were intensified.

TIDES AND TIDAL CURRENTS

The tide moves into B. I. S. as a progressive wave. Low water at Block Island precedes low water in the eastern end of L. I. S. by an hour and a half. This in turn precedes low water in the western end of L. I. S. by two hours. Here the tide becomes essentially a standing wave. Throughout the central and western parts of L. I. S., the time of slack water nearly coincides with high and low tides, but toward the eastern end, the ebb current follows high tide by an hour and a half or more. The mean range of the tide is about 0.75 m along the shore of B. I. S. and the eastern part of L. I. S. and increases in a westerly direction to 2.2 m. The corresponding spring ranges are 0.95 and 2.6 m. Theoretical aspects of the tides in this region have been treated by Redfield (1950), and further discussion is unnecessary.

Surface tidal currents have been measured by the U. S. Coast and Geodetic Survey and published in the form of hourly charts covering a complete tidal cycle. These are summarized in Fig. 6 as average flood and ebb velocities. The original Survey charts show that the current turns at nearly the same time throughout both Sounds. Thus the lag in the time of the tide, described above, is a fairly precise indicator of the degree of transition of the tidal wave from the progressive to the standing type.

Data on the height and time of the tide from the U. S. Coast and Geodetic Survey tide tables provide a means of estimating the magnitude of tidal transport in L. I. S. A 24-hour period was chosen when the predicted tides approximated the mean range. The tidal height was computed for hourly intervals during this period throughout L. I. S. By summing hourly changes in volume for successive small areas, the total inflow and outflow during a tidal cycle was found to be 8.2% of the volume below mean low water.

Tidal exchanges in B. I. S. cannot be determined with any degree of precision. The change in the volume of water is only 2–3%. But since it also supplies and receives the tidal volume of L. I. S. and Gardiners Bay, the total exchange of water may be nearly an order of magnitude greater.

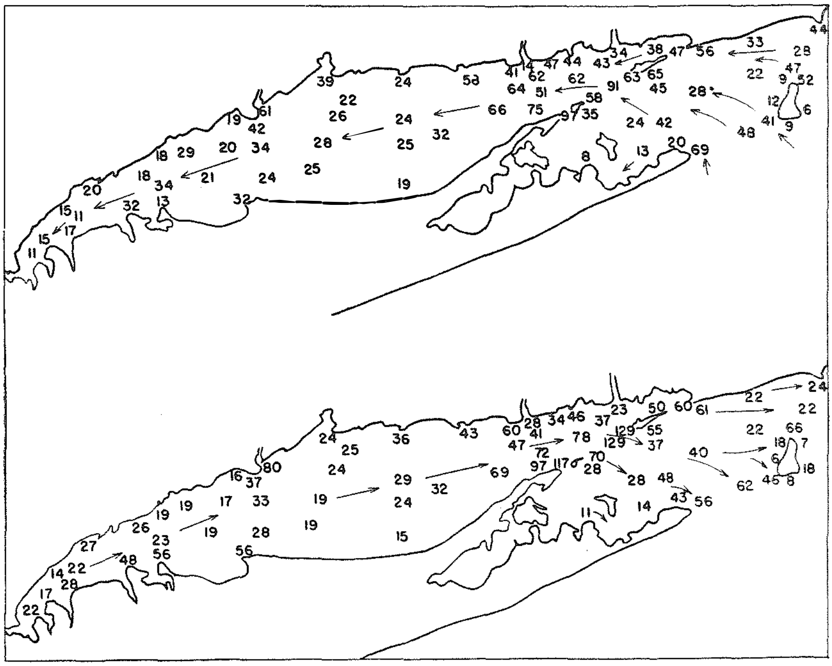


Figure 6. Average velocity in cm per second of the flood (top) and of the ebb (bottom) surface currents.

The volume computations described above were used to estimate the average east-west tidal velocity through half a dozen cross-sectional areas of L. I. S. The calculated velocities in any given area were in most cases within the limits of variation of the measured surface values given in Fig. 6. Average surface values were somewhat higher, as might be expected. The difference ranged from about 10%

in the eastern and central parts of the Sound to nearly 50% in the constricted western portion.

NONTIDAL SURFACE MOVEMENTS

Fig. 6 reveals differences between flood and ebb velocities which are in some cases very marked. Such differences may be ascribed to the following causes:

1. Errors of measurement.
2. Small-scale oceanographic variations. These may be of a random nature, such as eddies and wind drifts, or they may be consistent differences of a very local nature due to peculiarities of bottom topography.
3. Rotation of the tides. While the predominant tidal movement is an east-west oscillation, the Coriolis force must tend to produce a clockwise rotary movement. Prytherch (1929) measured tidal currents with an Ekman meter in a limited area along the Connecticut shore and found a clockwise rotation during the latter half of the flood. However, in neither the current measurements in Fig. 6 nor in Redfield's (1950) theoretical treatment of the subject is there an indication of a broad-scale rotary movement.
4. Large-scale nontidal movements generated by the pressure distribution.

The present section will deal with the question of whether there exists in this region a consistent or prevailing residual drift, and if so, what the pattern of circulation and the generative forces might be. Drift bottle records, current measurements, and the distribution of conservative concentrations will be brought to bear on these problems.

Drift Bottles. Prytherch (1929) described a series of experiments in which 500 drift bottles were released during the period of September 18–21, 1926 near the Connecticut shore east of the mouth of the Housatonic River. The majority of recoveries during the first week or two were on the Connecticut shore, east and west of the point o release. At progressively later intervals there were returns from th opposite shore, from the eastern part of L. I. S., and from the shores B. I. S. There were 203 recoveries during the first month and a tot of 290 in ten months. Prytherch presented charts of the positions release and recovery in six of the experiments. Fig. 7 summar these experiments as numbers of recoveries within designated st of the shore line.

The drift bottle data were supplemented with current meter observations in the general area of bottle releases. There was an indication of a residual drift to the east. The evidence as a whole led Prytherch to the conclusion that the predominant drift in L. I. S. is a large-scale clockwise eddy, with a discharge of surface water out through the eastern passes.

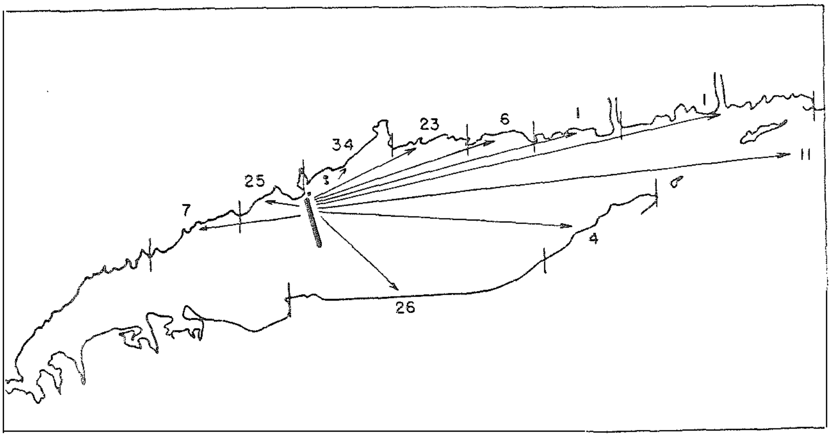


Figure 7. Summary of Prytherch's (1929) drift bottle experiments. Black spots show points of release. Figures indicate the number of recoveries along strips of shoreline delimited by vertical lines.

Current Measurements. The hourly current measurements of the U. S. Coast and Geodetic Survey were summed, and the resultant drift during the 12-hour tidal cycle was converted to an estimate of average residual velocity. The results are shown in Fig. 8A. It is only with considerable reservation that they can be accepted as evidence of a general circulation pattern. Random variability and errors of measurement are such that a nontidal movement cannot be detected unless it constitutes a sizable fraction of the tidal velocity. It is apparent in Fig. 8A that a considerable number of the velocities are large enough to reduce technical errors to insignificance. It is not so easy to evaluate small-scale oceanographic variability. The only criterion available is consistency of the results. As a specific example, in the north central part of L. I. S. there is an estimated velocity of [illegible] cm/sec eastward along the Connecticut shore. The observation was [illegible]ined in a channel between the mainland and an offshore island [illegible] reef. It disagrees as to current direction with other coastal observations to the east and west. It might be regarded as a local aberration. However, two stations in more open waters to the south and west also indicate an easterly drift. It so happens that both of these have small and relatively insignificant velocities. But, although all of the observations are open to suspicion individually, the existence of three consistent results increases the statistical probability of a general eastward drift in this part of L. I. S.

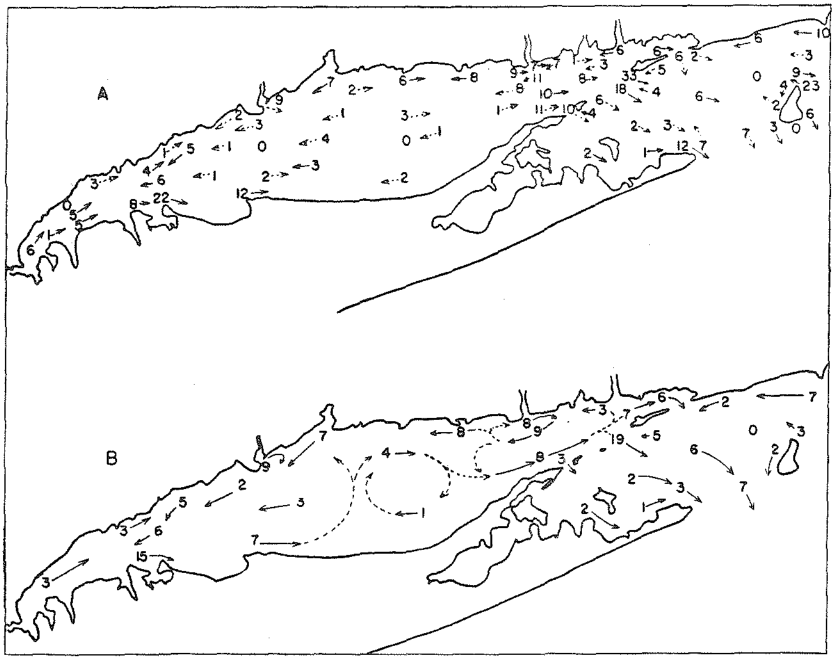


Figure 8. Residual surface drift in cm per second. *A.* Difference between flood and ebb velocities (Fig. 6) averaged for a complete tidal cycle. Solid arrows indicate that the residual drift is more than 15% of the tidal displacement; broken arrows, less than 15%. *B.* Schematic diagram of currents obtained by combining and averaging data in *A.*

Fig. 8B shows a simplified and schematic current diagram obtained by combining and averaging adjacent observations in Fig. 8A. It is apparent that this treatment entails subjective judgments as to which observations are best combined. Its only purpose is to facilitate examination and discussion; possible distortions should be borne in mind.

The results thus far obtained suggest a complicated circulation pattern in L. I. S. which is briefly summarized as follows: There appears to be a surface drift into L. I. S. at the western end which merges with a counterclockwise current following the shore line in the western third of the area. This gives way to weak and confused currents in the broad central portion. Here the requirements of continuity and the measured drifts, such as they are, suggest that there may be a weak clockwise eddy. Another clockwise eddy, of small size but with strong currents, is found between the mouth of the Connecticut River and Long Sand Shoal. Both of these eddies probably supply water to an eastward drift that follows the Long Island shore and moves out through the eastern passes. In B. I. S. there appears to be a predominant westward drift between Point Judith and Block Island which eventually merges with the L. I. S. effluent and passes out to sea between Block Island and Montauk Point.

The Relation between Currents and Density Distribution. Possible agencies in the generation of currents in L. I. S. are (a) the Coriolis effect on tidal flow, and (b) horizontal density gradients. Rotary tides might produce a simple clockwise residual drift of the type postulated by Prytherch. But the more extensive observations by the U. S. Coast and Geodetic Survey indicate that this type of circulation, if it exists at all, is limited to the central part of L. I. S. Elsewhere, if the circulation pattern outlined in the previous section is correct, it must be primarily a system of density currents. It is desirable, therefore, to examine the distribution of density in L. I. S. to see whether or not it provides a reasonable explanation for the observed currents that were shown in Fig. 8.

Fig. 9A shows the surface density distribution during the cruise of August 20–25, 1946, calculated from temperature and salinity data previously illustrated in Fig. 4. It differs only in minor details from the pattern that would be derived by considering only the effect of salinity on density. During the remainder of the year, temperature gradients were even less important, and the salinity distribution in Figs. 2 to 5 will provide an adequate basis for the discussion of density gradients.

So far as can be determined from the available data, horizontal variations in density are not simply surface phenomena; a similar degree of variability occurs in the bottom waters. This is illustrated in Fig. 9B, which is redrawn from a chart by Galtsoff and Loosanoff (1939) whose data on bottom waters were more complete than those obtained in the present survey.

In deep oceanic waters, density gradients of the magnitude observed in L. I. S. would allow no doubt as to the existence of currents. For example, assume a layer of water 10 m thick with a lateral change in density of one sigma-*t* unit in four miles. Assuming a surface of no motion at the bottom of the layer, dynamic computations show that the mean velocity at the sea surface (in the latitude of L. I. S.) would be of the order of 12 cm/sec. Along the northern shore of L. I. S. it is common to find density gradients equal to or greater than the one postulated. Farther off shore, where the density gradients are smaller, similar calculations lead to estimates of 5 cm/sec or less.

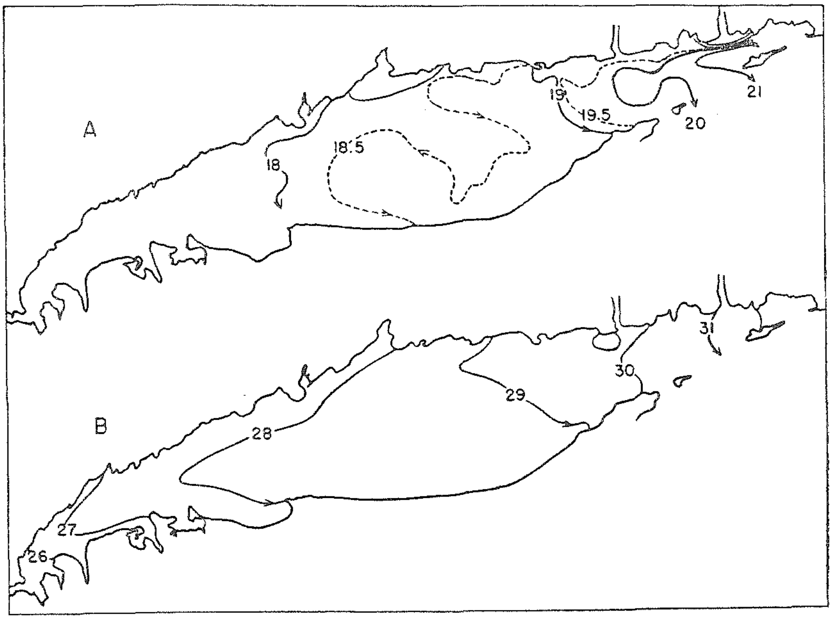


Figure 9. *A*. Surface density distribution, August 20–25, 1946. *B*. Bottom salinity distribution during August–September 1935 (after Galtsoff and Loosanoff, 1939). Arrows indicate the direction of propagation of currents related to the distribution of density.

The hypothetical cases are suggestive of the magnitude of the forces tending to produce density currents in L. I. S. However, it is not possible to make due allowance for frictional terms nor to designate a correct depth for the surface of no motion, if any. Hence, simple dynamic theory cannot be applied to these waters with any degree of accuracy, and even the qualitative interpretation is somewhat uncertain. In deep water one would expect that the lines of equal density would approximate the dynamic topography of the sea surface and that the movement of water would follow the arrows as indicated in Fig. 9. While the major part of this pattern agrees with the current measurements in Fig. 8, the scheme as a whole is impossible from the standpoint of continuity. It seems possible that water movements generated in the northern part of L. I. S. where the density gradients are strongest, evolve into a persistent but non-steady state distribution of currents in which continuity is established by movement across isobaric surfaces in the southern part of L. I. S. where the density structure is weakest.

In brief, freshwater drainage tends to set up a simple counterclockwise movement of water in L. I. S. However, the necessary pattern of density distribution is never quite realized; it is continually weakened by lateral diffusion associated with the strong tidal oscillation, particularly along the Long Island shore where the freshwater supply is least. The net result is a series of eddies instead of one.

Summary of Surface Currents. A variety of evidence has been brought to bear on the problem of surface currents—drift bottles, current measurements, and density distribution. These cannot be synthesized into an entirely consistent picture; nevertheless, the composite diagram shown in Fig. 10 indicates general agreement as to the major features of the circulation pattern. The long solid arrows in Fig. 10 indicate the direction of propagation of density currents as determined by a more or less typical salinity distribution (Fig. 4, supplemented by data on the western part of L. I. S. from 9B). In the southern part, these arrows are terminated well offshore, since the isohalines cannot indicate properly the direction of flow, and the density distribution probably impedes movement rather than propagating it.

The short solid arrows are the residual drifts from Fig. 8A. Short dotted arrows postulate an onshore set in two areas where most of Prytherch's drift bottles were grounded. Of the bottles recovered in L. I. S., 85% were returned from these two strips, which constitute less than 50% of the shore line. None was recovered west of Darien, Connecticut nor on the Long Island shore west of Port Jefferson.

Such a complete separation cannot be accounted for simply by the distance from the point of release. Hence an offshore set is indicated by short dotted arrows in the western area.

In the central part of L. I. S. the observations are less complete than elsewhere. Long dotted arrows indicate a possible pattern of currents which is based on the weak density gradients shown in Fig. 9A. Obviously a drift to the north is necessary in order to satisfy continuity. Moreover, the postulated pattern requires a convergence of currents on both the Long Island and Connecticut shores (and subsequent deflection offshore) at points which mark approximately the centers of the major drift bottle recoveries.

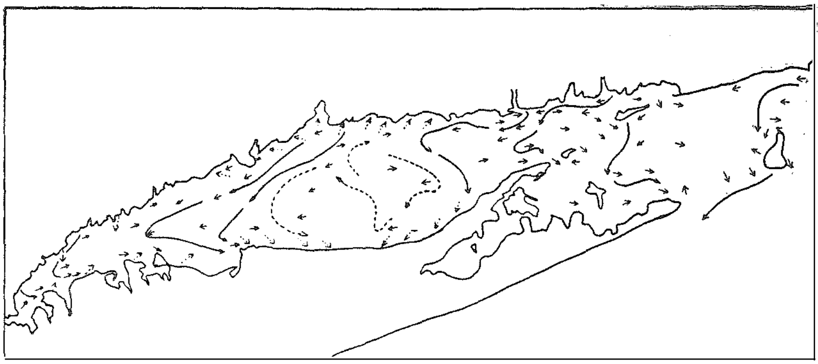


Figure 10. Composite diagram of surface currents. For explanation, see text.

Some of the features that have been discussed may be quite variable. During periods of heavy river drainage, the fresh water is sometimes carried well out into the Sound. Probably it forms clockwise eddies that alter the circulation pattern locally. The effect is likely to be greatest off the mouth of the Connecticut River. Ordinarily there appears to be a pool of fresh water and a clockwise eddy between the mouth of the river and Long Sand Shoal. But when the fresh water extends far beyond the Shoal, as in Fig. 3, the compact system of currents in the eastern end of L. I. S. must be changed considerably. Fig. 3 also suggests that such eddies may break away intact and move out into B. I. S.

Currents in the central part of L. I. S. are probably particularly variable. The salinity distribution changed from one cruise to the next, but the possible changes in currents are too uncertain to warrant discussion. The early recoveries in the drift bottle experiments, first to the east and then to the west of the point of release, are not entirely explained by the pattern of currents in Fig. 10. The results would seem more reasonable if the central eddy were displaced some ten miles westward at the time of the experiments.

THE CONSERVATION OF MASS AND SALT WITHIN LONG ISLAND SOUND

Freshwater Drainage. Further inquiry into the physical oceanography of L. I. S. will include estimates of mass transport, the exchange of water and salt between L. I. S. and B. I. S., and effects of turbulence. A prerequisite to all such work is a quantitative knowledge of the rate of addition of fresh water to L. I. S. Data largely from Suttie (1928) show that three rivers supply the major inflow. The Connecticut River ranks first with a drainage basin of 11,200 sq. mi. (statute); the Housatonic River drains 1,930 sq. mi. and the Thames River 1,400. Smaller rivers and streams of Connecticut, Long Island, and the mainland of New York State contribute drainage from 1,290 sq. mi. Thus the total drainage basin of L. I. S. is 15,900 sq. mi.

Data on river discharge during 1946 were obtained from the water supply papers of the U. S. geological Survey, as follows: (a) Observations on the monthly discharge of the Connecticut River from a gauging station at Thompsonville, Connecticut, which measures the drainage from 9,661 sq. mi. of the basin. (b) Similar observations for the Housatonic River at Stevenson, Connecticut, drainage basin 1,545 sq. mi. (c) Data on average monthly discharge per square mile of drainage basin for three smaller rivers, the Shetucket, Quinnipiac, and Saugatuck (respectively 401, 109, and 77.5 sq. mi.). Items (a) and (b) were used directly; they constitute 70% of the total drainage basin of L. I. S. It was assumed that the remaining 30% could be estimated with sufficient accuracy by applying the average of (c). The results are shown in Fig. 11. The average fresh water drainage during 1946 was 679 m^3/sec. The total was 214 x $10^8 m^3$, or about 35% of the volume of L. I. S. below mean low water.

The total freshwater increment includes rainfall on the surface of the Sound as well as river drainage. According to the Monthly Weather Review, the mean rainfall in New England in 1946 was 38.41 inches (98 cm).

In problems involving the conservation of mass and salt, an allowance must be made for the loss of water by evaporation. It has not

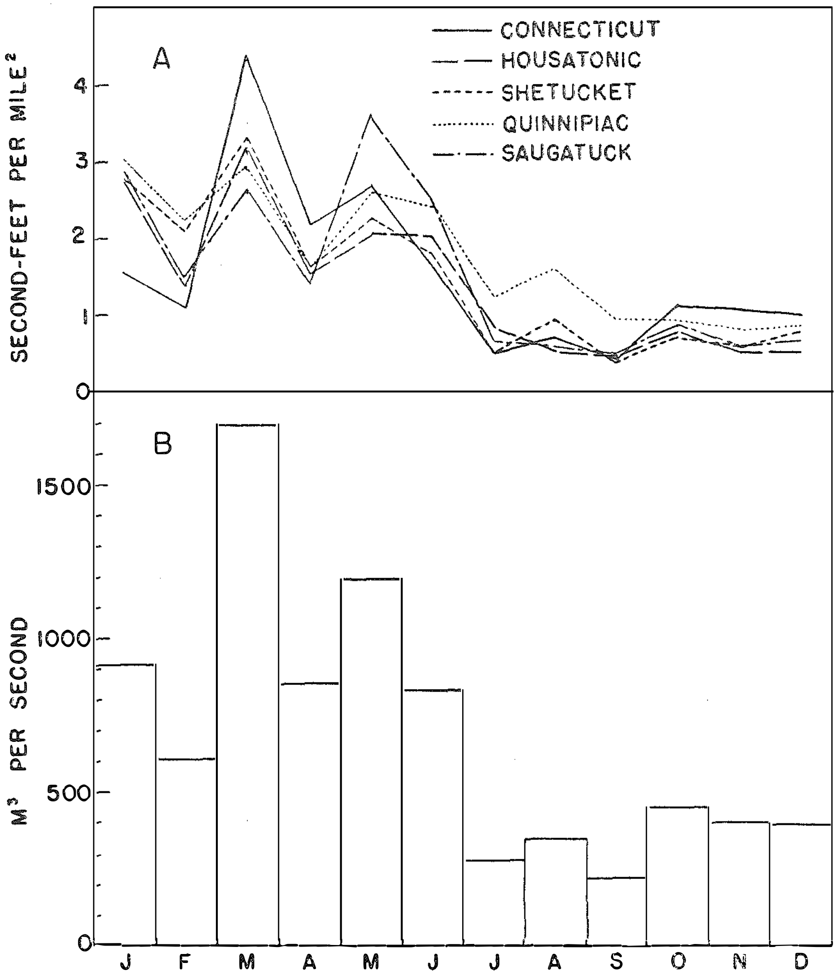


Figure 11. Freshwater drainage. *A*. Runoff in cubic feet per second from each square mile of the drainage basin of five Connecticut rivers. *B*. Estimated mean monthly drainage into L. I. S. during 1946.

been computed or measured, but general information on oceanic evaporation (Sverdrup, et al., 1942: 123) indicates that the total evaporation loss is about the same as the 1946 rainfall. Therefore the net increment of fresh water will be assumed to equal the river drainage in Fig. 11.

Mass Transport. Freshwater drainage creates a small hydraulic head of water such that over a period of time there must be a corresponding net transport of water from L. I. S. Superimposed upon the net transport is a series of exchange transports between L. I. S. and the adjacent waters. The largest of these of course is the tidal exchange. Only the net and tidal transports can be described with a satisfactory degree of accuracy. However, certain other aspects of the transport system are so important that an attempt must be made to evaluate them.

Fig. 8 shows that surface water moves through L. I. S. from west to east. At the westernmost point of current observation in the Sound, the residual surface velocity was 6 cm/sec. The cross section of the channel at this point is about 37,000 m^2. Thus, if the current extended from surface to bottom and averaged about two-thirds of the surface velocity (cf. Sverdrup, et al., 1942: 568), the mass transport into L. I. S. at this point would be about 1,500 m^3/sec. However, farther to the west, in the constricted part of the channel known as the East River, current observations have indicated a residual drift in the opposite direction, toward New York Harbor and the open sea. The source of these divergent surface movements must be upwelling water from deeper layers. Thus there is no certainty of a mass transport into L. I. S. at the western end. Probably there will be no great error if the transport is assumed to be negligible.

In the eastern passes both the observed surface velocities and the cross-sectional areas are much larger than those in the western channel. A calculation that assumes, as before, a mean eastward velocity in the passes equal to two-thirds of the surface velocity yields a transport of 34,000 m^3/sec. This is 45 times the net transport, a difference that could hardly be due to ordinary observational error. Possible alternatives are that the movement occurs only in a very thin surface stratum 1–2 m thick, or that there is a two-layered transport system such that water flows out at the surface and into L. I. S. at a deeper level.

Fig. 8 shows that surface currents followed lines of equal density where it was possible to do so without violating continuity. In the eastern end of L. I. S., the density structure agrees with observed currents; the outflow is probably essentially a density current. It would not be realistic to suppose that the usual mathematical relations between dynamic topography and current velocity are quantitatively applicable to an area where the water is squeezed through a series of channels and is subjected to intense bottom friction. However, it may be useful to prepare a maximum estimate of transport by the application of dynamic theory to the observed density distribution. For this purpose, two stations were chosen from each cruise (except Cruise 5, in which the data were inadequate), one in B. I. S. a few miles to the east of the passes (at about 41° 12′ N, 71° 50′ W), the other in the eastern part of L. I. S. (at about 41° 15′ N, 72° 10′ W). The first column in Table II shows the southward transport between these stations relative to the 30-meter depth, which is near bottom in B. I. S. and approximates the mean depth of L. I. S. at this longitude.

TABLE II. Transport Computations—Exchange between the Long Island and Block Island Sounds in m^3/sec.

Cruise	*Maximum transport*	*Drainage*		*Surface outflow*	*Bottom inflow*
		Period	*m^3/sec*		
1	70,800	Jan.	910	18,860	17,950
2	73,500	Feb-Mar.	1,150	20,820	19,670
3	86,000	Mar.-Apr.	1,270	23,730	22,460
4	28,100	Apr.-May	1,020	8,660	7,840
6	54,500	July-Aug.	310	11,610	11,300
7	28,600	Sept.-Oct.	330	6,970	6,640
8	35,500	Oct.-Nov.	420	7,960	7,540
9	40,200	Nov.-Dec.	390	9,930	9,540

The average of the transport computations is larger than the rough estimate of 34,000 m^3/sec based on observed currents in the passes. It is much larger than the generalized estimate of drainage during the preceding month or two, which is shown in the next part of Table II. However, there are reasons for believing that the transport estimates are much too large, aside from the matter of frictional effects. In the first place, the effect of freshwater drainage is not merely to create a hydraulic head by the addition of mass to L. I. S. It also tends to create a slope in the free surface by reducing the density of the water mass as a whole. It follows that the surface outflow will exceed the net transport, and to maintain continuity of mass there must be a compensating inflow of deeper water.

Second, it is arbitrary to fix 30 m as a depth of no motion. It is more realistic to assume that the net transport is correct. In that case the average depth of the surface of no motion must be reduced; there will be a southerly transport above this depth and a northerly one below. The dynamic computations are readily altered to fit this concept by subtracting a systematic correction from the transport values for successive depth intervals. The results are shown in the last two columns of Table II.

The figures so obtained are still maximal estimates, since no allowance has been made for frictional retardation. However, the discrepancy between net and total transport has been removed, and the computed surface currents are of the order of magnitude of the observed values. Total transports in the upper 5 m, divided by the cross-sectional area of the upper 5 m of the passes, yield estimates of 5–16 cm/sec, as compared with observed velocities of 6–33 cm/sec. Moreover, the concept that dilution by river drainage is fundamentally responsible for the maintenance of a two-layered transport system is supported by the fact that there is a correlation between the amount of drainage and the mass transport data in the last column of Table II.

TABLE III. Mean Salinity at a Station in B. I. S. at About 41° 12′ N, 71° 50′ W and in L. I. S. within the Listed Longitude Ranges

	Cruise							
L. I. S.	*1*	*2*	*3*	*4*	*6*	*7*	*8*	*9*
72–10 to 72–20 W	28.46	28.12	28.97	28.35	29.76	29.60	30.80	30.28
72–20 to 72–30 W	28.73	26.99	27.14	27.44	28.31	29.56	30.40	29.80
72–30 to 72–40 W	27.83	26.80	27.74	26.52	27.61	28.46	28.80	28.94
72–40 to 72–50 W	27.11	26.66	27.01	26.72	27.52	27.86	28.50	28.47
72–50 to 73–00 W	27.11	26.40	27.08	26.75	27.04	27.72	28.20	28.38
73–00 to 73–10 W	26.78	26.31	26.52	26.06	27.13	27.50	28.20	28.20
72–10 to 73–10 W	27.59	26.81	27.35	26.91	27.71	28.34	29.00	28.91
B. I. S.	31.03	30.17	30.54	29.61	30.59	31.23	31.90	32.02

If the postulated mechanism is correct—that freshwater drainage regulates the amount of inflow of more saline water from B. I. S.—it regulates the salinity at a more nearly uniform level than would otherwise be possible.

The Total Exchange of Water and Salt between the Two Sounds. If the net transport described above were the only movement of water in the eastern passes, L. I. S. would be diluted about 35% each year. Maintenance of an approximately constant salinity through the years requires the transfer of salt from B. I. S., by mass transport or by diffusion, in sufficient quantity to offset the tendency toward dilution. An elementary application of the principle of salt continuity is sufficient to determine the total amount of B. I. S. water that must be brought into L. I. S. during a given period in order to maintain the observed salinity.

Table III lists salinity data that will be used for the exchange computation and for other calculations later. Values for B. I. S. were obtained by averaging the salinity, surface to bottom, at a station a few miles east of the mouth of L. I. S. Within L. I. S. the observations were averaged on a volumetric basis; i. e., the product of the mean salinity of successive layers and the volume of water in each layer was summed from surface to bottom and divided by the total volume of water. By this method it is possible to deal with the salinity of the water mass as a whole and to ignore, for the moment, the effects of vertical diffusion.

TABLE IV. COMPUTATION OF EXCHANGE BY THE METHOD OF PROPORTIONAL PARTS

	Cruises						
	1–2	*2–3*	*3–4*	*4–6*	*6–7*	*7–8*	*8–9*
Mean salinity B. I. S.	30.60	30.35	30.08	30.10	30.91	31.57	31.96
Fresh water, 10^6 m^3	4,547	3,666	3,352	3,352	1,171	1,315	1,546
m^3/sec.	1,080	1,020	1,200	470	280	440	390
% of L. I. S.	7.34	5.93	5.42	5.42	1.90	2.13	2.50
B. I. S. inflow, m^3/sec.	4,610	12,400	7,060	8,380	6,700	10,240	3,050
L. I. S. outflow, m^3/sec.	5,690	13,420	8,260	8.850	6,980	10,680	3,440

Further steps in the exchange computation are shown in Table IV. The first line is the mean salinity between successive cruises at the B. I. S. station, obtained by averaging the data in Table III. The next line is the total freshwater drainage between cruises, which is listed also as mean flow in cubic meters per second and as a percentage of the total volume of L. I. S. If mixing processes in L. I. S. are rapid enough so that the fresh water is distributed fairly uniformly, the following type of calculation is permissible:

In the east-central part of L. I. S., where the mean salinity was $27.59^{\circ}/_{oo}$ during the first cruise, addition of 7.34 parts of fresh water per 100 parts of L. I. S. water between Cruises 1 and 2 would reduce the salinity to $27.59 \times 100/107.34 = 25.74^{\circ}/_{oo}$. However, the observed salinity at the time of the second cruise was $26.81^{\circ}/_{oo}$. If the difference were due to the introduction of x parts of B. I. S. water with a mean salinity of $30.60^{\circ}/_{oo}$, then

$$100\ (27.59) + 7.34\ (0) + 30.60x = (107.34 + x)\ 26.81,\ x = 31.3\%.$$

Thus the estimated introduction of B. I. S. water between Cruises 1 and 2 was 31.3% of the volume of L. I. S. From the volume of L. I. S. and the time interval between cruises,

$$\text{Inflow from B. I. S.} = \frac{.313 \times 6{,}184 \times 10^7 \text{m}^3}{4.2 \times 10^6 \text{ sec}} = 4610 \text{ m}^3\text{/sec.}$$

To maintain a constant mass of water in L. I. S., the mean outflow must equal the sum of drainage and inflow, or 5,690 m^3/sec. This and similar calculations for other cruise intervals yield the estimates shown in the last two lines of Table IV.

The method that has been described is simpler and less precise than Ketchum's (1951) treatment of the flushing of estuaries. The latter is not easily applied to L. I. S., with its complicated drainage and circulation pattern. Nearly 80% of the drainage (Connecticut and Thames Rivers) is introduced into L. I. S. within a few miles of the eastern passes. Its influence on the western part of L. I. S. is uncertain and probably variable. The method that has been described is perhaps the most accurate way of obtaining an estimate of the total exchange between the two Sounds, but it is not easily elaborated into a study of the exchange through successive cross sections of L. I. S.

The data in Table IV have meaning only as a statistic; they tell nothing about the processes effecting the transfer of salt. If the latter resulted solely from mass movements, the transport would be less than the maximum estimate based on dynamic topography. The nontidal velocities in the passes would be of the order of 4–10 cm/sec. On the other hand, if the two-layered transport system postulated in the previous section were quantitatively insignificant, the transfer of salt might be accomplished by the random interchange of small water masses. The transfer would be described in terms of the salinity gradient and a coefficient of lateral eddy diffusivity. The latter is readily determined from the transport data as the product of the mean velocity of exchange per unit cross-sectional area of the passes (1.9–5.2 cm/sec) and the distance between the B. I. S. station and the eastern part of L. I. S. (about 2.7×10^6 cm). Thus the estimated range in the diffusion coefficient is 5×10^6 to 1.4×10^7 cm^2/sec.

The truth must lie somewhere between these extremes. Lateral diffusion is inevitable in an area of strong tidal exchange. The existence of a two-layered transport system is supported by the analysis of the density distribution and by the accompanying theoretical considerations. The dynamic computations provide a method of making a tentative estimate of the relative importance of advection and of diffusion. For example, (a) assume that the relative variation in transport in Table II is correct, but that the estimates are systematically too large (i. e., frictional retardation reduces the transport to a certain fraction of the values listed); (b) assume that there is no consistent relation between diffusion and transport. If these assumptions are correct, the actual transport can be estimated by a statistical comparison between the dynamic computations and the total transfer as determined in Table IV. A least squares treatment[3] indicates that the transport is 20% of the values obtained by dynamic computation and thus ranges from 1,400–4,200 m^3/sec. The remainder of the inflow, which is assumed to be part of the diffusion mechanism, has a mean value of 4,960 m^3/sec. The estimated average coefficient of eddy diffusivity is 6×10^6 cm^2/sec in the passes and 3.3×10^6 in the less constricted area in the eastern part of L. I. S., between 72° 00′ and 72° 10′ W.

LATERAL DIFFUSION IN LONG ISLAND SOUND

The mean salinity, surface to bottom, previously shown in Table III, will be used to estimate the magnitude of lateral diffusion in the central body of L. I. S. water between 72° 20′ and 73° 00′ W. The change in salinity from one cruise to the next will be examined by means of the simplified equation

$$\frac{\partial S}{\partial t} = \frac{A_x}{\rho} \cdot \frac{\partial^2 S}{\partial x^2} - V\frac{\partial S}{\partial x} + \frac{\partial S_f}{\partial t},$$

in which the time rate of change of salinity S is postulated to depend upon three factors: (a) horizontal diffusion, the product of the coefficient of eddy diffusivity A_x and the change in the salinity gradient per cm of horizontal distance x along the long axis of L. I. S., taken as positive eastward; (b) advection, the product of the net transport velocity V and the salinity gradient; and (c) the rate of change of salinity due to the addition of fresh water to the Sound $\partial S_f/\partial t$.

Table V shows the mean values for the terms in the equation, calculated for the periods between successive cruises. Details of the method of calculation are appended to Table V, showing the transformation of the original differential form to terms of finite differences. The values listed are used to solve for the one unknown term A_x, and the results are shown in the last line of Table V. The calculated coefficients are of the order of magnitude of the ones obtained by a slightly different method in the previous section. They also fall within the general limits of previously computed values for surface

---

[3] The statistical method as applied here compares the average transport of two successive cruises (Table II) with the average inflow (Table IV) between cruises.

TABLE V. COEFFICIENTS OF HORIZONTAL EDDY DIFFUSIVITY IN L. I. S.*

	Cruises						
	1–2	*2–3*	*3–4*	*4–6*	*6–7*	*7–8*	*8–9*
Time, 10^6 seconds	4.2	3.6	2.8	7.1	4.2	3.0	4.2
$\Delta\bar{S}$	−0.78	0.54	−0.44	0.80	0.63	0.66	−0.09
$10^{11}\partial\bar{S}/\partial t$	−18.6	15.0	−15.7	11.3	15.0	22.0	−2.1
$10^3\Delta S_f$	−2.00	−1.61	−1.47	−1.48	−0.53	−0.61	−0.72
$10^{11}\partial S_f/\partial t$	−47.5	−44.6	−52.5	−20.8	−12.7	−20.3	−17.2
$10^{11}\partial S/\partial x$, 72-10 to 73-10	25.4	31.0	34.5	35.8	34.5	34.3	34.2
72-10 to 72-40	35.0	43.4	48.3	57.0	53.0	52.4	54.4
72-40 to 73-10	16.0	18.6	20.6	14.5	16.0	16.3	14.0
V, cm/sec.	0.20	0.19	0.22	0.09	0.05	0.08	0.07
$10^{11}V\partial S/\partial x$	4.9	5.9	7.6	3.2	1.7	2.7	2.4
$10^{17}\partial^2 S/\partial x^2$	5.5	7.2	8.1	12.4	10.8	10.5	11.7
$10^{-6}A_x$	6.1	9.1	5.5	2.9	2.8	4.3	1.5

* From the time between successive cruises in line 1 and the change in the mean salinity in L. I. S. between 72-10 and 73-10 W (cf. Table III) in line 2, the time rate of change $\partial\bar{S}/\partial t$ is calculated in g/cm³/sec. ΔS_f is the product of the mean salinity and the percentage volume of freshwater drainage (Table II), which is then divided by the time to give the time rate of change of salinity due to dilution $\partial S_f/\partial t$. Next are listed three sets of east-west salinity gradients, based on the mean values in Table III. The first group is the difference between the salinity at 72-10 to 72-20 W and at 73-00 to 73-10 W, divided by the distance between the midpoints of these groups, 72-15 to 73-05, or 6.88 x 10^6 cm. Similarly, the gradients in the eastern and western halves of this area are determined separately by establishing an estimated mean salinity at the midpoint (72-40) as the mean of the data from 72-30 to 72-50. The velocity of net transport V is calculated from the total drainage in m³/sec and the mean cross-sectional area of the Sound. The next line shows the product of the velocity and the salinity gradients between 72-10 and 73-10. $\partial^2 S/\partial x^2$ is the difference between the second and third gradients divided by the distance between the centers of the areas, 3.44 x 10^6 cm. Application of these data to the equation yields the coefficients of eddy diffusivity shown in the last line.

waters of the oceans, which Sverdrup, et al. (1942: 485) listed as about 10^6–10^8 g/cm/sec. That they lie near the lower limit of this range is to be expected in a relatively small body of water. The suggested seasonal variation, with the largest values in spring, may or may not be valid. The results are subject to considerable variation due to sampling error. Moreover, it is apparent that the net transport may be a serious over-simplification of the advection term. If the central part of L. I. S. has a two-layered transport system, such as was previously postulated for the eastern passes, the mixing effects of this transport will be included in the estimates of the diffusion coefficients. Therefore, the latter may be too high by an unknown and possibly variable amount. It is reasonable to suppose that lateral diffusion is primarily governed by the strength of the tidal currents. If this is so, the coefficients should be smaller in the central part of L. I. S. than in the eastern end, where the previous section suggested an average value of 3.3 × 10^6. Thus the lower values in Table V are probably more realistic than the higher part of the range.

VERTICAL EDDY CONDUCTIVITY

The seasonal temperature change provides a convenient means of estimating vertical turbulence, and the calculations can be carried out in greater detail than in the previous section because of the larger quantity of temperature records available.

For purposes of analysis, the part of L. I. S. between 72° 00′ and 73° 10′ W was divided into seven areas, each comprising 10 minutes of longitude and extending in a north-south direction across the width of the Sound. In each case the eddy conductivity was determined at depths of 10, 20, and 30 m, or at as many of these as the depth of water permitted.

In the absence of modifying effects due to advection and lateral conduction, the rate of passage of heat through a unit horizontal surface at a given depth z_1 is given by

$$A_z \frac{\partial \vartheta}{\partial z} = \int_{\text{bottom}}^{z_1} \frac{\partial \vartheta}{\partial t} dz ,$$

in which the product of the coefficient of vertical eddy conductivity A_z and the vertical temperature gradient $\partial \vartheta / \partial z$ at depth z_1 is equal to the time rate of change of temperature in the underlying water column. Tables VI and VII show the observed mean temperature gradients and the temperature change in the lower water between successive cruises. Application of these values to the equation yields the coefficients shown in Table VIII.

It is apparent that the equation is severely simplified. In the presence of horizontal temperature gradients in the lower water, horizontal diffusion and transport will modify the rate of change of heat and may cause a serious error in the estimate of vertical turbulence. A few calculations were made to assess these errors in terms of observed horizontal temperature gradients and of the previous estimates of net transport and lateral eddy diffusion. In no case did these effects account for as much as 1% of the observed temperature change. Nevertheless, Tables VI, VII, and VIII show that more serious errors exist. Question marks are inserted in Table VIII in places where the calculations yield negative values for the eddy coefficient. All such values were obtained in the eastern part of L. I. S., where it has been suggested previously that transport varies significantly with depth, thus invalidating the use of a mean transport

TABLE VI. Mean Temperature Decrease in °C x 10^{-2} per Cm of Depth in the Depth Range Listed. Each Value Is the Average for the Pair of Cruises. Cruise 5 Is Omitted because of Incomplete Data, and Cruise Intervals 1–2 and 6–7 Are Omitted because They Occurred Near the Minimum and Maximum Points of the Seasonal Temperature Cycle, When the Method Is Likely to Yield False Results.

Cruises	*Depth range (m)*	*72–00 to 72–10*	*72–10 to 72–20*	*72–20 to 72–30*	*72–30 to 72–40*	*72–40 to 72–50*	*72–50 to 73–00*	*73–00 to 73–10*
2–3	0–20	3.33	4.72	5.97	6.71	6.21	9.65	11.38
	10–30	−0.14	0.86	0.38	—	—	4.71	4.43
	20–45	−1.43	0.57	—	—	—	—	—
3–4	0–20	3.90	4.53	5.26	3.81	6.13	10.11	9.16
	10–30	−0.22	1.29	1.10	—	—	6.12	6.87
	20–45	0.70	0.95	—	—	—	—	—
4–6	0–20	2.73	3.08	3.95	4.93	6.05	9.34	6.98
	10–30	−0.35	1.06	0.98	—	7.01	7.97	7.85
	20–45	0.85	1.01	2.03	—	—	—	—
7–8	0–20	0.25	0.25	−1.52	−0.93	−1.72	−1.80	−0.46
	10–30	−0.78	0.05	−1.42	−0.79	−1.68	−2.25	−1.43
	20–45	−0.96	0.17	−1.08	—	—	—	—
8–9	0–20	−0.11	−0.57	−1.01	−1.85	−3.57	−3.03	−0.51
	10–30	−1.54	−0.73	−1.03	−1.32	−2.04	−3.13	−1.97
	20–45	−1.82	−0.69	−0.96	—	—	—	—

value for the whole vertical column. Here also, Table VII shows that the apparent rate of passage of heat through the 20 and 30-m levels sometimes exceeded that of the 10-m level. This presumably indicates advection. It probably means that warm surface water from B. I. S. sank and moved into L. I. S. along the bottom.

TABLE VII. Rate of Accumulation of Heat in Calories x 10^{-4}/Cm^2/Sec below the 10, 20, and 30-M Levels.

Cruises	*Depth (m)*	*72–00 to 72–10*	*72–10 to 72–20*	*72–20 to 72–30*	*72–30 to 72–40*	*72–40 to 72–50*	*72–50 to 73–00*	*73–00 to 73–10*
2–3	10	25.0	23.9	18.1	17.8	19.7	16.4	19.5
	20	24.5	17.2	12.8	—	—	12.8	15.0
	30	23.1	9.7	—	—	—	—	—
3–4	10	44.4	36.5	25.4	20.0	20.7	21.8	22.5
	20	54.0	25.8	18.6	—	—	13.2	15.4
	30	51.9	15.0	—	—	—	—	—
4–6	10	24.0	25.6	18.6	16.8	18.9	18.2	19.4
	20	26.8	18.7	13.5	—	11.6	12.7	15.4
	30	25.9	10.4	11.0	—	—	—	—
7–8	10	−24.0	−18.7	−18.3	−18.7	−23.0	−21.7	−23.0
	20	−25.7	−18.4	−13.3	−9.3	−13.3	−14.7	−16.7
	30	−24.0	−9.0	−11.0	—	—	—	—
8–9	10	−67.9	−47.4	−34.8	−27.4	−31.6	−31.2	−41.6
	20	−56.7	−34.5	−25.7	−13.6	−19.3	−22.1	−24.3
	30	−55.0	−20.0	−22.1	—	—	—	−15.5

TABLE VIII. COEFFICIENTS OF VERTICAL EDDY CONDUCTIVITY IN G/CM/SEC.

Cruises	*Depth* (*m*)	*72–00* *to* *72–10*	*72–10* *to* *72–20*	*72–20* *to* *72–30*	*72–30* *to* *72–40*	*72–40* *to* *72–50*	*72–50* *to* *73–00*	*73–00* *to* *73–10*
2–3	10	7.5	5.1	3.0	2.7	3.2	1.7	1.7
	20	?	20.	34.	—	—	2.7	3.4
	30	?	17.	—	—	—	—	—
3–4	10	11.	8.1	4.8	5.3	3.4	2.2	2.5
	20	?	20.	17.	—	—	2.2	2.2
	30	74.	?	—	—	—	—	—
4–6	10	8.8	8.3	4.7	3.4	3.1	2.0	2.8
	20	?	18.	14.	—	1.7	1.6	2.0
	30	31.	10.	5.4	—	—	—	—
7–8	10	?	?	12.	20.	13.	12.	50.
	20	33.	?	9.4	12.	7.7	6.5	12.
	30	25.	?	10.	—	—	—	—
8–9	10	615.	83.	35.	15.	8.9	10.	82.
	20	37.	47.	25.	10.	9.5	7.1	12.
	30	30.	29.	23.	—	—	—	7.9

The existence of a few patently invalid results suggests that there may be considerable error in the rest of the calculations. However, in general the variability in the results is consistent with oceanographic concepts. The coefficients were smaller in summer than in winter, which is presumably a stability effect. But the stability is not great at any time in L. I. S., nor are the eddy coefficients as small as the values that have been derived in more stable waters (cf. Sverdrup, et al., 1942: 484). The coefficients tend to increase toward the eastern end of L. I. S. It is suggested that this is due to the increasing tidal current, which probably is the major factor in the generation of turbulence in these waters. There are also two depth relations. First, the eddy coefficient is greatest at 10 m and least at 30 m except in certain cases in which the stability changes markedly with depth. Second, at any given depth the coefficient is least when the depth of the underlying water column is small, as in the central part of L. I. S. between 72° 30′ and 73° 00′ W. The effect of bottom friction on current velocity is a possible explanation of this result.

A cursory examination was made of coefficients of vertical eddy conductivity in B. I. S. for comparison with L. I. S. and for use in later analyses. Table IX lists the calculated values for the station that was previously used in the study of transport between the two Sounds. The calculations are based on the rate of change of the heat content below the depths listed in Table IX and upon temperature gradients averaged for 5-m intervals. Thus the gradient from 0–5 m was used to derive the value for the 2.5-m depth, etc. The last line of Table IX,

TABLE IX. COEFFICIENTS OF VERTICAL EDDY CONDUCTIVITY IN B. I. S. (CA. 41° 10′ N, 71° 50′ W), 1946 DATA.

Cruises	*2.5 m*	*7.5 m*	*12.5 m*	*17.5 m*	*22.5 m*	*27.5 m*
2–5	3.2	4.9	4.5	4.6	4.7	3.6
5–7	1.5	1.7	1.4	1.9	1.2	0.5
7–9	10.0	12.0	14.0	16.0	18.0	13.0
9–2	9.0	11.0	12.0	12.0	12.0	8.0

representing the midwinter period, is based on the assumption that the temperature cycles repeat from one year to the next with sufficient precision to warrant combining data from different years.

The central part of B. I. S. was examined on 13 occasions from January 11 to December 19, 1949. One to five bathythermograms and surface thermometer readings were taken each time, and the data were used to derive coefficients of vertical eddy conductivity. It was found that the gradients were small and variable in the surface layer in summer and in the whole vertical column in winter. Since it was intended to apply the results to a later analysis of oxygen and phosphate distribution, it seemed advisable to obtain a simplified and generalized set of data on eddy conductivity. Therefore all winter observations were combined into an average temperature gradient, and all summer observations in the upper 10 m were similarly combined. The remainder was averaged at 10-m intervals for each date. These simplified gradients were applied to the average temperature change in the preceding and following time interval, and the coefficients so obtained are shown in Table X. These differ only in minor details from the estimates previously shown in Table IX.

TABLE X. COEFFICIENTS OF VERTICAL EDDY CONDUCTIVITY IN B. I. S., 1949 DATA.

Date	*5 m*	*15 m*	*25 m*
19/XII, 11/I—24/II	11.0	7.0	2.0
24/III	9.0	5.0	2.0
9/IV	2.5	5.0	2.0
7/V	2.5	1.9	1.5
2/VI	2.5	1.6	2.9
9/VIII	2.5	0.5	0.7
28/VIII	2.5	1.0	0.7
17/IX	2.5	2.9	0.5

CURRENTS AND SALINITY DISTRIBUTION IN BLOCK ISLAND SOUND

Fig. 10 shows that surface water moves westward into B. I. S. between Point Judith and Block Island, traverses most of B. I. S., and then joins the southeasterly flow from L. I. S. The discussion of exchange between the two Sounds has indicated that some of the water entering B. I. S. continues as a subsurface drift into L. I. S. The average mass transport might be as much as 7,500 m^3/sec (mean of values in Table IV) or it might be only a third as much (from estimates of the relative importance of advection and diffusion). These figures provide a rough estimate of current velocities in the deeper water. If the estimated transport occupied half of the cross section of B. I. S. at the longitude of the station used for analysis, the mean velocity would be 0.7–2.0 cm/sec.

A more detailed analysis of the currents may be obtained from an examination of the salinity distribution. Three stations were chosen for this purpose. The first was east of Block Island (ca. 41° 10′ N, 71° 12′ W). The second was the station previously used for studies of the exchange between the two Sounds, and the third was located in the eastern part of L. I. S. The three stations lay nearly in line along an east-west axis that approximately corresponds with the postulated direction of flow of the major current system. An equation was written to describe the rate of change of salinity S at a given point on this axis:

$$\frac{\partial S}{\partial t} = \frac{A_x}{\rho} \cdot \frac{\partial^2 S}{\partial x^2} + \frac{\partial}{\partial z} \cdot \frac{A_z}{\rho} \cdot \frac{\partial S}{\partial z} - V \frac{\partial S}{\partial x},$$

in which A_x and A_z are the coefficients of eddy diffusivity along the horizontal x-axis, directed positively eastward, and the vertical z-axis directed downward, and V is the horizontal current velocity. In applying the equation to estimate the currents at the center station, the following assumptions are proposed.

(1) The effect of lateral diffusion and advection at right angles to the x-axis is assumed to be negligible. This is probably false, but the necessary data for including the third axis are not available.

(2) The coefficient of lateral eddy diffusivity is designated as 3×10^6 g/cm/sec throughout, a value essentially in agreement with the L. I. S. estimates and probably of the right order of magnitude for B. I. S. (also cf. p. 63).

(3) The coefficients of vertical eddy diffusivity are assumed to equal the conductivity coefficients in Table IX.

The equation was applied in the form of finite differences. The methods were the same as those used in previous analyses that have been described in detail, and therefore the procedures will not be

TABLE XI. ESTIMATED CURRENT VELOCITIES IN B. I. S. (41° 10′ N, 71° 50′ W). POSITIVE VALUES ARE EASTERLY, NEGATIVE WESTERLY.

	10 m	*20 m*	*25 m*	*Mean*
March–July	0.2	0.3	−3.0	−0.57
July–October	−0.5	−0.5	−0.6	−0.53
Oct.–Jan. .	6.4	5.6	−32.0	−3.4
Jan.–March	−1.5	6.5	−8.4	−1.2

tabularized. The results are shown in Table XI. They confirm the existence of a westerly flow in the deeper water. The velocity seems to vary greatly, but part of this may be due to errors of sampling or of assumptions. The October to January period is particularly open to suspicion. During the remainder of the year, mass transport estimates developed from these velocities would be of the order of magnitude of the requirements for exchange between the two Sounds.

Table XI also indicates an easterly movement in the upper waters during most of the year, which presumably is part of the L. I. S. outflow. However, the eastward flow is weak; the average velocities for the water column as a whole (last column) are westerly. This agrees with previous evidence that most of the L. I. S. outflow passes out near Montauk Point and has relatively little effect on the central and eastern part of B. I. S.

The calculations suggest that the current pattern varies during the year. While the methods are such that not much confidence can be placed in the details of the analysis, certain aspects of the variability agree with other oceanographic information.

The period from July to October was the one time of the year when there was no evidence of any eastward transport through the central part of B. I. S. Freshwater drainage and the calculated L. I. S. outflow were smaller than average. Moreover, the lateral density gradient between the eastern part of L. I. S. and the center of B. I. S. was slightly stronger than at any other time of the year, largely because of the higher temperature of L. I. S. in summer. These phenomena logically would limit the outflow to a small and compact density current around Montauk Point. Finally, the plankton studies that follow will show that B. I. S. during this period had a greater than average abundance of organisms of offshore origin. This is part of a general phenomenon, for Bigelow and Sears (1939) have reported a maximum offshore influence in late summer and autumn in the whole coastal area. However, a vertically diffuse westerly drift of the kind shown in Table XI appears to be particularly favorable for bringing these organisms into B. I. S.

The L. I. S. outflow increased in midwinter, and it had a pronounced freshening effect on B. I. S. The outflow continued to be strong through the spring months, although the freshening effect lessened. Therefore, although the outstanding characteristic of the midwinter period was the magnitude of the L. I. S. influence, this was due primarily to the diffuse nature of the circulation pattern rather than to the volume of the outflow. While Fig. 3 indicates that most of the outflow passed around Montauk Point, as in other seasons, the major gradients in temperature and salinity were pushed eastward to the middle of B. I. S., and the density gradients were weaker than in summer. In the central and eastern part of B. I. S., about two-thirds of the winter stations showed a salinity minimum at mid-depths. Similar minima were observed also during the winter of 1949. These minima indicate that the effect of the L. I. S. outflow was most pronounced at mid-depths. In the zone of active admixture of the two water masses, there are areas, particularly in the northwestern part of B. I. S., where such admixture can produce water that is slightly fresher and colder than the main body of B. I. S. water but within the same density range. There are no density barriers to prevent this water from moving eastward through B. I. S. The quantitative analysis of the January–March period in Table XI indicates that this mid-depth movement is a definite current rather than lateral diffusion.

REFERENCES

Bigelow, H. B. and Mary Sears
1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Harv. Mus. comp. Zool., *54* (4): 183–378.

Galtsoff, P. S. and V. L. Loosanoff
1939. Natural history and method of controlling the starfish (*Asterias forbesi*, Desor). Bull. U. S. Bur. Fish., *49:* 75–132 (Bull. No. 31).

Ketchum, B. H.
1951. The flushing of tidal estuaries. Sewage and Industr. Wastes, *23:* 198–208.

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

REDFIELD, A. C.

1950. The analysis of tidal phenomena in narrow embayments. Pap. phys. Oceanogr. Meteorol., *11* (4): 1–36.

RILEY, G. A.

1941. Plankton studies. III. Long Island Sound. Bull. Bingham Oceanogr. Coll., *7* (3): 1–93.

SUTTIE, R. H.

1928. Report on the water resources of Connecticut. Bull. Conn. geol. nat. Hist. Surv., *44*: 1–168.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING

1942. The oceans. Prentice-Hall, Inc., N. Y., 1087 pp.

PHYTOPLANKTON OF BLOCK ISLAND SOUND, 1949

By Gordon A. Riley

Bingham Oceanographic Laboratory
and
Woods Hole Oceanographic Institution[1]

TABLE OF CONTENTS

ABSTRACT

Observations were obtained in the central part of Block Island Sound[2] on 12 occasions during 1949. They consisted of the following: measurements of temperature with surface bucket thermometer and bathythermograph; analyses of salinity, oxygen, and phosphate at a series of five or six depths between surface and bottom; phytoplankton cell counts at the same depths and analyses of plant pigments in the surface water; Secchi disc readings; collections of zooplankton and bottom fauna, which will be described by other writers.

Minimum concentrations of phytoplankton were found in midwinter and in midspring. There was a flowering of moderate size in February and other flowerings of slightly smaller proportions in the summer. The phosphate concentration had a midwinter maximum and declined sharply during the spring flowering. These phenomena are typical of temperate coastal waters.

The phosphate concentration was not at any time much less than 0.5 mg-at P/m^3, and the quantity of zooplankton was not correlated in an obvious way with the phytoplankton concentration. Probably neither of these factors was very important in determining the form of the seasonal cycle of phytoplankton. There was some

---

[1] Contribution No. 579 from the Woods Hole Oceanographic Institution.

[2] Hereafter Block Island Sound will be referred to as B. I. S., Long Island Sound as L. I. S.

evidence that the phytoplankton was partly controlled by undetermined chemical or biological factors; however, it also seems likely that physical oceanographic processes had a drastic effect on the quantity and composition of the flora.

The species composition is described and discussed from the standpoint of dominant species, seasonal succession, and comparison with adjacent waters. A few growth experiments during the period of the spring flowering provided information on the potential growth rates of the dominant species. In two of the three experiments, the growth rates were correlated with the observed growth in B. I. S. waters.

A quantitative analysis of oxygen and phosphate distribution has been used as the basis for a rough estimate of productivity. The average rate of increase of the phytoplankton in the upper 20 m is estimated to be of the order of 26% of the population per day, in excess of the immediate requirements of zooplankton and bacteria in the surface layer. The average consumption by zooplankton is probably not more than 4% of the phytoplankton population per day; bacterial requirements have not been estimated. Some of the excess phytoplankton production of the surface layer is transferred downward and is utilized by animals and bacteria on and near the bottom. The calculations indicate that not more than 19% of the phytoplankton population is so utilized each day. It is postulated that the remaining 7% of the daily excess production is lost by lateral dispersal (exchange with sparser populations offshore). The productivity estimates and the available data on phytoplankton distribution are used to determine the magnitude of the coefficient of lateral eddy diffusivity necessary to produce the estimated amount of physical dispersal. The result agrees with previous calculations of eddy diffusion obtained by analyzing the salinity distribution.

ACKNOWLEDGMENTS

The B. I. S. collections described herein were obtained aboard the commercial dragger ELEANOR of Stonington, Connecticut. To the owner and master, Captain Ellery Thompson, the writer is deeply grateful, not only for permission to use the vessel and for help in every phase of the field work, but also for much useful information about B. I. S. and a thoroughly enjoyable association.

The phytoplankton survey was part of a cooperative program. Georgiana B. Deevey (1952) discusses the zooplankton collections; at a later date Frederick E. Smith will publish an analysis of the bottom fauna. To the former, the writer is indebted for permission to use some of the zooplankton data in the present paper, to the latter for help in the field work, and to both for valuable discussions of our various problems. Other members of the laboratory, Daniel Merriman, E. F. Thompson, and Y. H. Olsen, have been helpful in many ways.

The paper summarizes some hitherto unpublished observations on L. I. S. This work was made possible by the cooperation of Victor L.

Loosanoff of the Milford Laboratory of the U. S. Fish and Wildlife Service, who provided collecting facilities and laboratory space. This opportunity is taken to thank him and his staff for their help.

METHODS

On 12 occasions during 1949, samples were obtained from the central part of B. I. S. at either Station A or B (Fig. 1). The collections for phytoplankton counts and chemical analyses ordinarily consisted of five or six samples between surface and bottom. Other observations included a surface temperature reading with a bucket thermometer, a bathythermogram, a Secchi disc reading, and oblique tows with a Clarke-Bumpus sampler, using no. 2 and no. 10 nets. Additional surface samples and zooplankton tows were sometimes obtained at other positions indicated in Fig. 1.

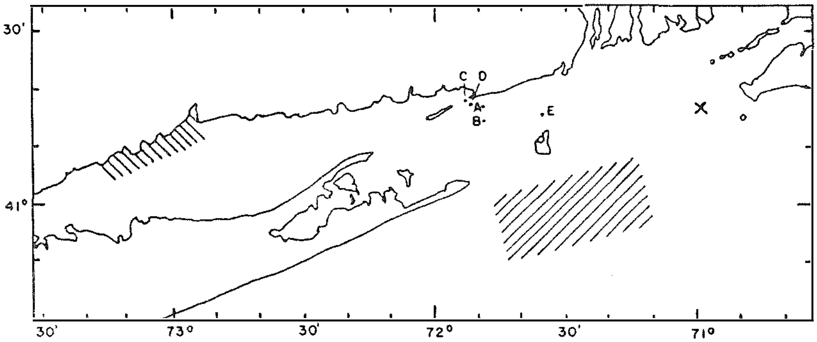


Figure 1. Positions of phytoplankton observations. A to E, stations in B. I. S.; x, Lillick's (1937) collections; hatched areas, previous measurements by the writer in L. I. S. and in the coastal water south of B. I. S.

Salinity samples were titrated with silver nitrate standardized against Woods Hole standard sea water. An ordinary burette was used. The probable error of the determinations is of the order of $\pm 0.03\,^{\circ}/_{\circ\circ}$, which is considered to be sufficiently accurate for work in neritic waters.

Oxygen and phosphate were determined by the usual Winkler and Atkins-Deniges methods, respectively. A visual colorimeter was used to read the phosphates, and a salt error correction of 1.35 was applied throughout.

For phytoplankton examination 350 ml of water were preserved with neutral formalin. After the bottles had been allowed to stand several days, the samples were concentrated by slowly siphoning off the water until about 20 ml remained in the bottom of the bottle. This was quantitatively removed to a large vial. Later the sample was further concentrated to about 3 ml; the volume was measured and 1 ml was drawn off for counting in a Sedgwick-Rafter cell. At least one sample from each day's collection was prepared as a semipermanent Hyrax mount for identification purposes.

In addition to the counts, a liter of surface water was filtered through no. 50 Whatman paper, and the residue was extracted with acetone for colorimetric comparison with the Harvey plant pigment standard.

QUANTITATIVE ASPECTS OF THE PHYTOPLANKTON POPULATION

Plant Pigments. Fig. 2 illustrates the seasonal cycle of phytoplankton, as indicated by plant pigment determinations, together with some pertinent environmental factors. There was a midwinter minimum, a small and early spring flowering, and a moderately large population during the late summer. All these characteristics are common in neritic temperate waters.

The seasonal cycle of phosphate was also fairly typical, with its midwinter maximum and a severe decline during the flowering period. The midsummer concentration of phosphate was larger than that in many other areas described. It hardly seems likely that phosphate was a strongly limiting factor.

The zooplankton observations are discussed in detail by Deevey (1952). It suffices for the moment to say that no obvious relation exists between the quantities of phytoplankton and zooplankton. In particular, there is no evidence of an increase in zooplankton during and after the spring flowering, such as has been found in the English Channel and in various other localities. There is no clear evidence that zooplankton grazing controlled the size of the phytoplankton population at any time.

Cell Counts. Fig. 3 summarizes the total cell numbers in the surface water and the mean number of cells in the upper 20 m. The general form of the seasonal cycle resembles what has been described above, but the cell numbers are more variable than the plant pigment estimates. This variability is largely the result of differences in species composition. The largest numbers were obtained at times

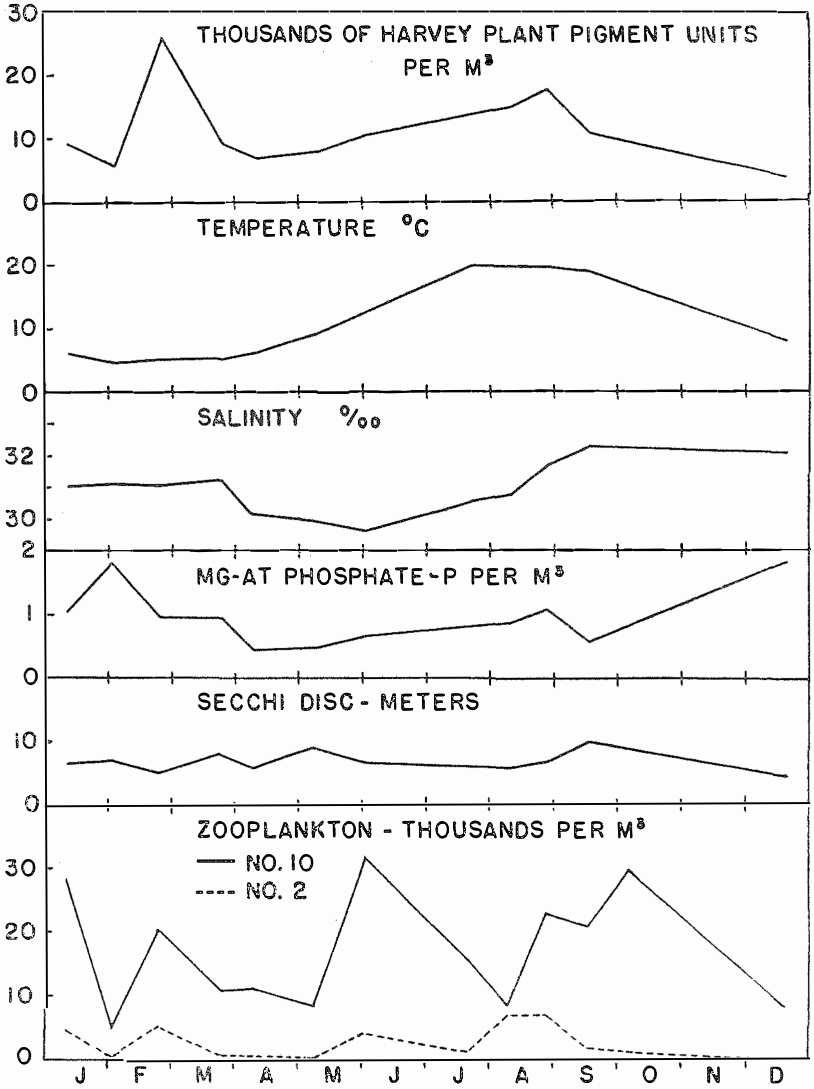


Figure 2. Surface measurements of plant pigments, temperature, salinity, and phosphate at Station A or B, transparency as determined by the Secchi disc, and the number of zooplankton organisms obtained by oblique tows with no. 2 and no. 10 nets.

when the population was dominated by small diatoms.

Fig. 4 shows examples of the three main types of vertical distribution that were found. The winter and early spring period of minimum

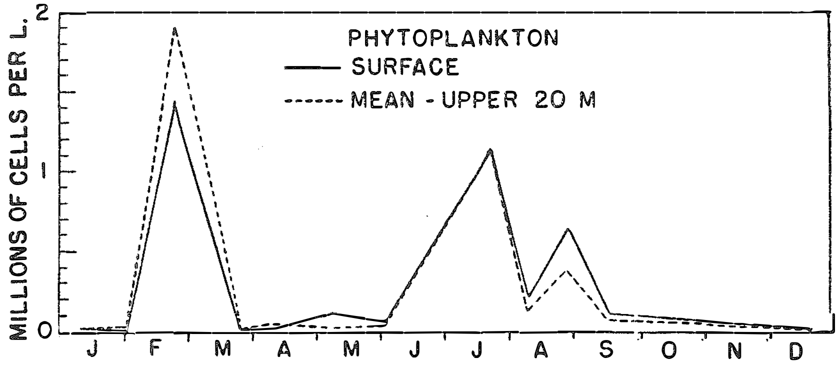


Figure 3. Seasonal variation in phytoplankton concentration at Station A or B.

stability was characterized by a population that increased with depth to a maximum at 10–20 m. After the onset of vernal warming, the population tended to decrease from the surface downward, except that in some cases there was another maximum in the thermocline.

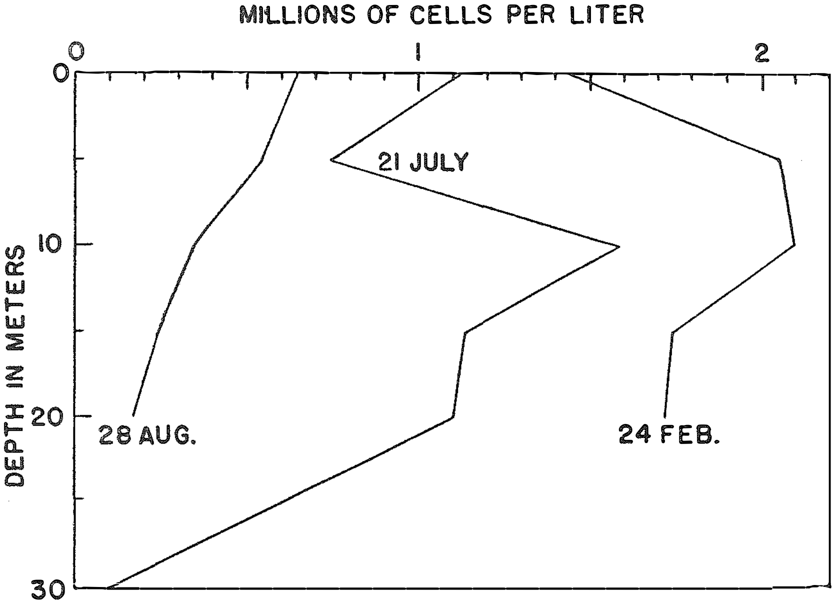


Figure 4. Vertical distribution of phytoplankton.

The surface and 5-meter cell numbers at stations A and B are compared in Table I with surface numbers at other positions previously designated in Fig. 1. There are two examples of extreme variability (E, January 11; B, May 7), but otherwise the cell numbers are fairly uniform, with perhaps slightly larger populations at the inshore stations C and D. In the surface water at station B, May 7, the population differed from the remainder of the water column in species composition as well as in quantity, and the salinity of the water was 0.3°/₀₀ higher than at 5 m. It is an obvious example of a water mass that differed in origin and history from the other water sampled on that date.

TABLE I. THOUSANDS OF CELLS PER LITER AT STATIONS A TO E IN B. I. S.

Date	*meters*	*A, B*	*C*	*D*	*E*
11/I/49	0	22	20	—	132
3/II	0	10	73	45	31
	5	26			
24/II	0	1,442	2,051	1,448	1,623
	5	2,104			
24/III	0	16	52	63	22
	5	20			
7/V	0	117	18	14	—
	5	16			

Comparison with Adjacent Waters. In previous years the writer has obtained a few measurements of plant pigments in the coastal waters south of B. I. S. These are summarized in Table II. They average less than half the mean quantity in B. I. S. There is little information on the form of the seasonal cycle. A spring flowering has not been observed. In March 1947, one very large value of 56,000 Harvey units was obtained at a depth of 60 m at a coastal water station. It might have been a remnant of an earlier flowering of large proportions, but there is no certainty that the phytoplankton was of local origin. In August 1947, two stations near the edge of the

TABLE II. SURFACE PHYTOPLANKTON CONCENTRATIONS RECORDED AS HARVEY UNITS PER M³ IN WATERS 10–30 MILES SOUTH OF B. I. S.

	Number of observations	*Mean Harvey units*
May 1939	2	2,500
March 1947	2	6,700
August 1947	2	5,000
December 1949	2	4,000

continental shelf had surface concentrations of 11,000 and 18,000 Harvey units, the order of magnitude of the summer population in B. I. S.

Lillick (1937) published an account of the phytoplankton population in the coastal waters near Vineyard Sound. While the area investigated was near shore in a depth of only 30 m, the temperature and salinity records indicate that it was more nearly typical of the open coastal waters of the region than is B. I. S. The seasonal cycle differed only in minor details from what has been described above, but the cell numbers were markedly less. The annual mean was of the order of 20,000 cells/l as compared with 325,000 in B. I. S. The comparison is biased by the fact that the latter flora was dominated by the small diatom *Skeletonema costatum,* while Lillick's data reveal relatively greater proportions of big diatoms. Excluding this one species, the annual mean in B. I. S. was about 45,000 cells/l.

In general, there seems to be little doubt that B. I. S. has a higher concentration of phytoplankton than the adjacent waters to the east and south, although the character of the data precludes any possibility of precise comparison.

The writer has obtained phytoplankton measurements of various sorts along the northern shore of L. I. S. in depths of 20 m or less. A nearly complete seasonal cycle was obtained between September 1938 and August 1939 (Riley, 1941). It was found that it consisted of an early winter minimum, a very long and intense spring flowering lasting from mid-January to April, other flowerings of smaller size in late summer, and a relatively smaller but by no means impoverished flora the remainder of the year. The phytoplankton was measured as milligrams of chlorophyll per m^3. According to a later series of measurements, one milligram of chlorophyll in the L. I. S. summer plankton is equivalent to about 3,100 Harvey units of plant pigments. Applying this conversion factor to the 1938–39 data yields the estimates of abundance shown in the first line of Table III. Subsequent measurements by the Harvey method are summarized in the remainder of Table III.

TABLE III. PLANT PIGMENT MEASUREMENTS (HARVEY UNITS PER M^3) IN THE SURFACE WATER IN THE NORTH CENTRAL PART OF L. I. S.

	Maximum	*Minimum*	*Mean*	*No. of obs.*
September 7, 1938–August 18, 1939	ca 194,000	ca 16,000	ca 55,600	65
July 8–November 13, 1940	125,000	7,500	45,200	54
June 16–September 22, 1941	79,000	18,000	45,600	51
May 17–July 26, 1950	75,000	12,000	31,500	9

Cell counts were made during the summer of 1941. The total quantity varied from 60,000–7,400,000 cells/l, with a mean of 1,630,000. The routine counts did not include naked flagellates and other small forms. Occasional examination of freshly preserved material revealed 10–16 millions of these small cells per liter.

The small area that has been studied probably is not typical of L. I. S. as a whole. A few measurements in the central water mass have yielded smaller concentrations than those of the inshore waters represented by Table III. The concentration presumably declines toward the east. Station C (Table I) lies within the boundary of Fishers Island Sound and is subject to strong L. I. S. influence on the ebb tide. However, it more nearly resembles B. I. S. than the central part of L. I. S. with respect to phytoplankton concentrations. The population in the richer parts of L. I. S. appears to be an order of magnitude larger than that in the outer coastal waters. The B. I. S. data represent an intermediate point in what is probably a general gradient of decreasing concentrations.

SPECIES COMPOSITION

The Dominant Species in Block Island Sound in 1949. Nine genera, listed in Table IV, constituted 98% of the total number of cells in the phytoplankton counts. The first column of Table IV is the number of dates (out of a total of 12) when the genus was included in the routine plankton counts. The methods were such that there was a

TABLE IV. Summary of Dominant Genera and Species.

	No. of dates present	*Mean no. of cells per liter*	*% of total population*	*Maximum % of population*
Skeletonema costatum	12	270,500	83.5	99
Chaetoceros spp.	11	19,700	6.1	80
C. didymus	—	—	—	80
C. curvisetus	—	—	—	10
C. decipiens	—	—	—	12
C. compressus	—	—	—	13
Leptocylindricus spp.	8	6,900	2.1	45
L. danicus	—	—	—	40
L. minimus	—	—	—	5
Thalassiosira spp.	11	5,800	1.8	41
T. subtilis	—	—	—	41
Thalassionema nitzschioides	12	5,400	1.7	92
Nitzschia spp.	11	5,300	1.6	39
N. closterium	—	—	—	39
N. seriata	—	—	—	23
Asterionella japonica	10	1,700	0.5	7
Rhizosolenia spp.	12	1,500	0.5	11
R. faeroense	—	—	—	10
Guinardia flaccida	9	1,000	0.3	20

TABLE V. SEASONAL VARIATION IN THE SPECIES COMPOSITION OF THE B. I. S. PHYTOPLANKTON. AN x INDICATES THAT THE SPECIES WAS SUFFICIENTLY ABUNDANT TO BE FOUND IN THE ROUTINE PLANKTON COUNTS.

	Collection Dates											
	1/II	*3/II*	*24/II*	*24/III*	*9/IV*	*7/V*	*2/VI*	*21/ VII*	*9/ VIII*	*28/ VIII*	*17/ IX*	*19/ XII*
Skeletonema costatum	x	x	x	x	x	x	x	x	x	x	x	x
Thalassionema nitzschioides	x	x	x	x	x	x	x	x	x	x	x	x
Rhizosolenia setigera	x	x	x	x	x	x	x	x	x	x	x	x
Pleurosigma normanii	x	x	–	x	x	x	x	x	x	x	x	x
Distephanus speculum	x	x	x	x	x	x	x	x	x	x	x	–
Asterionella japonica	–	x	x	x	x	x	x	x	x	x	–	x
Nitzschia closterium	–	x	x	x	x	x	x	x	x	x	x	x
Guinardia flaccida	–	x	x	x	x	x	x	x	x	x	x	–
Melosira sulcata	–	–	x	x	x	x	x	x	x	–	x	x
Licmophora abbreviata	–	–	x	x	x	x	x	x	x	–	–	x
Ditylium brightwellii	–	–	x	x	x	x	x	x	–	–	x	–
Corethron hystrix	–	–	x	–	–	x	–	–	x	x	x	–
Leptocylindricus danicus	–	–	–	x	x	x	x	x	x	x	x	–
Actinoptychus undulatus	–	–	–	x	x	–	x	–	–	x	–	x
Rhizosolenia alata	–	–	–	x	x	x	x	x	x	x	x	x
R. hebetata f. *heimalis*	–	–	–	–	x	x	–	–	–	–	–	x
R. hebetata f. *semispina*	–	–	–	–	x	–	x	x	x	x	x	x
Nitzschia seriata	–	–	–	–	x	x	x	x	x	x	x	–

probability of more than 0.5 of recording a species if the average cell count was more than 20 per liter. The second column lists the number of cells per liter, averaged from the surface to 20 m and averaged for all collection dates. This number is next converted to a percentage of the total population. Finally the data for individual dates are used to determine the maximum degree of dominance at any one time, expressed as a percentage of the total population on that date.

Four of the genera were represented by a single species, as indicated. The remainder are given with a summary of the abundance of the genus as a whole, and in addition, individual species are listed if at any time they constituted as much as 5% of the total population.

Several other species were moderately important during a particular season, although in terms of mean annual cell numbers they did not warrant inclusion in Table IV. The following species at one time or another made up at least 5% of the population: *Ditylium brightwellii*, *Corethron hystrix*, *Melosira sulcata*, *Coscinodiscus subtilis*, and *Distephanus speculum*.

While the cell number is the most convenient criterion for examining population composition, certain other measurements might be used, no one of which would give precisely the same results. In terms of total cell contents, *Ditylium*, *Coscinodiscus*, and *Rhizosolenia* would be more important than is indicated by cell numbers. Conversely, the relative significance of the small diatoms would be reduced, although *Skeletonema costatum* would still be the dominant species.

Seasonal Cycles. *Skeletonema costatum*, *Thalassionema nitzschioides*, and *Rhizosolenia setigera* were present in every set of plankton samples. Six other species were present on at least nine of the twelve sampling dates. A total of 17 species, listed in Table V, were present on a broad seasonal basis and apparently were capable of tolerating almost the entire range of variability of the B. I. S. environment. Nevertheless, six of the species, in spite of their persistence, did not achieve a significant degree of dominance at any time.

Species of more transient occurrence are listed in Table VI in the order of their appearance throughout the year. Again the list includes forms that achieved a considerable degree of dominance and others that were present only as a few scattered cells.

Tables V and VI serve only to describe the most significant aspects of species occurrence and succession. As a species list, the data are incomplete. The material examined on prepared slides and during

TABLE VI. SEASONAL VARIATION IN THE SPECIES COMPOSITION OF THE B. I. S. PHYTOPLANKTON. AN x INDICATES THAT THE SPECIES WAS SUFFICIENTLY ABUNDANT TO BE FOUND IN THE ROUTINE PLANKTON COUNTS.

	Collection Dates											
	1/II	*3/II*	*24/II*	*24/III*	*9/IV*	*7/V*	*2/VI*	*21/ VII*	*9/ VIII*	*28/ VIII*	*17/ IX*	*19/ XII*
Thalassiosira nordenskiöldii	x	x	x	x	x	x	–	–	–	–	–	–
Prorocentrum micans	x	x	x	x	x	x	x	–	–	–	–	–
Coscinodiscus excentricus	–	x	x	x	x	–	–	–	–	–	–	–
Biddulphia aurita	–	x	x	x	–	–	–	–	–	–	–	–
Peridinium spp.	–	x	x	x	x	x	–	–	–	–	–	–
Stephanopyxis palmeriana	–	–	x	–	–	–	–	–	–	–	–	–
Grammatophora marina	–	–	–	x	–	–	–	–	–	–	–	–
Rhizosolenia faeroense	–	–	–	x	x	–	–	–	–	–	–	–
Coscinodiscus centralis	–	–	–	–	x	–	–	–	–	–	–	–
Streptotheca thamensis	–	–	–	–	x	x	–	–	–	–	–	–
Thalassiothrix frauenfeldii	–	–	–	–	x	x	–	–	–	–	–	–
Thalassiosira gravida	–	–	–	–	x	–	–	–	–	–	–	–
T. rotula	–	–	–	–	x	x	x	x	–	–	–	–
Grammatophora angulosa	–	–	–	–	–	x	–	–	–	–	–	–
Striatella sp.	–	–	–	–	–	x	–	–	–	–	–	–
Chaetoceras brevis	–	–	–	–	–	x	x	–	–	–	–	–
C. decipiens	–	–	–	–	–	x	x	–	–	x	–	–
C. compressus	–	–	–	–	–	x	–	–	–	x	–	–
C. didymus	–	–	–	–	–	x	–	x	x	x	x	–
Dinophysis sp.	–	–	–	–	–	x	x	–	x	–	–	–
Ceratium lineatum	–	–	–	–	–	x	x	x	x	–	–	–
C. fusus	–	–	–	–	–	x	x	–	x	–	–	–
C. tripos	–	–	–	–	–	x	x	x	–	–	–	–
Lauderia borealis	–	–	–	–	–	x	x	–	–	–	x	–
Gonyaulax sp.	–	–	–	–	–	–	x	x	x	–	–	–
Rhizosolenia calcar—avis	–	–	–	–	–	–	–	x	x	–	x	–
Eucampia cornuta	–	–	–	–	–	–	–	x	x	x	x	–
Leptocylindricus minimus	–	–	–	–	–	–	–	–	x	x	x	–
Chaetoceros curvisetus	–	–	–	–	–	–	–	–	–	x	x	–
C. constrictus	–	–	–	–	–	–	–	–	–	x	–	–
Thalassiothrix longissima	–	–	–	–	–	–	–	–	–	x	–	–
Cerataulina sp.	–	–	–	–	–	–	–	–	–	x	–	–
Bacteriastrum delicatulum	–	–	–	–	–	–	–	–	–	–	x	x
Coscinodiscus subtilis	x	–	–	–	–	–	–	–	–	–	x	x
C. marginatus	–	x	x	x	x	–	–	–	–	–	–	x
Thalassiosira subtilis	–	–	–	–	–	–	–	–	–	–	–	x

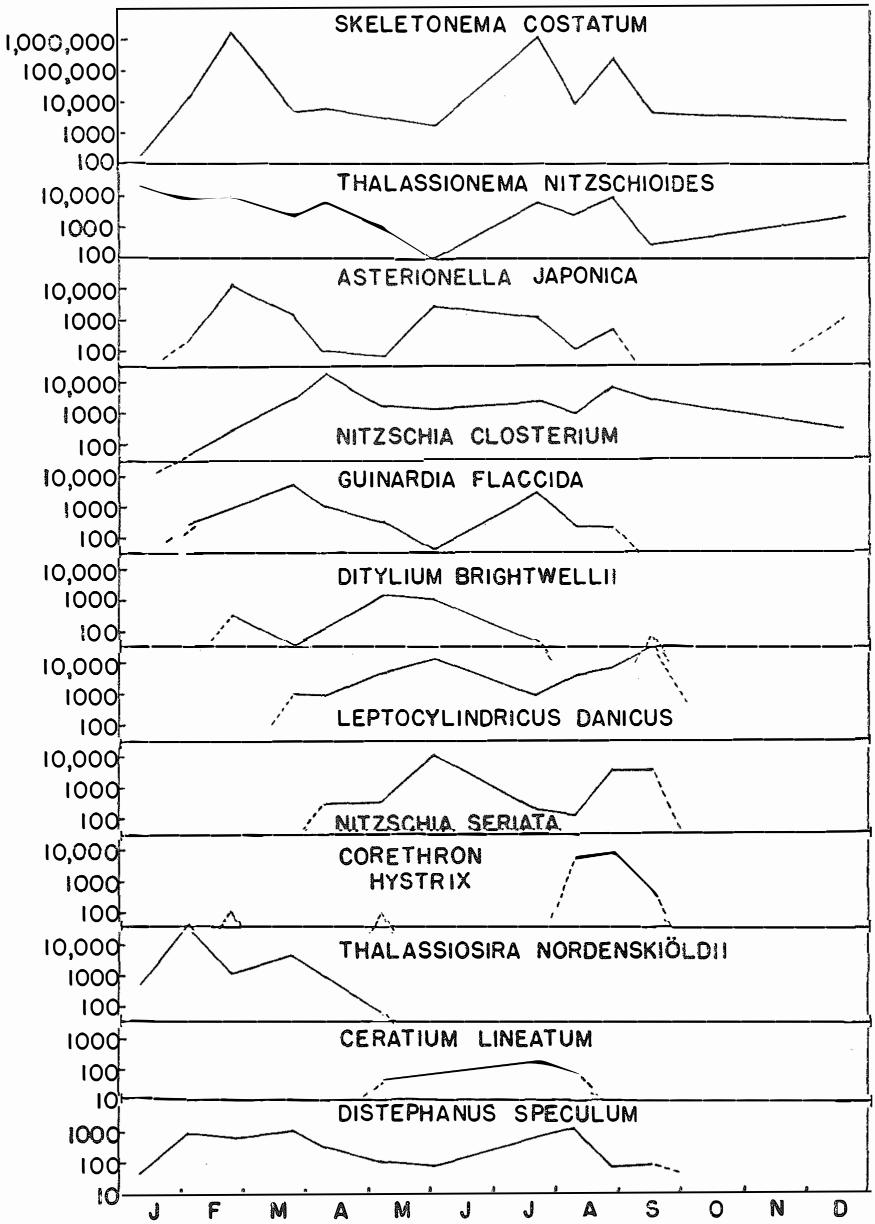


Figure 5. Seasonal variation of representative species of phytoplankton; the mean number of cells in the upper 20 m is plotted on a logarithmic scale.

the routine counts was the population occurring on each collection date in a volume of 150–500 ml of water. Examination of net tows and larger water samples presumably would increase both the size of the list and the period of occurrence of some species. Also, the writer was unable to derive satisfactory specific identifications for some of the forms. particularly when only a few specimens were available for study. It will be noted in Table IV that *Chaetoceros* and *Thalassiosira* spp. were present on 11 collection dates. The distribution of species indicated in Tables V and VI represents more limited periods of sufficient abundance to warrant identification by a nonspecialist. Similarly, most of the dinoflagellates are listed by genera.

Fig. 5 shows seasonal variations in abundance of some of the species. *Skeletonema* was so thoroughly dominant that its seasonal cycle differed little from that of the population as a whole (Fig. 3). More than half of the other persistent species also exhibited a tendency toward a bimodal seasonal cycle, with a maximum sometime between January and April and another during the summer. Some of these are illustrated in Fig. 5, together with representative examples of unimodal seasonal distribution.

Comparison with Adjacent Waters. Occasional examinations of net tows and water samples from L. I. S. indicate that *Skeletonema costatum* is the dominant species there as well as in B. I. S., at least during the spring and summer. Complete counts and species lists are not available for L. I. S. on a year-round basis. The comparison must be based largely on counts made during the summer of 1941. At that time *Skeletonema* averaged 1.2 million cells/l, or 72% of the total population, and reached a maximum concentration of 6.5 million cells/l in late summer. Other major constituents were *Thalassionema nitzschioides, Nitzschia closterium, Leptocylindricus danicus, L. minimus,* and *Asterionella japonica.* The only important species that was not found in the later survey of B. I. S. was a small *Rhizosolenia,* probably *R. delicatula.* Other *Rhizosolenia* and *Chaetoceros* spp. were found in about the same numbers in both Sounds, but were less significant percentagewise in L. I. S. The species in these genera were not fully identified during the L. I. S. survey, so that precise comparison is not possible.

For detailed comparison of B. I. S. with the waters to the eastward, the reader is referred to Lillick's (1937) work on the phytoplankton south of Vineyard Sound. It suffices here to say that the two floras are remarkably similar with the one major exception that *Skeletonema* was not excessively dominant in Lillick's counts.

GROWTH EXPERIMENTS

At the time of the spring flowering, a few simple experiments were performed to determine the reproductive capacity of the various species of phytoplankton. During the routine collection of samples for phytoplankton counts, a half-gallon bottle was filled with surface water, and at the end of the day's operations it was hung from a pier in Stonington Harbor just below low tide level. After three to seven days, formalin was added, and the phytoplankton was subsequently counted. Table VII shows the initial and final cell counts for the most important species and for the population as a whole in the first two experiments. From these counts the coefficient of increase k was determined according to the formula

TABLE VII. Cell Counts and Growth Coefficients in Bottles of Surface Water.

	Feb. 2–5			*Feb. 24–Mar. 3*		
	Initial	*Final*	*k*	*Initial*	*Final*	*k*
Skeletonema costatum	2,780	110,000	1.23	1,340,000	3,750,000	.15
Thalassionema nitzschioides	5,200	17,200	.40	9,400	9,600	.003
Prorocentrum micans	780	500	−.15	100	1,100	.34
Thalassiosira nordenskiöldii	290	1,200	.48	53,500	32,500	−.07
Guinardia flaccida	290	500	.19	2.800	300	−.32
Distephanus speculum	120	1,000	.71	600	300	−.10
Coscinodiscus marginatus	40	800	.33	800	200	−.20
Asterionella japonica	100	1,300	.86	28,000	66,000	.12
Total cell count	9,600	135,000	.89	1,442,000	3,864,000	.14

$$k = \frac{\ln F - \ln I}{T},$$

where I and F are the initial and final cell counts, respectively, and T is time in days.

The k values show that the population as a whole increased 89% per day at the time of the first experiment. Individual species varied widely in their reproductive capacity. During the period of February 2–24, a flowering developed in B. I. S. The average daily increase was 23% of the total population. Increases in individual species in B. I. S. were roughly proportional to their reproductive capacity at the beginning of the period, as indicated by the first experiment. This relationship is shown in Fig. 6A. However, the

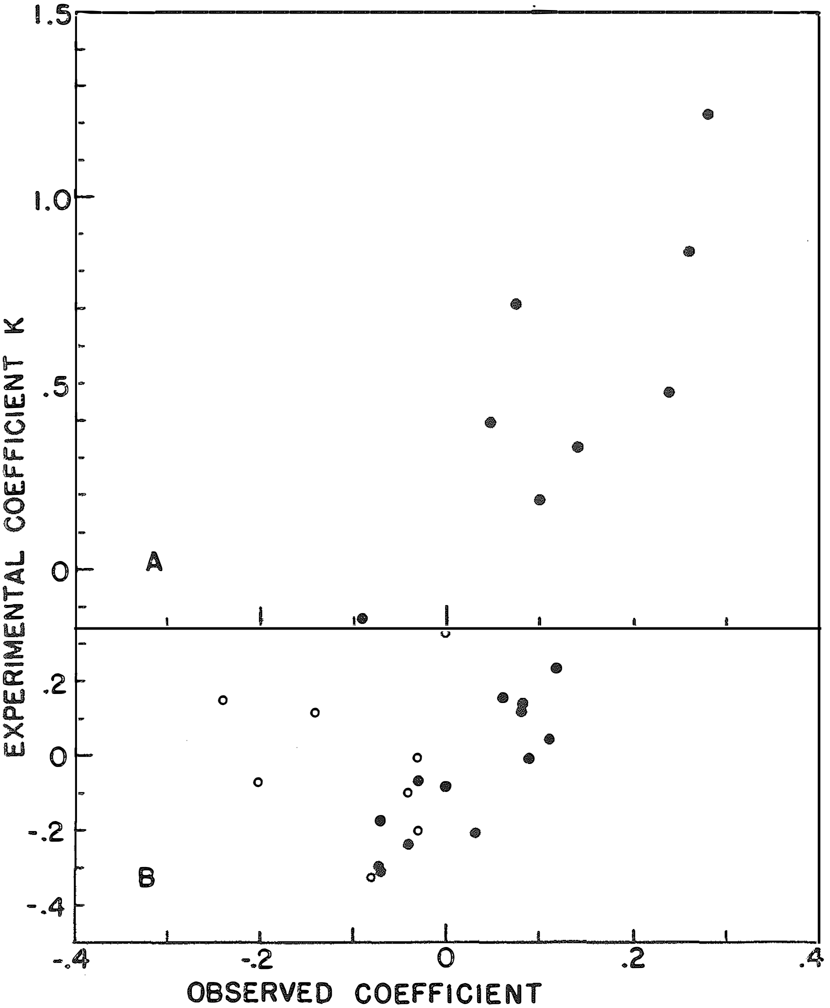


Figure 6. Coefficient of daily increase in cell number *k* in experimental bottles compared with the observed increase in B. I. S. *A*. Experiment of February 2 to 5. *B*. Circles, February 24 to March 3; dots, March 24 to 30. Each point represents a particular species.

experimental *k*'s were higher than the observed coefficient of increase in B. I. S. This was to be expected, since the light intensity was higher in the experimental bottles than in the water column as a whole and since the phytoplankton was protected during the experiment from processes of physical dispersal.

TABLE VIII. Cell Counts and Growth Coefficients in the Experiment of March 24–30. The Surface Water Population of April 9 Is Listed for Comparison of Experimental Results with Subsequent Events in B. I. S.

	Initial	*Final*	*k*	*April 9*
Skeletonema costatum	1,700	4,700	.17	4,600
Thalassiosira gravida	3,000	1,800	−.08	3,200
Nitzschia closterium	300	200	−.06	190
Peridinium sp.	600	100	−.30	200
Rhizosolenia alata	600	100	−.30	200
R. setigera	300	400	.05	1,800
R. faeroense	300	1,300	.24	2,100
Chaetoceros sp.	2,800	1,000	−.17	900
Guinardia flaccida	300	700	.14	1,000
Thalassionema nitzsch.	3,600	1,100	−.20	5,500
Coscinodiscus marginatus	400	100	−.23	200
Leptocylindricus danicus	300	600	.12	1,000
Ditylium brightwellii	100	100	.00	400
Total cell count	15,700	14,500	−.006	24,700

A third experiment, begun on March 24 (Table VIII, Fig. 6B), showed a similar relation between experimental reproductive coefficients and observed changes in the B. I. S. population. But in the second experiment, also plotted in Fig. 6B, there was no significant relation. All of the important species of February 24 declined during the subsequent month, irrespective of their reproductive capacity, and Table VIII shows that several other species joined the population. The most obvious explanation of the difference between this experiment and the others is that the water sampled on February 24 was swept away and replaced by another water mass with a somewhat different species composition.

CHEMICAL DATA

TABLE IX. Seasonal and Vertical Distribution of Oxygen in Ml/L and Phosphate in Mg-At P/M³

Depth	*Collection Date*										
m	*11/ I*	*3/ II*	*24/ II*	*24/ III*	*9/ IV*	*7/ V*	*2/ VI*	*9/ VIII*	*28/ VIII*	*17/ IX*	*19/ XII*
0	——	7.31	7.19	7.13	7.12	6.61	6.15	5.35	5.10	5.11	6.70
5	——	7.45	7.47	7.76	7.19	6.83	6.21	5.10	5.33	5.55	6.40
10	——	7.78	7.25	7.66	8.11	6.75	6.30	5.79	5.13	5.36	7.00
15	——	8.06	8.13	7.86	7.87	6.30	5.75	6.09	4.96	5.52	6.67
20	——	8.48	7.71	7.21	7.65	6.33	5.50	5.54	4.76	5.53	6.97
30	——	——	——	——	——	——	——	5.27	——	4.96	6.72
0	1.06	1.81	.98	.95	.45	.48	.67	.89	1.08	.58	1.84
5	——	1.39	.74	.83	.43	.48	.67	.80	.90	.53	1.71
10	——	1.93	.61	.90	.47	.52	.64	.87	.88	.57	1.63
15	——	2.29	.63	.90	.58	.48	.70	1.00	1.02	.57	1.71
20	——	1.52	.76	.93	.60	.50	.73	1.06	1.00	.62	1.71
30	——	——	——	——	——	——	.99	1.28	——	.72	1.84

Oxygen and phosphate determinations are shown in Table IX. Certain aspects of the data reveal the character of the biological agencies that affect oxygen and phosphate distribution. From February 24 to September 17 there was a mid-depth oxygen maximum at 5, 10, or 15 m, indicating that the production of oxygen by photosynthesis exceeded its utilization by the respiration of the whole biological association. During most of the year, the minimum phosphate concentration occurred between the surface and 15 m, suggesting net utilization by the population inhabiting the surface layer. Below 15 m the oxygen tended to decrease and the phosphate to increase with depth, indicating a predominance of katabolic processes in the lower water. As is commonly observed, there was a decline in the amount of soluble phosphate in the water column as a whole during the spring months, suggesting that phosphate regeneration did not keep pace with utilization.

Quantitative interpretation of these observations is uncertain because of the lack of detailed information on regional variations and because of the possible effects of currents and lateral mixing. Previous chemical observations in L. I. S. and in the offshore waters (Riley, 1939, 1941) suggest that the oxygen distribution is relatively uniform laterally. Probably there will be no great error if it is assumed that variations in oxygen are caused by local processes. Phosphate is not so easily generalized. There are no large differences between the Long Island and Block Island Sounds, but the phosphate concentration offshore tends to be less at the surface and greater in the bottom water. The effects of interchange between B. I. S. and offshore water are not easily predicted.

If advection and lateral diffusion are ignored, the rate of change of oxygen at a particular location is given by

$$\frac{\partial O^2}{\partial t} = \frac{\partial}{\partial z} \cdot \frac{A}{\rho} \cdot \frac{\partial O_2}{\partial z} + R\,,$$

in which A is the coefficient of vertical eddy diffusivity, z is the vertical axis, which is directed positively downward, and R is the biological rate of change of oxygen. The simplified determinations of eddy conductivity (Riley, 1952: table X) will be used as numerical values of A. Table IX provides the remainder of the data necessary for estimating the biological production and consumption of oxygen. The eddy coefficients were calculated for the depth ranges 0–10 m and

10–20 m, and the oxygen gradients will be determined for the same depths (in terms of finite differences). However, since the maximum oxygen concentration did not always occur at 10 m, it seems advisable to prepare two sets of estimates as follows: (a) The maximum observed concentration between 5 and 15 m is designated as the 10-meter concentration, and the derived biological rate of change will be called a maximum estimate. (b) The mean of the 5, 10, and 15-meter values will be called the 10-meter concentration, and the result will be regarded as a minimum estimate.

As a numerical example of the method of calculation, on April 9 the oxygen concentrations at 0, 10, and 20 m were respectively 7.12, 8.11, and 7.65 ml/l (for the maximum estimate). The calculated coefficients of eddy conductivity are 2.5 g/cm/sec between 0 and 10 m and 5 between 10 and 20 m. The rate of change of oxygen is determined from the preceding and following periods. The maximum concentration between 5 and 15 m declined from 7.86 ml/l on March 24 to 6.83 ml on May 7, a period of 44 days. Fitting these data to the equation,

$$\frac{6.83 - 7.86}{44 \times 86400} = \frac{1}{10^3}\left[\frac{5\,(7.65 - 8.11)}{10^3} - \frac{2.5\,(8.11 - 7.12)}{10^3}\right] + R\,,$$

$$-.3 \times 10^{-6} = (-\,2.3 - 2.5)\,10^{-6} + R\,,$$

$$R = 4.5 \times 10^{-6}\ \mathrm{ml/l/sec}\,,$$

or 0.39 ml/l/day at a depth of 10 m. The calculation implies that oxygen is transferred downward through the 20-meter level and upward through the sea surface at rates of 2.3 × 10^{-6} and 2.5 × 10^{-6} ml/cm^2/sec, respectively. It is also apparent that the total excess of production over consumption in the surface layer is 4.5 × 10^{-6} ml/cm^2 of sea surface per second (0.39 ml/day). Furthermore, if lateral transfer can be ignored, the downward transport of oxygen must equal the biological utilization below 20 m; this amounts to 0.20 ml/cm^2/day, or about half of the excess in the surface layer.

Table X summarizes similar calculations for the whole year. Maximum and minimum values are determined according to the criteria cited previously. The results indicate that the net oxygen production during the period from February 3 to December 19 came to a total of between 34 and 102 ml/cm^2. Estimates of consumption in the bottom water ranged from 18–29 ml/cm^2. The latter are probably too low. A more detailed examination of the lowest part of the water column that was sampled, from 15–20 m, or from 20–30 m whenever possible, yielded a total of 41 ml/cm². This value, too, seems to be less than the excess produced in the surface layer. The calculations suggest that B. I. S. exists in a state of ecological imbalance, in which the production of phytoplankton exceeds its consumption.

TABLE X. OXYGEN PRODUCTION AND CONSUMPTION IN MILLILITERS PER CM² OF SEA SURFACE PER DAY. THE FIRST HALF OF THE TABLE LISTS MAXIMUM AND MINIMUM ESTIMATES OF PRODUCTION IN THE UPPER 20 M IN EXCESS OF THE RESPIRATORY REQUIREMENTS OF THE BIOLOGICAL ASSOCIATION. THE SECOND HALF IS THE CALCULATED CONSUMPTION BELOW 20 M

Date	*Production*		*Consumption*	
	Max.	*Min.*	*Max.*	*Min.*
3/II	.49	.01	−.25	−.43
24/II	1.16	.35	.25	−.05
24/III	1.02	.74	.44	.24
9/IV	.39	.14	.20	.03
7/V	.12	.03	.09	.05
2/VI	.14	.05	.11	.08
9/VIII	.17	.07	.03	.01
28/VIII	.10	.05	.05	.03
17/IX	.11	.08	.01	−.01
19/XII	.32	−.19	.02	−.18

The biological rates of change of phosphate were determined by the same kind of methods and will be summarized briefly, although, for reasons expressed previously, they are open to suspicion. The maximum estimate of phosphate utilization at 10 m was 0.15 mg-at P/m³/-day, averaged for the entire period of the investigation, and the total utilization in the upper 20 m was 550 mg-at/m² of sea surface. Compared with the maximum oxygen estimate, the mean ratio of oxygen production to phosphate consumption is 231 : 1 by atoms. This figure can be regarded as approximately normal; however, estimates for individual dates varied widely. All O : P ratios for the period from February 24 to August 9 were above average, and the remainder were abnormally low. The mean for the spring-summer period was 510 : 1, and for the autumn-winter period it was 107 : 1.

DISCUSSION

In any area where a so-called seasonal cycle is observed, the changes from one sampling date to another are partly due to local ecological reactions and are partly the result of physical dislocation of the populations by transport and diffusion. The physical oceanographic survey has shown that there is continual transport of water through B. I. S. and a variable degree of admixture of the adjacent water masses. It is expected that the phytoplankton will be susceptible to significant physical effects. The present limited set of data cannot provide an adequate quantitative explanation of the observed seasonal variations of phytoplankton in terms of this interplay between ecological and physical oceanographic processes. However, the major features of the physical oceanographic influence can be clarified by brief analysis and discussion.

About 80% of the phytoplankton species and over 98% of the total number of individuals were typically littoral or neritic organisms. A few oceanic species were always present, but the only ones that achieved any degree of numerical importance were *Chaetoceros decipiens*, *Corethron hystrix*, and *Thalassiosira subtilis*. The number of individuals of presumably oceanic origin was greatest during the period from August to December and in the surface sample of May 7. On these occasions, salinity samples and other observations also indicated an oceanic influence. Thus there are numerous indications of excursions of oceanic water into B. I. S., although they appear to be less important quantitatively than the interchanges of adjacent neritic waters.

Among the neritic and littoral species there were some marked changes in composition and numbers from one sampling date to another. The most striking example is the vast fluctuations of *Skeletonema costatum* with respect to absolute numbers (Fig. 5) and degree of dominance. During the period from June to September it ranged from 3–98% of the total population. It has been mentioned before that this species is a dominant form in L. I. S. and is much less significant in the coastal waters to the east. Other important species such as *Asterionella japonica*, *Thalassionema nitzschioides*, and *Nitzschia closterium* appear to be more nearly uniform throughout the area. Probably *Skeletonema* can be regarded as an indicator of water mass exchange, although any such interpretation requires caution because this species has been known to produce flowerings in all of the nearby waters.

In the first two experiments described above, *Skeletonema* had a higher growth rate than any other species; in the third it was reduced to second place by *Rhizosolenia faeroense*, a transient species that attained a significant degree of dominance at this particular time. The experiments imply that *Skeletonema* is well adapted to live in B. I. S. Its removal or reduction may be generally indicative of the entrance of water masses from offshore, as in the period from February 24 to March 24 (cf. GROWTH EXPERIMENTS). It may then be reseeded by L. I. S. outflow; however, an increase of this species in B. I. S. cannot be regarded as evidence of a large influx of L. I. S. water unless other evidence shows that the observed increase is too large to be accounted for by ordinary growth.

TABLE XI. ESTIMATES OF PHYTOPLANKTON PRODUCTION IN THE UPPER 20 M (IN EXCESS OF UTILIZATION BY ZOOPLANKTON AND BACTERIA)

Date	*Phytoplankton*		*Production*	
	HU/m³	*Mg C/l*	*Mg C/l/day*	*%Phyt.*
3/II	5,700	.10	.066	66
24/II	26,000	.44	.20	45
24/III	9,100	.15	.23	153
9/IV	7,100	.12	.071	59
7/V	8,100	.14	.021	15
2/VI	10,800	.18	.026	14
9/VIII	15,000	.25	.032	13
28/VIII	17,700	.30	.021	7
17/IX	10,900	.19	.026	14
19/XII	4,100	.07	.016	23
Mean	11,200	.19	.050	26

The data on oxygen distribution provide a method of roughly estimating the rate of increase in the organic content of the phytoplankton population. The first two columns in Table XI list the surface concentration of phytoplankton as Harvey units per m^3 and its estimated carbon content, the latter derived from the former by the application of an average conversion factor (cf. Riley, Stommel, and Bumpus, 1949). The next column is an estimate of average daily carbon production in the upper 20 m, obtained by applying the oxygen : glucose-carbon ratio to the average of the maximum and minimum estimates of oxygen production in Table X. The final column shows the calculated daily production as a percentage of the surface phytoplankton crop.

From the method of deriving these figures from observed oxygen concentrations, it is apparent that they represent the difference between phytoplankton production and the total utilization of organic matter *in situ*. Deevey (1952) indicates that the average consumption by zooplankton is at most about 4% of the phytoplankton crop per day; bacterial respiration has not been determined. Thus the average estimate for phytoplankton production is somewhat more than 30% per day.

Some or all of the excess phytoplankton production of the surface layer is removed to the deeper water and is oxidized there by bacteria and animals. The data in Table X and the accompanying discussion suggest that the utilization in the lower layer may be markedly less than the excess production of the overlying water. The calculations are obviously crude and not thoroughly dependable; nevertheless, the question arises as to whether it is reasonable for such an unbalanced ecological system to exist in B. I. S. The only likely alternative to complete biological utilization is lateral dispersal by physical means. It is generally recognized that the large concentrations of neritic localities must be subject to reduction by interchange with more sparsely populated offshore waters, but estimates have not been made of the magnitude of such losses.

In B. I. S., the mean quantity of phytoplankton as determined by the plant pigment method was more than twice the average of the available offshore observations. Both lateral diffusion and the transport of offshore water into the Sound would reduce its phytoplankton concentration. On the other hand, the B. I. S. population might be increased by the addition of L. I. S. water. But since the latter primarily influences the westernmost part of B. I. S., its effect will be ignored in the first approximation.

A simple problem is postulated as follows:

(1) Assume that within the ten-mile (1.8×10^6 cm) width of B. I. S. there exists a uniform concentration of 11,200 Harvey units per m^3, or about 190 mg of phytoplankton carbon per m^3, while ten miles to the south the concentration is 4,500 Harvey units (mean of the observations in Table II) or 76 mg of carbon.

(2) The offshore water is assumed to move into B. I. S. at a speed of 1 cm/sec. There is also a turbulent exchange which will be analyzed later.

(3) The excess production of phytoplankton in the surface layer is postulated to produce 68 ml O_2/cm^2/year (average of the maximum and minimum values in Table X), while the utilization of phytoplankton on or near the bottom results in the consumption of not more than 41 ml/cm^2/year. The difference between these figures is postulated to represent the production of phytoplankton that is lost from B. I. S. by physical dispersal. It corresponds to a production of 13

mg glucose-carbon/m^3/day in a 30-meter column of water, or 150×10^{-6} mg C/sec.

(4) The equation for the rate of change of the phytoplankton population is written

$$\frac{\partial P}{\partial t} = R + \frac{A}{\rho} \cdot \frac{\partial^2 P}{\partial x^2} - V \frac{\partial P}{\partial x} ,$$

where R is the biological rate of change of the phytoplankton concentration P, A is the coefficient of lateral eddy diffusivity, V is the current velocity, and x is lateral distance. According to the first assumption, the problem deals with a simplified steady-state distribution, such that $\partial P / \partial t = 0$. From the data that have been given, the equation may be written in terms of finite differences,

$$150 \times 10^{-6} + \frac{A}{\rho} \frac{(76 - 190) - (190 - 190)}{(1.8 \times 10^{6})^2} - \frac{(-1)(76 - 190)}{2 \times 1.8 \times 10^{6}} = 0 ,$$

$$A = 3.3 \times 10^{6} \text{ g/cm/sec} .$$

This value of the lateral eddy coefficient agrees closely with estimates derived in the previous paper (Riley, 1952) from examination of the salinity distribution. It indicates that the estimated average loss of phytoplankton (about 7% of the population per day) by physical processes is credible. However, two phases of the problem require further examination before the result can be fully accepted. One is the quantity of phytoplankton in the eastern part of L. I. S. and its effect on the B. I. S. population. The other is the question of the source and rate of supply of phosphate and other nutrients that must be transported into B. I. S. in order to replace the loss that occurs when these substances are carried away in organic combination in the plankton.

While the discussion has been mainly concerned with physical oceanographic factors, it is apparent from the experiments that the seasonal cycle is partly controlled by biological or chemical factors. Growth rates were high during the time when the spring flowering was developing; later they became much lower. The change cannot be accounted for by any of the observed environmental factors. However, the existence of reduced growth rates in the experiments subsequent to the flowering is sufficient evidence that the population was kept at a low level by physiological limitations as well as by physical dispersal.

Field observations yield little information about the nature of the ecological control of the population. The minimum phosphate concentration was larger than is ordinarily the case in either L. I. S. or in the offshore waters. It seems unlikely that phosphate was an important limiting factor. Nevertheless, the abnormally large ratios of oxygen production to phosphate utilization in spring and summer indicate that the phosphate uptake declined even though there was a large quantity available. Possibly this phenomenon can be explained in terms of the availability of other essential nutrients, but at the moment the reason remains obscure.

The previous discussion has indicated that removal of phytoplankton by zooplankton grazing is less significant than physical dispersal. These two phenomena are closely related. If grazing were more important, so that it reduced the phytoplankton crop to the same concentration as that in the offshore waters, the exchange would cause no net loss of phytoplankton from B. I. S. The fundamental problem is the reason for the inability of the animal population to consume the phytoplankton as rapidly as it is produced. The zooplankton investigation in a future paper of the series is a necessary prerequisite to a discussion of this problem.

REFERENCES

DEEVEY, GEORGIANA B.
1952. Quantity and composition of the zooplankton of Block Island Sound, 1949. Bull. Bingham oceanogr. Coll., *13* (3): 120–164.

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

RILEY, G. A.
1939. Plankton studies. II. The western North Atlantic, May–June, 1939. J. Mar. Res., *2:* 145–162.
1941. Plankton studies. III. Long Island Sound. Bull. Bingham oceanogr. Coll., *7* (3): 1–93.
1952. Hydrography of the Long Island and Block Island Sounds. Bull. Bingham oceanogr. Coll., *13* (3): 5–39.

RILEY, G. A., HENRY STOMMEL, AND D. F. BUMPUS
1949. Quantitative ecology of the plankton of the western North Atlantic. Bull. Bingham oceanogr. Coll., *12* (3): 1–169.

A SURVEY OF THE ZOOPLANKTON OF BLOCK ISLAND SOUND, 1943–1946

By Georgiana Baxter Deevey

Bingham Oceanographic Laboratory

CONTENTS

ABSTRACT

Surface zooplankton samples, collected usually at monthly intervals from August 1943 to June 1946 with a No. 2 silk net one foot in diameter, were obtained mainly from various localities in Block Island Sound,[1] although a few were taken at the eastern end of Long Island Sound.[1] Since most of the tows were of 15 minutes' duration at 1.75–2 knots, the numbers of organisms are expressed as per 15 minute tow. Fourteen trawl wing samples were also obtained. Surface and bottom salinity and temperature data were procured with the samples. During the first half of the period studied, the surface salinity varied around 32°/₀₀, but during the second half it decreased, and this change was reflected in the general picture of the zooplankton.

B. I. S., a fairly open body of water, acts as an intermediary between the neritic waters of the continental shelf and the littoral waters of L. I. S. in particular. Both the salinity and the composition of the zooplankton provide clues to the origin of the water masses sampled. Oceanic, neritic, littoral, and estuarine organisms were observed in the plankton.

Zooplankton volumes varied throughout the year and at different stations, but they consistently showed maxima in midwinter and minima in early spring and late autumn or early winter. In 1944 there was also a maximum in midsummer, but in 1943 and 1945 this occurred in midautumn.

The copepods were the dominant organisms in the surface zooplankton, although cladocera, crustacean larvae, tunicates, chaetognaths and hydromedusae were taken in numbers at various times. The seasonal variation in abundance of all these forms is considered. *Centropages typicus* was the dominant copepod, although it decreased in numbers as the salinity fell. Other copepods that appeared seasonally included *C. hamatus, Pseudocalanus minutus, Temora longicornis, Acartia tonsa, Calanus finmarchicus, Labidocera aestiva,* and *Monstrilla anglica.* The remaining copepods were categorized as (1) strays from offshore waters, (2) strays from brackish waters, (3) species possibly indigenous to B. I. S. that appeared periodically but in small numbers, (4) species not adequately sampled by the net, (5) parasitic forms.

Podon intermedius was the most important cladoceran, appearing consistently during the summer and fall months, while *P. leuckarti, Evadne nordmanni* and *Penilia avirostris* occurred less regularly. *Oikopleura dioica* and *Doliolum nationalis* were the most important species of pelagic tunicates. *Sagitta elegans* was the only chaetognath observed.

Adult individuals of *Centropages typicus* and *C. hamatus* exhibited a seasonal variation in mean length. The largest individuals of *C. typicus* occurred in midwinter, those of intermediate size in early summer, while small ones appeared in late summer and early fall. Presumably these size periods denote three main generations during the year. Wet and dry weight determinations were obtained for 13 samples of 300 or 400 individuals; although they showed that there was a fairly close correlation between mean length and wet weight, larger size was not necessarily correlated with a high dry weight, for in some instances this simply meant a higher water content. Of the two generations per year observed for *C. hamatus,* the winter generation was considerably larger than the late spring genera-

---

[1] Throughout this report, Block Island Sound will be referred to as B. I. S., Long Island Sound as L. I. S., and Fishers Island Sound as F. I. S.

tion. Correlation coefficients between mean length and temperature showed that an inverse correlation exists between temperature and size in these two species of *Centropages.*

INTRODUCTION

During the three-year period from August 1943 to July 1946 a study of the species of fish taken by the trawl fishery in B. I. S. was undertaken by members of the staff of the Bingham Oceanographic Laboratory. The first report on this material has been published by Merriman and Warfel (1948). On all occasions when sample catches of fish were obtained, zooplankton samples were also collected and these form the basis of this report. Since the zooplankton of B. I. S. has not been systematically investigated previously, the present study will serve to outline the seasonal variations of the organisms occurring in this region. The fish eggs and larvae were removed from the plankton samples for separate study, and the results of that investigation (Merriman and Sclar, 1952) form one of the companion reports to this work.

Since the primary objective in this survey of the B. I. S. area was to obtain knowledge of the fish, and since the collections were made from a commercial dragger, the zooplankton samples do not depict the seasonal variations occurring at one definite location but were taken throughout the region. Also, in the spring the fishing fleet moved in near the mouths of the Thames and Connecticut rivers, so that the samples taken in May 1944 and 1945 and in March 1946 were collected at the eastern end of L. I. S. in waters of lower salinity. The circled areas on Fig. 1 indicate the stations where the samples were obtained, while Table I lists the station numbers with the dates and localities.

B. I. S. is a fairly open body of water, its salinity varying from place to place and at different depths depending on the origin of the water masses which enter from the Atlantic on the south and southeast and from the littoral areas on the west. It is partially protected on the south from the open waters of the Atlantic Ocean by Block Island and by the eastern extremity of Long Island. On the west its waters merge with those of Fishers Island Sound[2] and L. I. S., while on the east it is adjacent to Narragansett Bay which opens into the Atlantic (see inset on Fig. 1). Brackish water from L. I. S. flows mainly in the surface layers across the western part of B. I. S. around Montauk Point and into the Atlantic. More saline water from offshore comes

---

[2] See footnote 1.

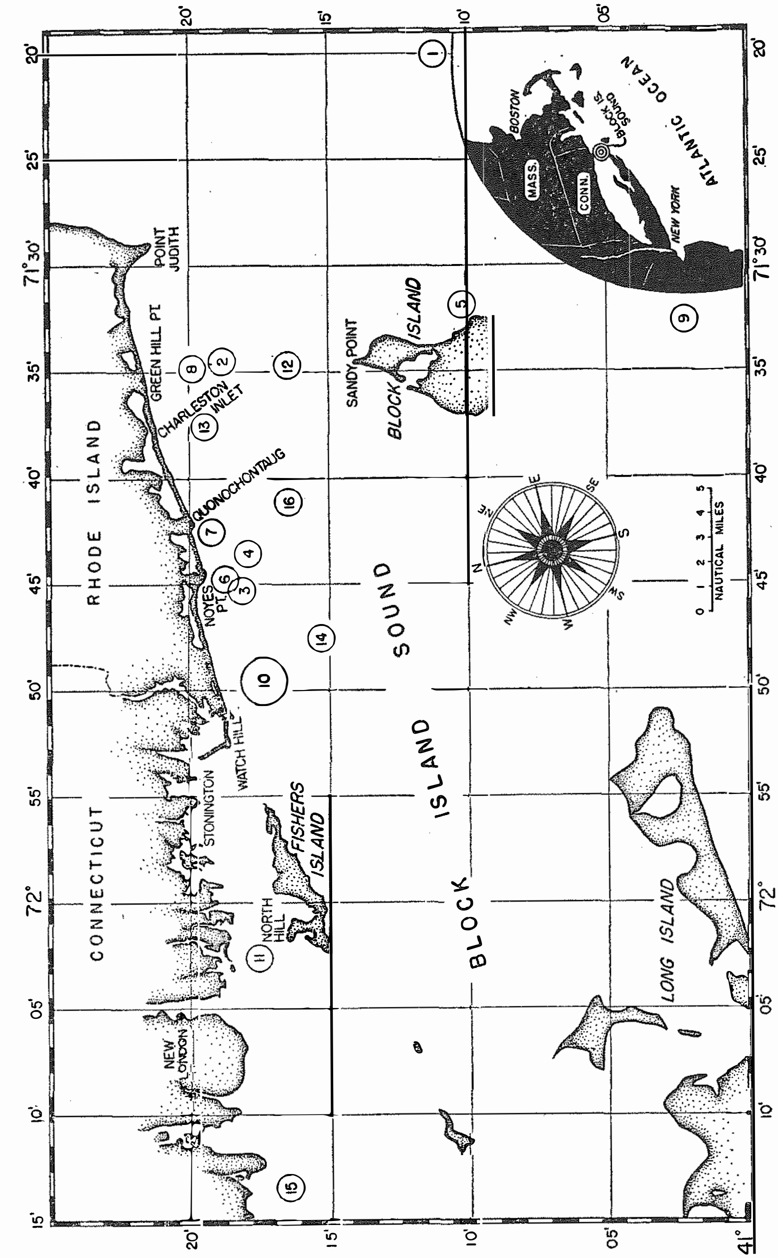


Figure 1. Block Island Sound. The numbered circles indicate the localities where samples were obtained. Drawn by Elizabeth Howe Constable.

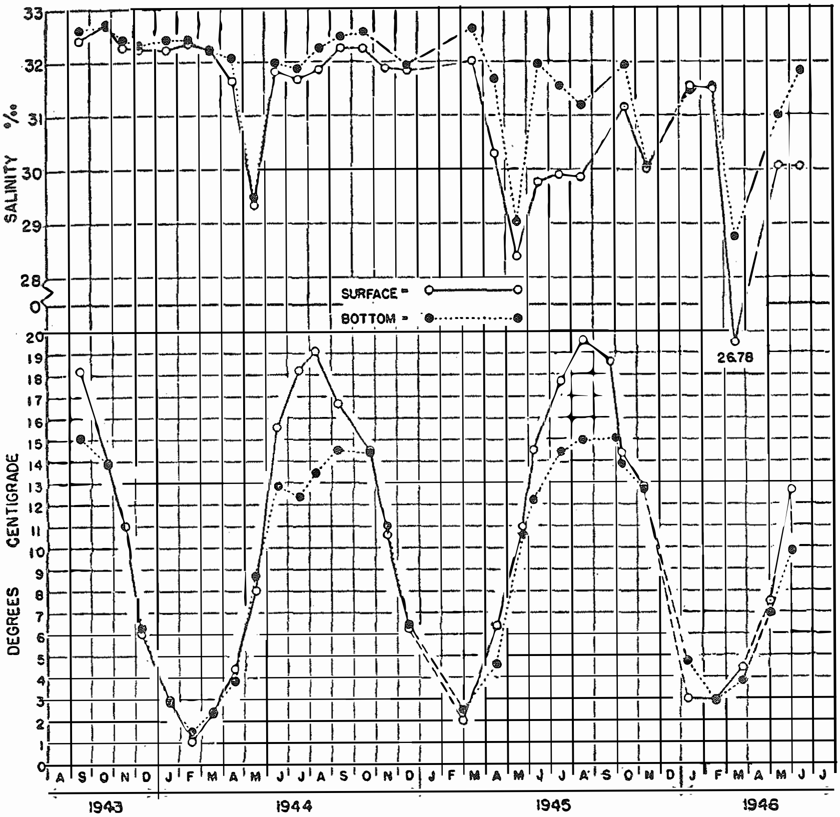


Figure 2. The surface and bottom salinities and temperatures recorded for Block Island Sound from August 1943 to June 1946. Reproduced from Merriman and Warfel, 1948: fig. 4.

into B. I. S. from the southeast, primarily in the bottom layers. The offshore waters are probably mainly of northern origin, derived from Georges Bank and the Gulf of Maine, although there is evidence for the inflow of Gulf Stream water, especially during the late summer and early fall. Since waters of such varied origin are found within B. I. S., changes in the plankton picture should and do occur concurrently with the fluctuations of the water masses. Some littoral and neritic species complete their life histories within B. I. S., while the occasional presence of alien organisms provides further evidence for the general hydrographic scheme just outlined.

The variations in salinity and temperature noted during the three-year period are shown in Fig. 2. The three low points on the salinity curve indicate the months when the fishing fleet moved into the eastern end of L. I. S. Omitting these three points, it is apparent that a gradual but definite decrease in the salinity of the surface layers of the areas sampled in B. I. S. took place from 1943–1946. An increasing difference between the surface and bottom salinity also occurred. This suggests a local change in current pattern resulting in a larger proportion of L. I. S. water traversing the region rather than a general decrease in salinity over a wide area. This lowering of the salinity is reflected in the general picture of the zooplankton, as will be noted on subsequent pages. Coincident with the decrease in the salinity, the troughs and peaks of the temperature curve show a slight increase.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the advice and assistance generously given by the staff and students of the Bingham Oceanographic Laboratory during the course of this investigation. I am especially indebted to Gordon A. Riley for placing at my disposal his extensive knowledge of the hydrography of the B. I. S. region and of plankton problems in general, for the determination of the wet and dry weights of *Centropages typicus*, and for his considered criticism of the manuscript. I am grateful also to Willard D. Hartman for the identification of the sponges taken in the trawl wing samples, to Frederick E. Smith who identified several of the small crustacea from these samples and who checked my identifications of the amphipods in particular, to Howard Sanders for aid in the identification of the crustacean larvae, and to Elizabeth Howe Constable for the careful preparation of the figures. Several valuable suggestions were made by Daniel Merriman, Grace E. Pickford, Ernest F. Thompson, and my husband, Edward S. Deevey, Jr.

METHODS

The zooplankton samples were collected at monthly intervals from August 1943 to July 1946. In a few instances, samples were taken twice in a month, while none was obtained in January, February, and December 1945 and in April and July 1946. Table I lists the dates, station numbers, and localities for the tows. Most of the samples were collected from Captain Ellery Thompson's dragger, the ELEANOR; one sample was taken from the RITA and one from the MARISE.

TABLE I. Dates, Station Numbers, and Localities for the Zooplankton Town

Date	*Station Number*	*Locality*
IX–12–1943	1	14 mi. SSE. of Pt. Judith, R. I.
X–31–1943	2	3 mi. S. of Green Hill, R. I.
XI–21–1943	3	5 mi. ESE. of Watch Hill, R. I.
XII–19–1943	4	5–8 mi. ESE. of Watch Hill, R. I.
I–2–1944	5	Old Harbour, Block Island, R. I.
I–23–1944	6	1 mi. S. of Noyes Pt., R. I.
II–20–1944	8	2 mi. S. of Green Hill, R. I.
III–19–1944	10	2 mi. SSE. of Watch Hill, R. I.
IV–19–1944	10	3 mi. S. by E. of Watch Hill, R. I.
V–18–1944	11	Between Fishers Island and Mouth of Thames River.
VI-23-1944	12	3 mi. N. of Sandy Pt., Block Island, R. I.
VII–16–1944	6	Yellow Bank, 1½ mi. from R. I. shore.
VII–23–1944	12	3 mi. N. of Sandy Pt., Block Island, R. I.
VIII–13–1944	12	3 mi. N. of Sandy Pt., Block Island, R. I.
IX–10–1944	12	3 mi. N. of Sandy Pt., Block Island, R. I.
X–26–1944	7	Off Noyes Pt. and Quonochontaug, R. I.
XI–19–1944	7	Off Noyes Pt. and Quonochontaug, R. I.
XII–18–1944	13	2 mi. S. of Charleston Inlet, R. I.
I–1945	—	——
II–1945	—	——
III–5–1945	2	4 mi. S. of Green Hill, R. I.
IV–16–1945	12	3 mi. NNE. of Block Island, R. I.
V–27–1945	11	Between Fishers Island and Mouth of Thames River.
VI–18–1945	10	2 mi. SE. of Watch Hill, R. I.
VII–17–1945	10	1½ mi. SE. of Watch Hill, R. I.
VIII–21–1945	14	5 mi. SSE. of Watch Hill, R. I.
IX–9–1945	10	2 mi. SE. of Watch Hill, R. I.
X–15–1945	7	1 mi. S. of Quonochontaug, R. I.
XI–11–1945	11	1 mi. N. of North Hill, Fishers Island, N. Y.
XII–1945	—	——
I–14–1946	13	2 mi. off Charleston Inlet, R. I.
II–19–1946	7	2 mi. W. of Noyes Pt., R. I.
III–24–1946	15	½ mi. W. of Hatchett's Reef, Conn.
IV–1946	—	——
V–6–1946	10	2 mi. S. of Watch Hill, R. I.
VI–9–1946	16	4 mi. S. of Quonochontaug, R. I.
VII–1946	—	——

These samples were collected with a No. 2 silk net one foot in diameter towed at the surface in the turbulent wake of the dragger 75 to 100 feet behind the boat at an average speed of 1.75 to 2 knots. Therefore it is probable that organisms from the upper 10 to 15 feet of water were sampled (see Merriman and Sclar, 1952). Strictly speaking, the zooplankton samples cannot be considered quantitative. However, for all but two of the samples the duration of the tows is known, most of them being 15 minutes in length; therefore all estimates of the numbers or volumes of the surface organisms are expressed as per 15 minute tow. Since the net tore while the August 1943 sample was being collected, this sample is only qualitative; for the January 1946 sample, for which the duration of tow was not listed, it is safe to assume that the standard 15 minute tow was made.

On occasions when tows were made on two different days in one month, as happened in January, February, and July 1944, the total number of organisms collected differed widely. On the other hand, as in the case of the fish eggs (see Merriman and Sclar, 1952), when consecutive hauls were made on one day consistent results were obtained. The two 10-minute tows made on November 21, 1943 yielded totals of 175 and 147 organisms. Two hauls made on July 16, 1944 showed total numbers of approximately 25,000 and 35,000 organisms, while three samples obtained on March 5, 1945 gave total numbers of 30 organisms for a 10-minute tow, 68 organisms for a 15-minute tow, and 248 organisms for a 20-minute tow. In each instance the total numbers of organisms obtained are of the same order of magnitude.

The total quantity of zooplankton taken in the surface samples was studied both volumetrically, by the displacement method, and numerically. To obtain the volume, the sample was strained through a piece of No. 2 silk and was allowed to drain on paper towelling for 15 to 30 minutes depending on the quantity, after which it was added to a known volume of water. The volumes obtained by this method were so small that as a rule only the total volume of a sample was estimated. When larger organisms such as sagittae or *Cyanea* were present, their volumes were estimated separately.

Numerical counts were made on all surface samples. At least 500 organisms and frequently 1,000 or more per sample were counted, the number counted varying greatly depending on the size of the sample and the heterogeneity of its composition. When the total sample consisted of several hundred organisms or less, the entire number was counted.

Fourteen bottom plankton samples were also obtained with a stramin net attached to the head line of the trawl. Volumetric determinations as well as percentage or total counts were obtained for these samples. Although many of the organisms obtained in the stramin net are not planktonic in habit, at least some of these invertebrates must play an important part as food for bottom-living fish; therefore they will be considered briefly in the APPENDIX. In presenting the material for the surface and bottom hauls, some of the data from the bottom hauls will be included with those from the surface tows. The organisms that live on or immediately over the bottom will be treated separately as bottom organisms, but the occurrence in the bottom hauls of any primarily planktonic forms such as copepods and sagittae will be noted in the section dealing with the surface zooplankton.

In this survey all members of the zooplankton population were not equally represented in the samples. Due to the fairly coarse mesh size of the net, neither small organisms such as *Oïthona, Paracalanus,* and *Oïkopleura* nor the immature stages of copepods were adequately sampled; hence the seasonal cycles and relative abundance of these forms cannot be estimated with any degree of accuracy. Also, since only surface tows were made, and although the upper 10–15 feet of water was probably sampled, there are no data for the occurrence of organisms throughout the entire water column. Although many planktonic species are usually found near the surface, others occur primarily at deeper levels; therefore the surface hauls may not be representative of the water column as a whole and in some instances they almost certainly are not. Thus some of the variability that superficially appears to be seasonal may actually be the result of failure to sample the whole population. Since the waters sampled each month constitute so small a proportion of the area as a whole, both horizontally and vertically, the possibility that important species may have been missed entirely by the net must be emphasized.

THE ZOOPLANKTON

Variation in Total Volume and Number

The total quantity of zooplankton varied throughout the year and at different stations. Fig. 3 shows in graphical form the total volume of the zooplankton in cubic centimeters per 15 minute tow, while Fig. 4 gives the estimated total number of zooplankton per 15 minute tow for the three-year period. In general, both of these figures show that the quantity of plankton was greater during the first half of the period studied. Zooplankton volumes consistently showed maxima in midwinter and minima in early spring and late autumn or early winter. For the remainder of the year the records were less consistent, with large peaks in midsummer of 1944 and in midautumn of 1943 and 1945. Fig. 4, giving the total numbers, mirrors the peaks and troughs shown in Fig. 3.

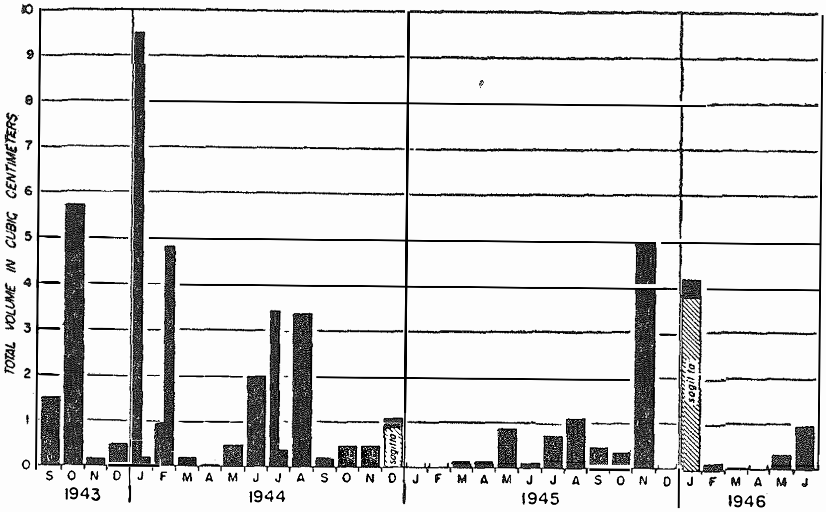


Figure 3. The total volume of the zooplankton in cubic centimeters per 15 minute tow from September 1943 to June 1946.

The general downward trend in the abundance of the zooplankton was coincident with the gradual lowering of the salinity, a factor undoubtedly of great importance to certain members of the plankton fauna. *Centropages typicus*, unquestionably the dominant form

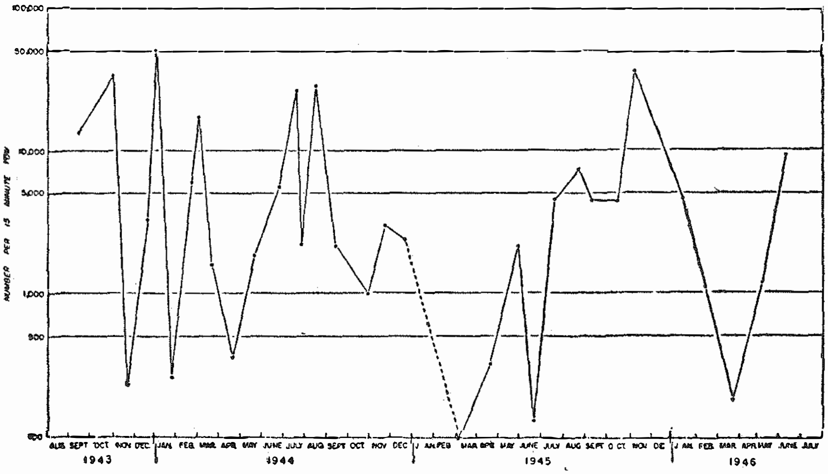


Figure 4. The estimated total number of zooplankton per 15 minute tow on a logarithmic scale for the three-year period.

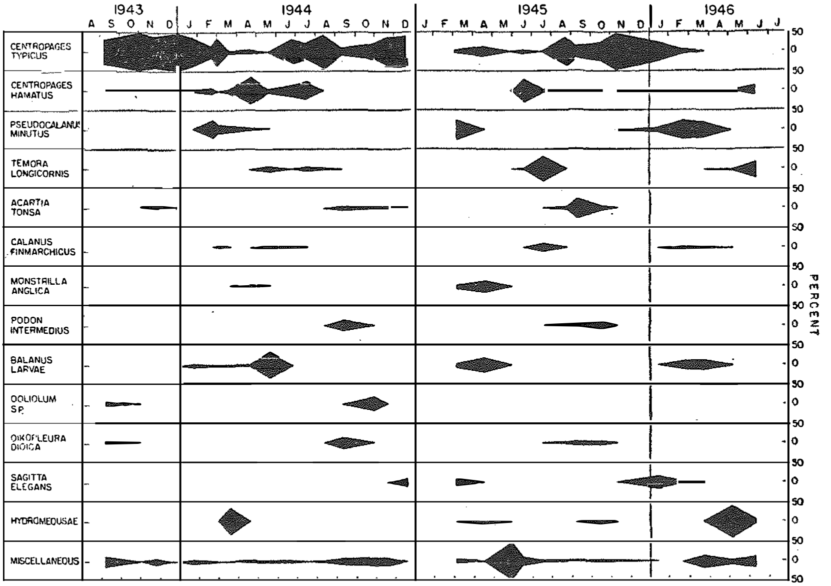


Figure 5. Relative percentages, by count, of the more important species of zooplankton collected during the three-year period.

throughout the first year of the observations, lost its year-round supremacy as the salinity fell, appearing in numbers in some months but not in others. Due to its absence there was no midsummer maximum in quantity of zooplankton in 1945, and in 1946 *C. typicus* was abundant only in January.

THE COMPOSITION OF THE ZOOPLANKTON

In all but two instances the copepods were the dominant group found in the surface zooplankton samples, although at various times cladocera, crustacean larvae, tunicates, chaetognaths, and coelenterates constituted appreciable percentages of individual samples. As already noted, *Centropages typicus* was by far the dominant organism throughout the period studied, even though it was found less frequently as the salinity fell. Other copepods which made up 5% or more of any of the samples, by count, include *Centropages hamatus, Pseudocalanus minutus, Temora longicornis, Calanus finmarchicus, Acartia tonsa,* and *Monstrilla anglica. Podon intermedius* was the

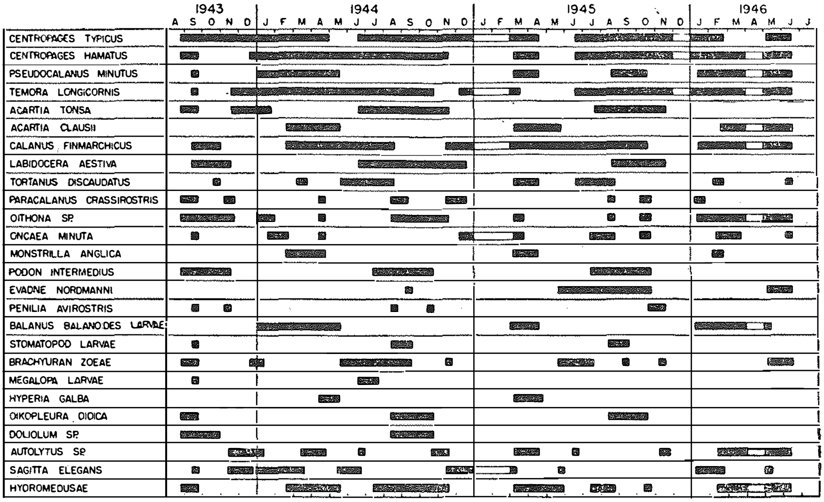


Figure 6. The seasonal occurrence of the organisms that appeared fairly regularly in the surface tows from Block Island Sound from August 1943 to June 1946.

most important cladoceran, occurring throughout the summer months and into the fall. Pelagic tunicates, especially *Oikopleura dioica* and two species of *Doliolum*, also appeared from August to October. *Sagitta elegans* was relatively numerous in the surface samples only during the winter months of 1945 and 1946, while hydromedusae were most abundant during the spring months. The crustacean larvae included in particular the nauplii and cyprids of *Balanus balanoides* and brachyuran zoeae. Fig. 5 portrays the percentages, by count, of the dominant species throughout the three-year period. The seasonal occurrence of the organisms that appeared in the surface tows with some degree of regularity is shown in Fig. 6. Most of these species will be considered separately.

It must be emphasized that in all probability some small species are important elements of the zooplankton of B. I. S., and it is unfortunate, therefore, that the mesh size of the net used was too large to retain these organisms. Occasional specimens of *Oithona* and *Paracalanus* were taken, presumably after the net had become clogged with larger plankton. Under the circumstances it is impossible to give an estimate of the relative importance of these forms. Other small organisms such as *Oikopleura* and *Podon* also could not have been adequately represented in the surface tows.

In the following sections where the various species are considered individually, constant use will be made of the terms oceanic, neritic, and littoral to describe the ecological preferences and salinity requirements of the organisms. It would be well, therefore, to define in advance the meanings of these words as they will be employed in this paper. Oceanic species are those that occur primarily beyond the continental shelf in the slope waters or in the Gulf Stream or beyond. Neritic species are most abundant over the continental shelf, though their distribution may extend into the slope water as well as into areas close to land where the salinity may be as low as 30°/oo or even slightly lower. Littoral species prefer sheltered waters such as bays and harbors where the salinity is usually within the twenties; when certain of these forms are found in neritic areas they may be considered indicators of coastal water. As thus defined, littoral species are brackish water forms, but since the salinity range of primarily littoral organisms need not be exceptionally wide, brackish water species may constitute a separate category including estuarine organisms which prefer waters where the daily or weekly salinity change is far greater than that in strictly littoral regions. There are, of course, planktonic organisms which cannot be definitely categorized as yet, and there are others that are known to appear almost indifferently in estuarine, littoral, and neritic areas. Among the species recorded from the B. I. S. region there were representatives from all four categories.

THE COPEPODS

Centropages typicus Krøyer

According to Bigelow and Sears (1939), *C. typicus* is one of the most common species found over the continental shelf from Cape Cod to Chesapeake Bay, where it was more numerous inshore than offshore. Although it was recorded at about 90% of all their stations for all months and years combined, the highest volumes of this copepod were obtained in February and October. In the Gulf of Maine, Bigelow (1928) reported that this species increased in numbers in August and was most generally distributed during autumn and early winter. The known temperature range of *C. typicus* noted by Bigelow is 3.05–24.4° C on the Atlantic Coast of North America. In B. I. S. it was taken, but not in numbers, at 1° C. The salinity range as given by Bigelow indicates that *C. typicus* is a relatively stenohaline species;

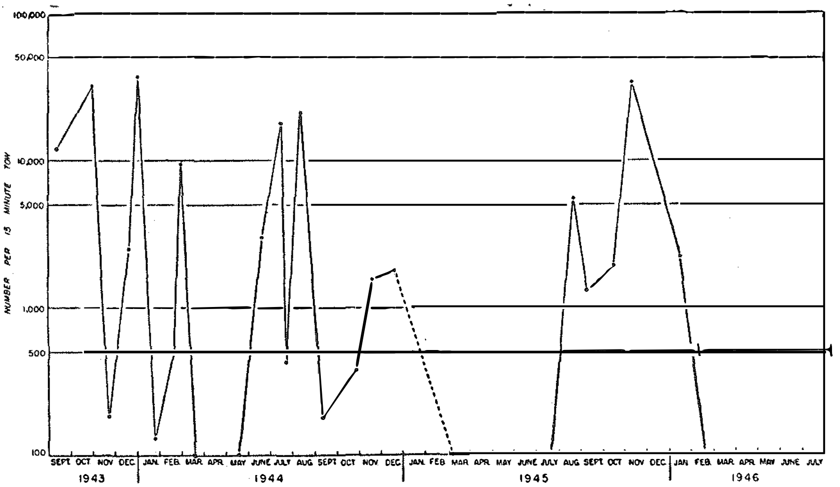


Figure 7. The estimated numbers of *Centropages typicus* per 15 minute tow on a logarithmic scale for the three-year period.

although it has been found to be common at Woods Hole, Massachusetts in salinities of 31–32°/oo, it has not been recorded in waters of lower salinity. Therefore its occurrence in numbers in August 1945 in B. I. S. at a salinity slightly below 30°/oo (see Fig. 2) may be the first record of its presence at such a low salinity. *C. typicus* is almost entirely restricted to the coastal areas (Clarke, 1940), and it is therefore a neritic form, confined to the waters over the continental shelf.

C. typicus was represented by at least a few specimens in every sample collected within the B. I. S. area throughout the three-year period studied, a distinction which it shared with no other member of the zooplankton. It was absent only from the spring samples taken at the eastern end of L. I. S. where the salinity was approximately 27–29°/oo. Throughout the year its abundance fluctuated sharply from sample to sample, but it always occurred in minimal numbers from March to May and, during the first year of the observations, it was fairly plentiful during the rest of the year. Fig. 7 gives the estimated numbers of *C. typicus* per 15 minute tow for the period studied. The great variation in numbers of zooplankton taken from station to station is exemplified by the two samples obtained in January 1944. The sample collected in early January contained approximately 50,000 organisms, the highest count for all of the samples, while the sample taken later in January consisted of only 258 organisms. In both of these samples, *C. typicus* was by far the dominant form, despite the great discrepancy in actual numbers counted. Similar differences in numbers were noted in the two February and two July 1944 samples.

Fig. 7 shows that fewer *C. typicus* were taken as the salinity decreased during the latter part of the period studied. This emphasizes the fact that the lower limit of salinity tolerance of this species must be between 30 and 31°/₀₀. The predominance of *C. typicus* over the other organisms in the surface hauls is apparent when Fig. 7 is compared with Fig. 4, which gives the total number of organisms. Except for the small peak in May 1945 and the maximum in June 1946, all the peaks in Fig. 7 match the peaks in Fig. 4. When *C. typicus* was absent, no other form appeared in comparable numbers.

A few *C. typicus* appeared on several occasions in the trawl wing samples. Individuals were observed in July, August and November 1944 and in March and October 1945. In the November haul, *C. typicus* made up 34.5% by count of the total number of organisms present.

Since the nauplii and early copepodid stages were not retained by the net, it is impossible to ascertain with certainty the times of year when *C. typicus* was breeding most actively. The *Centropages* population was always at its lowest ebb during the spring months, so it is improbable that any reproduction takes place at this time. Throughout the continental shelf, Bigelow and Sears (1939) also found that this species was of minor importance during this period, an observation which was corroborated by Clarke (1940). These investigators found *C. typicus* most abundant from summer into the late fall and winter. The presence throughout the year of at least a few late copepodid stages as well as adults in almost every sample from B. I. S. would seem to indicate that the reproductive activity is not strictly limited to certain months. This is borne out by the fact that females with spermatophores were observed during every month of the year except March, April, and May.

It is probable, however, that there are three main breeding periods during the year, and it is unfortunate that the data are too fragmentary to allow a conclusive statement about this. The variations in size of adults present the most valid clue to the number of generations, and this subject is discussed in a later section. Judging also from the relative number of females carrying spermatophores, from the percentage of immature stages, and from the abundance of the species, it is possible that the reproductive activities of *C. typicus* during the first half of the period investigated were concentrated in the early fall of 1943, and in the midwinter, early summer, and fall of 1944. Since the data for the B. I. S. area are confused due to the decreasing salinity, only the samples collected from September 1943 to March 1945 may be considered indicative of normal conditions for *C. typicus,* but as no samples were obtained during January and February 1945 there are no data for these months. In the Gulf of Maine, Bigelow (1928) assumed one chief breeding period in the summer for *C. typicus;* since this species increased in abundance in the upper 20 m when the waters had warmed to the maximum annual temperature, he gave 8–10° C as the lower limit for its active breeding. The temperatures in B. I. S. are lower than this from November or December to May or June, but the possibility of a midwinter breeding period should not be ignored. The abundance of *C. typicus* over the continental shelf in February, as well as the indications of reproductive activity found within the B. I. S. area in midwinter, points to a breeding period at this time. There is some evidence, therefore, that under normal conditions *C. typicus* may have three generations during the year, spawning occurring primarily in midwinter, early summer, and during the fall months. Since samples were collected only at the surface, the distribution of *C. typicus* with depth during the year is not known. Although experiments on the reactions of this species to light and gravity have shown that it may be expected to occur at the surface during the night and during the greater part of the day (Johnson and Raymont, 1939), possibly, as the salinity fell at the surface, the majority of the individuals may have gone to the deeper levels where the salinity was higher.

Centropages hamatus (Lilljeborg)

C. hamatus is more euryhaline than *C. typicus.* Although it has been found across the breadth of the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939), it was more abundant near shore. Its range is more northern than that of *C. typicus,* since the southern record of its occurrence on the Atlantic Coast of the United States is just above Cape Hatteras in the spring, while *C. typicus* has been found in the Gulf of Mexico (Foster, 1904). *C. hamatus* is a brackish water, littoral, and neritic copepod. Small numbers were present in Tisbury Great Pond, Massachusetts (Deevey, 1948) during the first half of the year, when the temperature rose from

0–24° C and when the salinity ranged from less than 1–31°/₀₀. According to Gurney (1928–1929), this species is characteristic of sheltered waters, together with *Acartia clausii* and *Temora longicornis.* Actually, the data collected in this region on the Atlantic Coast indicate that there are fine distinctions between the salinity preferences and ecological distribution of these three species. *C. hamatus* is capable of living in brackish, littoral and neritic situations, but it prefers less protected waters than *Acartia clausii. A. clausii* is most abundant in brackish and littoral regions, while *Temora longicornis* is primarily a littoral and neritic species.

At least a few individuals of *C. hamatus* were recorded from all but three of the samples collected in B. I. S., and this species was present in all but one of the samples taken within the limits of L. I. S. *C. hamatus* therefore ranked second, both in numbers counted and in its occurrence throughout the greater part of the year. It constituted 5% or more of the total sample (see Fig. 5) on a number of occasions during the first half of the year. *C. hamatus* was not found in the samples taken in October and November 1943, December 1944, and May 1945. It appeared in only one trawl wing sample, that obtained in May 1946.

Fig. 8 shows the estimated number of *C. hamatus* per 15 minute tow throughout the period studied. During the first year of the observations, *C. hamatus,* like *C. typicus,* occurred more consistently and in greater numbers, reaching its highest maximum in July 1944. In 1945 it was found in smaller numbers from June to November, no samples being collected in January, February, and December; in 1946 it was most numerous in January and June. Minimal numbers were found consistently during the late fall months. Maximal abundance of *C. hamatus* in June and July has also been noted off Marthas Vineyard (Clarke and Zinn, 1937), on the continental shelf (Bigelow and Sears, 1939), and in Oslo Fjord (Wiborg, 1940).

Undoubtedly at least two generations of *C. hamatus* are produced each year. Females with spermatophores were observed in June and July 1944 and 1945 and in January, February, and June 1946. In the samples collected in L. I. S., females with spermatophores were noted in May 1944, July 1945, and March 1946. Wiborg's data for Oslo Fjord indicated that individuals spawned in March or April reached maturity in June and July, there being, therefore, a spring and a summer generation. According to Marshall (1949), in Loch Striven

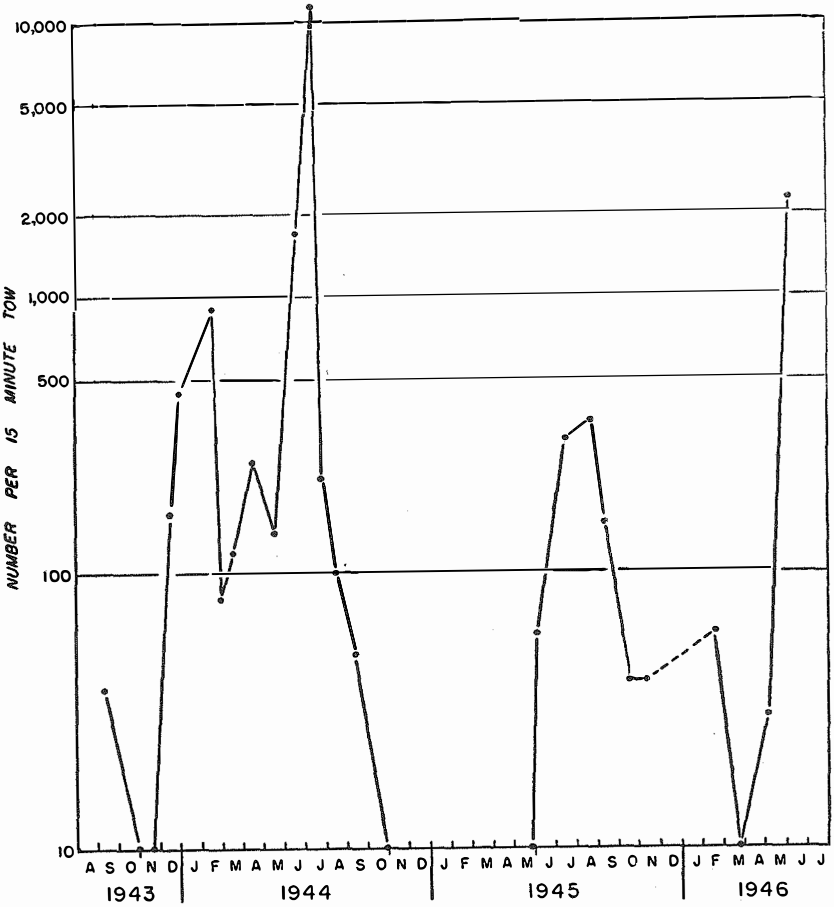


Figure 8. The estimated numbers of *Centropages hamatus* per 15 minute tow on a logarithmic scale for the three-year period.

five broods of nauplii were produced between April and the end of September, one of which failed to develop. Thus in Loch Striven there were four to five generations during the year. In the B. I. S. area, judging from the available data, reproduction occurred in the winter or early spring months, and again in June and July.

Pseudocalanus minutus (Krøyer)

P. minutus is a northern species, widespread throughout the North Atlantic region (Bigelow, 1928), with its southern boundary on our

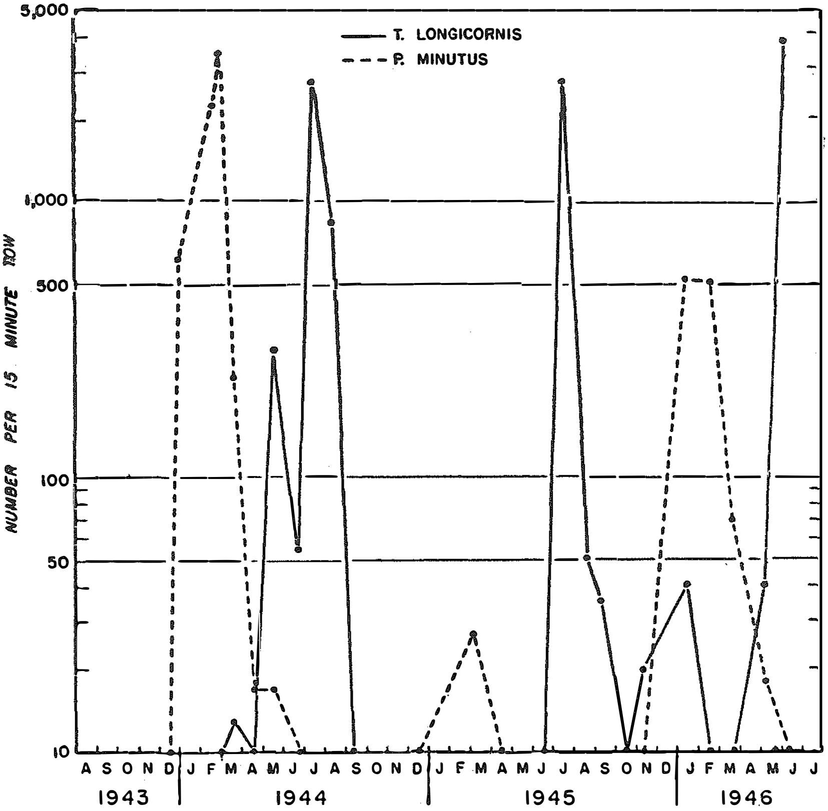


Figure 9. The estimated numbers per 15 minute tow on a logarithmic scale of *Pseudocalanus minutus* and *Temora longicornis* during the three-year period.

coast probably not far south of Chespeake Bay (Bigelow and Sears, 1939). It occurs throughout the year in the Gulf of Maine, but, according to Fish (1936), south of Cape Cod it virtually disappears from the neritic zone during the summer months, reappearing in the fall at Woods Hole. Bigelow (1928) gave its temperature range as 0–15° C, although it has been found at temperatures up to 20° C. According to Sewell (1948), its temperature range is −1.23–13° C, its known salinity range from 7.25–35.3°/₀₀.

In B. I. S., *P. minutus* was found in the surface samples from January to May, with maximum numbers in January and February. Fig. 9 gives the estimated numbers per 15 minute tow of both *P. minutus* and *Temora longicornis*. *P. minutus* was most abundant during the first year of the observations, but even at this time only moderate numbers were collected. During the period of its occurrence, the recorded temperature range was from 1–8° C, well within the limits set by Bigelow. Since both temperature and salinity should have been favorable for this species, it is odd that it was not found in numbers for a longer period each year. Its presence was detected in September 1943, and in August, September, and October 1945, but it was never plentiful during the fall months. It was also noted in the trawl wing samples obtained in May and July 1944, March 1945, and May 1946. Since it was fairly numerous during only one winter, it is impossible to state whether there was more than one generation per year. However, the presence of females with egg sacs in the trawl wing sample taken in May 1944 provides slight evidence for a spawning period in the spring and also indicates that the center of abundance of this species may have moved to the deeper layers. Digby (1950) recorded five generations per year for *P. minutus* in the English Channel, while Marshall (1949) reported that spawning occurred in late February, from April until July, and in early August in Loch Striven. The nauplii produced in July and early August had developed only to Stage IV copepodids by October, these representing the autumn stock which would mature by the following February. With regard to the vertical distribution of *Pseudocalanus,* Marshall found all stages above 10 m depth from April to June; from the end of June to the end of August, Stage III to Stage VI forms were taken almost entirely below the 10 m level.

Temora longicornis (Müller)

T. longicornis is a littoral and neritic species which may occur out to the edge of the continental shelf but is more frequently found near shore (Bigelow and Sears, 1939). In winter its range may extend southward to Cape Hatteras. Bigelow (1928) gave a wide salinity range for *T. longicornis,* from 6.54°/₀₀ in the Baltic to 35°/₀₀ in the open Atlantic, but according to Sewell (1948) the known upper salinity limit is 36.16°/₀₀. The recorded temperature range was from −1–20° C. In the Gulf of Maine this species has been found throughout the greater part of the year, but Fish (1925) listed *T. longicornis* as one of the three species characteristic of winter plankton at Woods Hole.

In B. I. S., *T. longicornis* appeared consistently in appreciable numbers only in June or July (see Fig. 9), although its presence was noted in every month except October 1943, November 1944, and April 1945. As shown in Fig. 9, like all the species already described, *T. longicornis* occurred in greater numbers during the first year of the observations. In July 1944 and 1945, when *Temora* was most abundant, the temperature was approximately 18° C, but it was less than 13° C at the time of the June 1946 peak.

Acartia tonsa Dana

A. tonsa is a littoral copepod which occurs primarily in somewhat sheltered waters and when found in the open ocean is always close to land. This preference for partially enclosed areas is emphasized by the fact that it was not found by Bigelow and Sears over the continental shelf from Cape Cod to Chesapeake Bay, except near the mouth of Delaware Bay. However, it is abundant in fresh, brackish, and salt water in the Woods Hole region (Sharpe, 1910; Wilson, 1932a) and is one of the most important members of the plankton fauna of Chesapeake Bay (Davis, 1944). Its range on the eastern coast of the United States is known to extend from Cape Cod to the Gulf of Mexico. In the partially enclosed areas which it prefers, such as the waters of Chesapeake Bay, it is a dominant form throughout the period of its occurrence.

In the B. I. S. area it was found from June or July into the late fall and winter. This region may be considered to be on the fringe of the more sheltered areas where *A. tonsa* occurs in greatest numbers, and it is of interest to note that this species constituted an appreciable percentage of the total sample only during the late summer and early fall of 1945 (see Fig. 5) when the salinity was approximately 30°/₀₀ and when *Centropages typicus* appeared in minimal numbers. Fig. 10 shows the estimated numbers of *A. tonsa* per 15 minute tow. This seasonal occurrence of *A. tonsa* from late spring or summer to early winter in these latitudes has been noted previously by a number of investigators. Off Marthas Vineyard it was found from April to December (Clarke and Zinn, 1937), while Fish (1925) reported adults from May to November at Woods Hole. In Tisbury Great Pond on Marthas Vineyard (Deevey, 1948) it appeared in June, but it virtually disappeared during the two summers studied, probably due to a sharp rise in salinity on both occasions. In L. I. S., *A. tonsa* has been found from July to January (unpublished data) and in Narragansett Bay during the summer months (Williams, 1907).

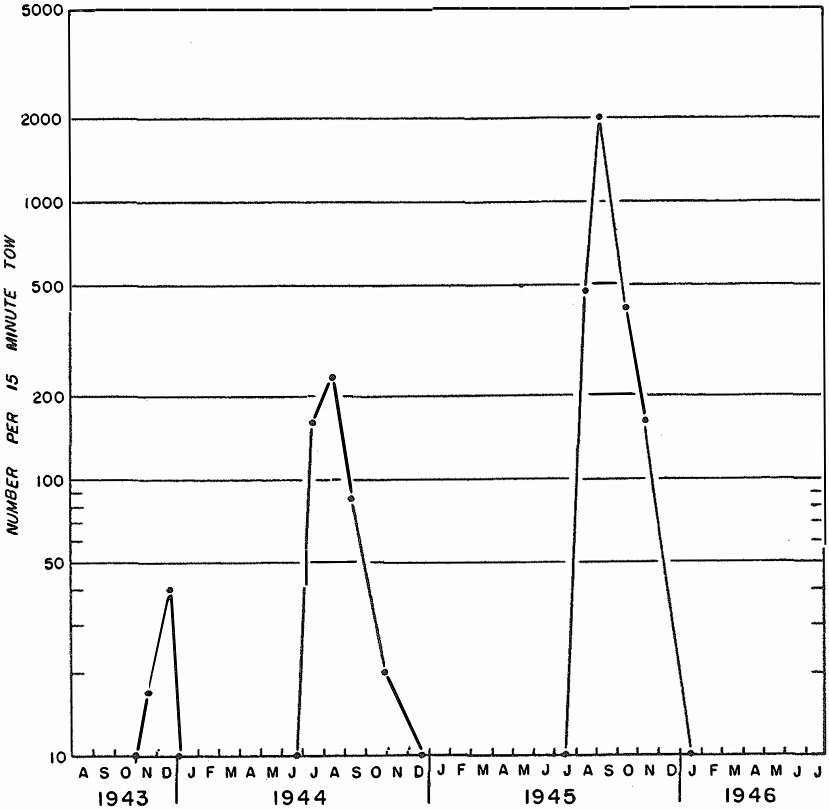


Figure 10. The estimated numbers of *Acartia tonsa* per 15 minute tow on a logarithmic scale for the three-year period.

During the fall of 1943 the presence of a few southern oceanic species indicated that offshore waters were moving into B. I. S. Although stray individuals of *A. tonsa* were noted from August 1943 to January 1944 (see Fig. 6), they were rarely numerous enough to appear in the counting chamber. This emphasized the fact that this species prefers littoral regions. The data do not show whether *A. tonsa* breeds extensively in B. I. S. In L. I. S., however, large numbers of females with spermatophores were found in a sample taken in July 1945 one mile south of Mamauguin, Connecticut. *A. tonsa* probably occurs in greatest abundance in the more sheltered waters adjacent to B. I. S.

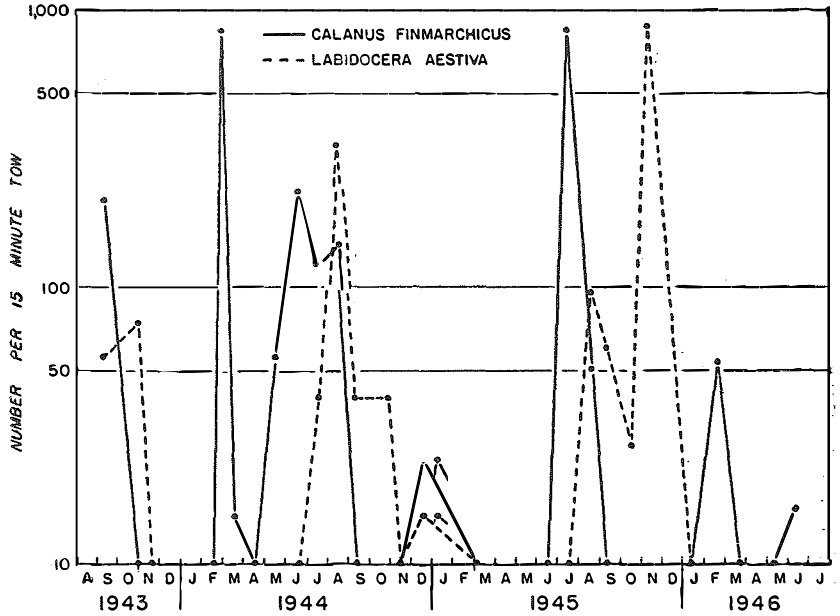


Figure 11. The estimated numbers per 15 minute tow on a logarithmic scale of *Calanus finmarchicus* and *Labidocera aestiva* for the three-year period.

Calanus finmarchicus (Gunner)

Over the continental shelf from Cape Cod to Chesapeake Bay, *C. finmarchicus* constituted a higher percentage of the total volume of zooplankton than any other form, *Centropages typicus* being the only other calanoid copepod of widespread importance (Bigelow and Sears, 1939). In this general region, *Calanus* is primarily neritic, although it is not as completely restricted to the waters over the continental shelf as *C. typicus* (Clarke, 1940). The relative abundance of *Calanus* is definitely seasonal in these latitudes, the greatest numbers occurring in spring and summer. According to Clarke and Zinn (1937), adults were most plentiful in May and June, a short-lived spring and a long-lived summer generation being produced yearly. It is probable that breeding occurs in the winter to early spring and in the early summer throughout this region (Clarke, 1940). Bigelow (1928) gave the temperature range of this species as approximately 0–20° C, while according to Sewell (1948) the salinity range is 29–35.3°/oo. *C. finmarchicus* is therefore able to tolerate slightly lower salinities than

C. typicus. This is also evidenced by the fact that individuals of *Calanus* have been taken within L. I. S.

In the B. I. S. area, *Calanus* was not plentiful in the surface tows, and since samples were not taken at various depths, its relative importance cannot be estimated further. Throughout the period studied, the presence of a few individuals was noted in every month of the year, more being observed from February to August or September. Fig. 11 shows the estimated numbers per 15 minute tow of *Calanus* and *Labidocera aestiva. Calanus* was most numerous in February and June 1944 and July 1945, so that its seasonal abundance agrees with the results obtained by other investigators. It was noted in the trawl wing samples in May and November 1944 and in May 1945, both May samples having been collected at the eastern end of L. I. S. Since both salinities and temperatures of B. I. S. were favorable for this species, it is surprising that it was not taken in greater numbers. Possibly the majority of the individuals may have been present at deeper levels. However, since marked fluctuations in the abundance of *Calanus*, apparently not related to changes in temperature or salinity, have been noted from year to year throughout the region south of Cape Cod (Sears and Clarke, 1940), the years 1944, 1945, and 1946 may have been "poor" for *Calanus.*

Labidocera aestiva Wheeler

L. aestiva is a littoral species, recorded only from the east coast of North America from the Gulf of St. Lawrence (Bigelow, 1928) to Chesapeake Bay (Wilson, 1932b). Like *Acartia tonsa,* this form is found primarily in sheltered waters and has not been reported from the coastal areas over the continental shelf. At Woods Hole, where it is known to occur from June to November, Fish (1925) characterized it as a typical summer form, but in Chesapeake Bay (Wilson, 1932b) it is abundant in summer, autumn, and winter, in the outer Bay particularly.

L. aestiva was not an important member of the zooplankton of B. I. S., but it occurred consistently during the summer and fall of each year (see Figs. 6 and 11). It is probable that two generations are produced each year, one in July or August and the other in October or November, but as yet there is no evidence that reproduction occurs actively in B. I. S. Females with spermatophores have been observed in July in L. I. S. and in November north of Fishers Island not far from the mouth of the Thames River (see Fig. 1). *L. aestiva* probably prefers more confined waters than those of B. I. S.

Monstrilla anglica Lubbock

M. anglica is the only species belonging to the Monstrilloidea that was taken in B. I. S. These forms are parasitic during the juvenile stages but free-swimming as adults. *M. anglica* deserves special mention, however, since, according to Wilson (1932a), the only other record of its occurrence on this coast is from the Gulf of Maine, where two males were collected in March 1920. In B. I. S., *M. anglica* appeared regularly in the surface tows obtained in February, March, and April (see Fig. 6). Due to the fact that the total volume of plankton was smaller in March and April than at any other time of year, the few *Monstrilla* that appeared at this time on occasion constituted an appreciable percentage of the total sample. This occurred in 1945 in particular (see Fig. 5) when 93 *Monstrilla* per 15 minute tow, the highest number recorded, were counted in the April sample. In 1944 *M. anglica* was present from February to April, but in 1946 it was taken only in February, the March sample having been collected in L. I. S. while no sample was obtained during April.

This definite seasonal appearance of *M. anglica* implies that there is but one generation a year. The individuals obviously reach maturity in late winter or early spring. According to Wilson, the adults are incapable of feeding and exist wholly to reproduce. Breeding must occur during the period from February to April, the young requiring nearly a year for their development. Most of the individuals examined were males; these varied in length from 1.3–2 mm. Only two females were observed. *Monstrilla anglica* is evidently an indigenous member of the B. I. S. fauna.

Other Copepods

The other copepods which appeared in the B. I. S. zooplankton tows were never important quantitatively. The majority of these were brought into the Sound from more saline or more brackish areas. These forms may be grouped under several headings: (1) strays from offshore waters, the majority from the Gulf Stream; (2) strays from brackish waters; (3) species possibly indigenous to the Sound that appeared periodically but in small numbers; (4) species not adequately sampled by the net; (5) parasitic forms.

The pelagic species that appeared in B. I. S. as strays from offshore waters were found only during the fall months of 1943 and 1944 during the period of higher salinity. Four Gulf Stream species were recorded only from the September 1943 sample which was collected 14 miles SSE. of Pt. Judith, Rhode Island, in the open waters of the continental shelf (see Fig. 1); several other species noted on this occasion also occurred later within the Sound. *Acartia danae* Giesbrecht, *Calocalanus pavo* (Dana), *Eucalanus attenuatus* (Dana), and *Mecynocera clausi* I. C. Thompson were observed only in September 1943. *Calanus minor* (Claus) appeared in September and November 1943 and December 1944. *Corycaeus venustus* Dana was noted only in October 1943. *Eucalanus monachus* Giesbrecht, *Temora turbinata* (Dana), and *T. stylifera* (Dana) were present from September to November 1943. *Rhincalanus nasutus* Giesbrecht was recorded only from the trawl wing sample collected in November 1944. All of these species are southern forms, but *Temora turbinata* has been reported as numerous in the outer part of Chesapeake Bay (Wilson, 1932b) and may have a wider salinity tolerance. It is of interest to note, however, that this species was not recorded over the continental shelf from Cape Cod to Chesapeake Bay, although this may not preclude its presence. It is safe to conclude that *T. turbinata* came into B. I. S. from more southern waters, while the other species listed are definitely known as Gulf Stream forms from waters beyond the continental shelf.

Two other species that arrived in the Sound from offshore waters are *Anomalocera patersonii* Templeton and *Candacia armata* (Boeck). Both of these species have a more northern distribution than the ones already considered, but both have been recorded from the Gulf Stream south of Nantucket or Marthas Vineyard (Wilson, 1932a). Bigelow (1928) found *A. patersonii* fairly widespread over the Gulf of Maine, especially during August, although it occurred for the greater part of the year; he concluded that it probably reproduced in the Gulf. Only occasional specimens of *Candacia armata* were taken in the Gulf of Maine, and Bigelow believed that these were of oceanic origin. Both species have been collected over the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939), but *C. armata* occurred more frequently than *A. patersonii*. Evidently *A. patersonii* is more numerous north of Cape Cod, while *C. armata* has been found abundant on rare occasions south of the B. I. S. area. Since both species occur over the continental shelf, they must have a somewhat wider salinity tolerance than the Gulf Stream forms that have been listed. *Anomalocera patersonii* was present in the B. I. S. samples in June, July, and October 1944. Adults were noted on all three occasions, while immature copepodids were found in June and October. *Candacia armata* appeared in September 1943 in the sample taken outside the Sound; it also occurred in October, November, and December 1944. Females with spermatophores were observed in September 1943 and in the trawl wing sample taken in November 1944. Immature stages were present in the surface samples for November and December 1944. It is possible, therefore, that some reproduction may occasionally occur in the Sound and that this takes place during the fall months.

Halithalestris croni (Krøyer) was collected on only one occasion, in March 1944. This is a large pelagic harpacticoid of northern distribution that has not been recorded hitherto south of Woods Hole, Massachusetts. This copepod is probably not a regular inhabitant of B. I. S. It is noteworthy that the species thus far mentioned occurred only during the period of higher salinity and provide evidence for the advent of offshore waters into the Sound at this time.

The copepods that appeared in the Sound as strays from brackish waters include two species of *Eurytemora, E. hirundoides* (Nordquist) and *E. americana* Williams. *E. hirundoides* was found only in February 1944, although it was taken north of Fishers Island in March 1946. *E. americana* was present only in the trawl wing sample for July 1944, but it too was taken north of Fishers Island in May 1944. Both are primarily brackish water species.

Acartia clausii Giesbrecht and *Tortanus discaudatus* Thompson and Scott are species that may be indigenous to B. I. S. but that were never numerous. The salinity preferences of these forms are similar to those of *Acartia tonsa* and *Labidocera aestiva*, and they may be classed as primarily littoral forms in these latitudes. The data are insufficient to allow a statement as to whether these species breed in B. I. S. or whether they are constantly carried into the Sound from nearby littoral waters such as those of L. I. S. *Acartia clausii* was present in small numbers from February to May or June (see Fig. 6). In Tisbury Great Pond, Massachusetts, *A. clausii* was also most numerous during the spring months, two generations being produced in April and June (Deevey, 1948). Individuals of *Tortanus discaudatus* were recorded most frequently during the spring and summer months (see

Fig. 6). In 1945 and 1946, most of the specimens noted were males; males constituted 2.5% of the June 1946 sample and many of these individuals appeared to be clutching small hydromedusae. This latter fact is mentioned, since evidence that copepods attack hydromedusae was not noted at any other time, although it is usual to find hydromedusae engulfing copepods. The seasonal distribution observed for *T. discaudatus* is similar to that recorded for it in the Woods Hole region where Fish (1925) found it to be a spring and early summer form.

Aside from *Halithalestris croni*, *Harpacticus chelifer* (Müller) was the only other harpacticoid noted in the samples. This was the dominant form in the sample taken in the latter part of July 1944, constituting 46% by count of the total number. Females with egg sacs were present at this time. This species may be indigenous to the B. I. S. area.

The copepods that were not adequately sampled by the net include species of the cyclopoids *Oithona* and *Oncaea* and the calanoid *Paracalanus*. *Oithona spinirostris* Claus, differentiated from *O. plumifera* Baird on the basis of the relative lengths of the anal segment and the caudal rami (see Wilson, 1932a), was definitely identified only from the November 1944 sample and may not occur regularly, but *O. similis* Claus and *O. brevicornis* Giesbrecht are in all probability indigenous to the B. I. S. region. Species of *Oithona* were observed in every month except May, July, and December (see Fig. 6), so it is probable that they are present throughout the year in B. I. S. *Oncaea* sp., probably *O. minuta*, was noted on a number of occasions (see Fig. 6) and may also be a year-round inhabitant of the Sound. Although *Paracalanus parvus* (Claus) might be expected to occur in B. I. S., it was taken only in August and September 1944 and in October 1945 and probably was not abundant during the period studied. On the other hand, *Paracalanus crassirostris* Dahl was noted more frequently, although it is the smallest calanoid known (see Fig. 6). In all likelihood it is an indigenous member of the B. I. S. fauna. On the eastern coast of the United States this species has been recorded only from Tisbury Great Pond, Massachusetts (Deevey, 1948), although Davis (1944) has described *P. crassirostris* Dahl var. *nudus* Davis from Chesapeake Bay.

In addition to *Monstrilla anglica*, a few more parasitic species were found. *Caligus rufimaculatus* Wilson was fairly common, especially in the trawl wing samples. Both sexes of this copepod are parasitic on the outside surface of the two species of *Fundulus* common at Woods Hole and on mullet, and this species hitherto has not been recorded outside the Woods Hole region. Individuals were observed in the surface tows collected in September 1943 and June 1944, and in the trawl wing samples for May, July, and November 1944, May 1945, and January and May 1946. Females and males were present in the majority of the samples, but only males were found in September 1943 and May 1946. Females with egg strings were noted in July 1944 and May 1945. The samples collected in May 1944 and 1945 were obtained at the eastern end of L. I. S., so this species is apparently widespread throughout the region studied.

Two specimens of *Argulus megalops* Smith, another parasite known only from Narragansett Bay (Williams, 1907) and the Woods Hole region, were found in the trawl wing sample for November 1944. The hosts of this species are all bottom living fish, including the winter flounder *Pseudopleuronectes americanus*, summer flounder *Paralichthys dentatus*, sand dab *Hippoglossoides platessoides*, spotted flounder *Lophopsetta maculata*, sea robin *Prionotus carolinus*, long-horn sculpin *Myoxocephalus octodecimspinosus*, and the goosefish *Lophius piscatorius*. This species, too, will probably prove to be widespread in the B. I. S. area.

One young specimen of *Lepeophtheirus*, probably *L. thompsoni*, an external parasite on the goosefish, was recorded in May 1946.

CLADOCERA

Four species of Cladocera were found in B. I. S., occurring seasonally. *Podon leuckarti* Sars appeared only in the late spring, in June 1944 and 1945, and in May and June 1946. It was most abundant in June 1946 when it made up 17% of the total number of organisms. *Podon intermedius* Lilljeborg was taken consistently during the summer and fall months throughout the period studied (see Fig. 6), and several times it constituted an appreciable percentage of the total sample. Fig. 12 gives the estimated number per 15 minute tow during the periods of its occurrence. In 1943 *P. intermedius* was present from August to November, but it was never plentiful. In 1944 it comprised 25% of the September sample and in 1945 14% of the October sample (see Fig. 5). Fish (1925) reported a similar seasonal periodicity for this species at Woods Hole, where maximal numbers were recorded in June and mid-September. Individuals of *P. leuckarti* were observed

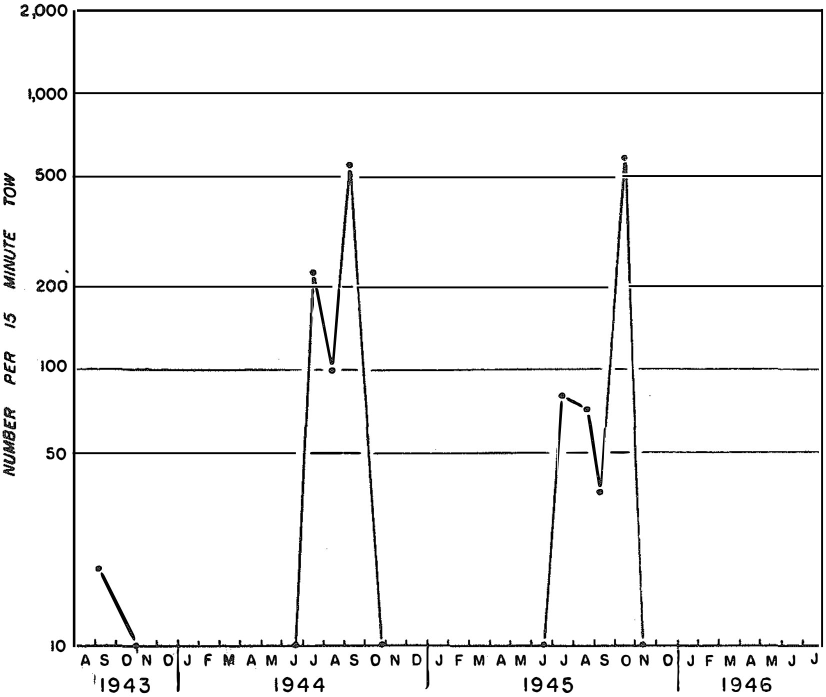


Figure 12. The estimated numbers of *Podon intermedius* per 15 minute tow on a logarithmic scale for the three-year period.

carrying resting eggs in June of every year, while many specimens of *P. intermedius* with resting eggs were observed in October 1945. It is probable that the smaller individuals were not retained by the net and that *Podon* was present in higher numbers than those recorded.

Evadne nordmanni Loven was found more frequently during the latter half of the period studied (see Fig. 6), but it was never as numerous as *P. intermedius*. In July 1945 and May 1946 it constituted 2% of the total sample. In the Woods Hole area this species was found from June to January (Fish, 1925). The fact that *E. nordmanni* occurred consistently only during the months when the salinity was lower indicates a preference for littoral areas, although Baker (1938) recorded a wide salinity tolerance for it, from 2–35°/oo. According to Bigelow (1928: 35), this genus is "an infallible index of coastal water."

Penilia avirostris Dana appeared in small numbers in the fall (see Fig. 6). It was numerous on only one occasion, in September

1943, when it constituted 16% of the sample and when an estimated 2,900 per 15 minute tow were collected. Since this was the sample which was taken in the open waters outside B. I. S., possibly *Penilia* prefers the higher salinities. However, individuals were found throughout the B. I. S. area and also north of Fishers Island. Although four species of *Penilia* have been described, all are now considered members of a single widespread species (see Calman, 1917; Cattley and Harding, 1949), the correct name for which is *Penilia avirostris* Dana 1849. There are few previous records for this cladoceran on our Atlantic Coast. It has been collected at Beaufort, North Carolina (Sudler, 1899) and off Winterquarter and Cape May (Bigelow and Sears, 1939). Its presence in B. I. S. is therefore the most northern record of its occurrence on this coast.

CIRRIPEDIA

Nauplii and cyprids of *Balanus balanoides* were taken each year during the winter and spring months (see Fig. 6). In 1944 they occurred regularly from January to May. In 1945, no samples were collected in January and February, nauplii appeared only in the March sample, while cyprids were present in March and April. In 1946, nauplii were taken from January to May, but cyprids were found from January to March, no sample being obtained during April. Cyprids were present in the bottom haul for March 1945, while nauplii appeared in the bottom haul for May 1946. In July 1944 and 1945, stray cyprids were observed that appeared similar in size and relative proportions to those of *B. balanoides;* since it is unlikely that *B. balanoides* cyprids would be found in the plankton at this time, these cyprids must belong to another species of *Balanus.*

Although nauplii and cyprids were never numerous, they occasionally constituted appreciable percentages of the samples due to the paucity in numbers of zooplankton during the spring months. Thus cyprids made up 10% of the March and 35% of the April 1945 samples, and 7% of the February and 24% of the March 1946 samples. Nauplii constituted 11% of the February 1946 sample. The actual numbers counted were highest during the 1944 season when a greater number of other organisms was present.

STOMATOPODA

During August and September the prevalent type of crustacean larva taken in the surface tows was the antizoea of stomatopods.

Antizoeae were observed in September 1943 and in August and September 1944 and 1945 (see Fig. 6). They were most numerous in August of both years, when over 200 per 15 minute tow were collected, and in August 1945 they constituted 3% of the total sample, the highest relative percentage obtained. Most of these larvae were Stage I antizoeae, although a few Stage II and Stage III forms were recorded. According to Gurney (1942), only the Lysiosquillinae have the earliest larva of the antizoea type. *Squilla empusa,* the common species of stomatopod in B. I. S., develops from a distinctly different larval type called a pseudozoea. The only *Lysiosquilla* reported from this general region is *L. armata* (see Bigelow, 1894), described by Smith in 1881 from two specimens found in the stomach of a flounder off Marthas Vineyard, Massachusetts. Aside from this species, the nearest recorded form is *L. scabricauda,* which has been found from South Carolina to Brazil and in the Bahamas and West Indies, and which has been reported recently from Bermuda. Since most of the antizoeae taken in the plankton were in their first pelagic stage, it seems unlikely that they had come any great distance from their point of origin. According to Kemp (1913), specimens of *Lysiosquilla* are rarely found, though they may possibly be quite abundant, since species of this genus live in deep burrows which they rarely leave. Because of this, quite a number of forms are known only from single specimens. It is possible, therefore, that these antizoeae may be the larvae of *L. armata,* which may be more common in this region than the record would suggest, or they may be the larvae of some other unrecorded species of *Lysiosquilla.* It seems less likely, despite the long larval life of stomatopods, that these very early larvae have been brought up from Bermuda or farther south, although they appear in B. I. S. at the time when alien warm water species are present.

DECAPODA

The only decapods that appeared in the surface tows were larval forms and the pelagic penaeid *Lucifer faxoni. L. faxoni* Borradaile was collected only in September 1943, when a few males and females were present. This was the sample obtained from the open waters outside B. I. S. which contained other oceanic species. *L. typus* was the species noted on several occasions over the continental shelf by Bigelow and Sears (1939), who did not record the occurrence of *L. faxoni.*

Brachyuran zoeae were found primarily during the summer months, while megalops larvae were taken much less frequently (see Fig. 6). Zoeae were more abundant in the samples obtained within L. I. S. in May and July 1945 than in those from B. I. S. They were recorded in the surface tows in every month except February, March, April, and October, but they were counted in greatest quantity during the summer of 1944, a maximum of 600 per 15 minute tow being obtained for August. Zoeae were present in the trawl wing samples for May of each year, although they were most numerous in July 1944 when they made up 20% of the total sample. Megalops larvae were observed on several occasions in the surface tows, and from July to September 1944 and in May 1945 they were taken in the trawl wing samples.

The zoeae of *Cancer irroratus* were recorded in July 1944, May and July 1945, and May and June 1946. *Carcinides maenas* zoeae were rare in the plankton, occurring in July 1944 and June 1946, while the zoeae of *Libinia* sp. were found only in September 1945 and those of *Pinnotheres maculatus* were noted only in September 1944. The zoeae of *Callinectes sapidus* were recorded most frequently: in August and September 1943, from June to September 1944; in July, September, and November 1945; and in June 1946. *Callinectes* zoeae were dominant in the July 1944 trawl wing sample.

Other decapod larvae that occurred in the plankton samples include *Crago septemspinosus*, *Eupagurus* sp., *Hippolyte* (?), and *Upogebia* sp. Of these *Crago* was the dominant form. It was found from July to September 1944, in July and October 1945, and in May and June 1946. *Eupagurus* larvae were taken in November 1943, July 1944, and May 1945, while *Upogebia* appeared in September 1945, and *Hippolyte* (?) was recorded in September 1943 and May 1946.

TUNICATES

Several species of pelagic tunicates appeared in late summer and early fall in B. I. S. These include in particular *Oikopleura dioica* Fol, *Doliolum nationalis* Borgert, and *Dolioletta gegenbauri* (Uljanin). A few aggregated zooids of the salp *Thalia democratica* (Forskål) were observed in August and November 1944. *T. democratica* is a widely distributed species that has been recorded from the Massachusetts and Rhode Island coasts (Metcalf, 1918). *Fritillaria* sp., found in February 1946, constituted 3.5% of the total number counted. These specimens were not sufficiently well preserved for species identifica-

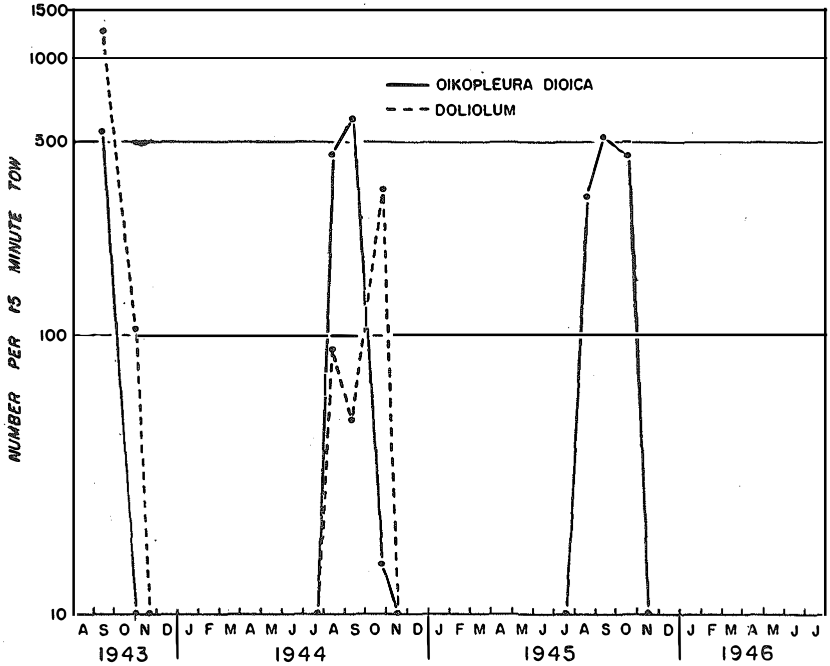


Figure 13. The estimated numbers of *Oikopleura dioica* and *Doliolum* per 15 minute tow on a logarithmic scale for the three-year period.

tion. A few stray appendicularians noted in April 1944 and March 1945 may have been *Fritillaria* also.

Of the pelagic tunicates that were collected, *Oikopleura dioica* occurred each fall with greatest regularity. Fig. 13 shows the seasonal abundance of this species and of the doliolids. *O. dioica* was taken from August to October in the surface samples (see Fig. 6) and in the trawl wing sample for October 1945. Although it was never obtained in large numbers (see Fig. 13), it was most abundant in September of each year. However, this organism is so thin and small that it is astonishing that the net retained this many. Undoubtedly the *Oikopleura* population was not adequately sampled. In September 1944, *O. dioica* made up 27.5% by count of the total sample, while it constituted 12% in September and 10.5% in October 1945 (see Fig. 5). Bigelow and Sears (1939) found this species over the continental shelf from Delaware Bay southward and therefore regarded it as a warm water indicator. The fact that it appeared in

B. I. S. in 1945 during the period of lower salinity when the other pelagic tunicates were not present in the samples may indicate that it was not necessarily brought into the Sound from offshore waters. On the other hand, it may mean only that lower salinities do not have a deleterious effect on this species. According to Essenberg (1926), *O. dioica* has been found in temperatures ranging from 3.2–29.5° C and in salinities varying from 11.4–36.7°/₀₀. She stated that in the warmer waters where it occurs throughout the year it apparently prefers waters near to shore to oceanic regions. Fish (1925) believed *O. dioica* to be the species of *Oikopleura* that appeared at Woods Hole in the summer.

Garstang (1933) revised the classification of the doliolids according to the arrangement of the alimentary canal in the gonozooids of the various species. On this basis he recognized four genera: *Doliolina*, *Dolioloides*, *Dolioletta* and *Doliolum.* According to this classification the two species that occurred in B. I. S. are *Doliolum nationalis* and *Dolioletta gegenbauri.* Garstang believed that *Doliolum nationalis* and *D. denticulatum* may be the same species (see also Thompson, 1948), since they are separated only on the basis of the extent of the branchial septa, which may vary somewhat depending on environmental influences. As yet all the stages between the two species have not been observed, and in all the specimens examined from B. I. S. the branchial septum ended ventrally just anterior to the fifth muscle band, as defined for *Doliolum nationalis. D. nationalis* was found in 1943 and 1944, while *Dolioletta gegenbauri* occurred only in 1943. *D. nationalis* appeared in August and September 1943 and from August to October 1944. In 1943, both gonozooids and phorozooids were present in the samples, but in 1944 only phorozooids were observed. *D. gegenbauri* was noted from August to the end of October 1943. Phorozooids were the only forms observed in the August sample, while only gonozooids were found in September. The two species of doliolids were not counted separately. An estimated total of over 1,100 per 15 minute tow for September 1943 was the highest number recorded (see Fig. 13); as previously noted, this was the sample obtained in the open waters outside B. I. S. In October 1944, when *D. nationalis* was the only species present, it constituted 34% of the total sample. The most northern record for doliolids recorded by Bigelow and Sears was on the continental shelf off Atlantic City, New Jersey. They stated that *Doliolum* must come into neritic areas from the continental slope. Doliolids have also been noted in the Gulf Stream outside the Gulf of Maine (Bigelow, 1928). The doliolids were found in B. I. S. only during the period of higher salinity, and it is undoubtedly true that they were brought into this area from offshore waters.

CHAETOGNATHS

Sagitta elegans was the only chaetognath found in B. I. S. A few sagittae were taken in the surface tows in every month except April, July, August and October (see Fig. 6), but they were fairly abundant only in February and December 1944 and in January 1946. *Sagitta* was collected in greater quantity in the stramin net samples, and it constituted an appreciable percentage, by count, of the organisms in some of the bottom hauls. Immature individuals were present on every occasion when the presence of *S. elegans* was noted, and, except for the winter months when mature specimens were taken at the surface, most of the individuals observed were immature. It is possible that there is a fairly large population of *S. elegans* in B. I. S. concentrated in the water column usually at some level beneath the surface, and it is unfortunate that the collecting methods were not designed to allow an analysis of these forms. The trawl wing samples were obtained too infrequently to give a consecutuve picture throughout the year.

Mature *S. elegans* were taken in surface and bottom hauls only during the period from December to May. In midwinter, when adults occurred at the surface, immature individuals were found at the bottom. During the spring months only a few young individuals were observed at the surface, but in May each year the highest volume of *Sagitta* was taken at the bottom where adults were numerous. In July 1944 medium-sized sagittae, the majority 13–17 mm in length, dominated the organisms in the bottom haul, constituting 50% of the total; but no other sagittae appeared either in the surface or bottom samples during the summer and early fall of that year. In November 1944, small and medium-sized sagittae up to 15 mm in length made up 28% of the bottom sample, only a few small individuals, up to 6 mm long, appearing at the surface. By December *S. elegans* constituted 18% of the surface tow, individuals of all sizes from 2.5–22 mm long being noted. During the three-year period, mature specimens were taken at the surface only during January, February, or March, while adults were observed in the bottom hauls in May.

Judging from the presence of the youngest stages, it is probable that reproduction occurred in the B. I. S. region at least from late fall to May, but the absence of definite data for the summer and early fall months precludes any further statement. According to Clarke, Pierce, and Bumpus (1943), on Georges Bank *S. elegans* has one major period of reproduction during the spring months, and a second smaller generation is produced in the late summer or autumn. Off Marthas Vineyard, Massachusetts, Clarke and Zinn (1937) obtained evidence for four breeding periods during the year, in January, May, July, and September. The presence of all stages of *S. elegans* in midwinter and spring corroborates the January and May periods, while the presence of early immature stages in the fall indicates that reproduction must have occurred during this period also.

POLYCHAETES

Autolytus sp. and *Tomopteris* sp. were the only polychaetes taken in the surface hauls, although a few spionid larvae were noted in February and May 1944 and February 1946. Polychaetes appeared in the samples as stray individuals and were never important members of the zooplankton as the larvae in particular are in more sheltered or brackish areas. The presence of *Tomopteris* was noted in the surface tows for February, April and October 1944 and January 1946. It occurred also in the bottom sample for April 1945. *T. catharina* has been found widely scattered over the continental shelf from Cape Cod to Cape Hatteras (Bigelow and Sears, 1939) and also in the Gulf of Maine (Bigelow, 1928), but it was always represented by a few individuals and was never taken in abundance.

Autolytus was observed more frequently than *Tomopteris;* it appeared in every month of the year except from July through September (see Fig. 6). This form must be indigenous to the B. I. S. area.

MOLLUSCS

Molluscs were taken infrequently in the surface tows. Lamellibranch veligers, much too small to be retained by the net ordinarily, were recorded from the surface haul for August 1943 and from the trawl wing sample for March 1945, while gastropod eggs appeared only in May 1944. Gastropod veligers were noted on a number of occasions during the year but were never numerous.

Three species of pteropods were found, but these too were represented by only a few individuals. In August and September 1943 the thecosomatous form *Creseis virgula* Rang appeared briefly. This species is typically tropical (Tesch, 1946) but has been recorded in these latitudes previously, borne north by the Gulf Stream. Bigelow and Sears (1939) have found this and other warm water pteropods scattered over the continental shelf, inshore and offshore, southward from off Atlantic City, New Jersey. Since a number of other oceanic forms have already been noted during the late summer and early fall of 1943, the presence of this tropical pteropod is added evidence of indrafts of Gulf Stream water.

Clione limacina (Phipps) and *Limacina retroversa* (Fleming) were the other pteropods observed during the period studied. *Clione limacina* was taken only in May 1946 when it constituted approximately 2% of the total surface sample; it was also collected in the stramin net. Most of these were young individuals. *C. limacina* has been found sporadically from February to October over the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939) both inshore and offshore, with greatest frequency in May and June. This is a northern species for which Bigelow and Sears found no evidence of reproduction later than June anywhere west of Cape Cod. A few young individuals of *Limacina retroversa*, another northern form, were also found only in the May 1946 sample.

Coelenterates

Hydromedusae were fairly numerous on several occasions, especially during the spring months, but no attempt has been made to identify them. Individuals were recorded in every month except December (see Fig. 6), the highest numbers occurring in March 1944 and May and June 1946, when approximately 1,000 per 15 minute tow were observed. The next highest numbers of about 700 per minute tow were found in July 1944. In 1944, hydromedusae constituted 65% of the total sample in March, 2.6% in July, and 1.8% in September; in 1945 the highest percentages were obtained in April (8.7%) and October (5%), while in 1946 hydromedusae were most abundant in May (80%) and June (11%). Aside from the maxima in spring and summer, there was a smaller peak in the fall. Leptomedusae, probably in large part *Obelia*, were observed especially in the spring and fall. Hydromedusae were present in the trawl wing samples in July and November 1944, April and May 1945, and January and May 1946.

On occasion during the fall months of 1943 and 1944 in particular, fragmentary siphonophores were found in the plankton samples.

Although they were in poor condition, it is a fairly safe assumption that these included specimens of *Muggiaea kochii.* The highest numbers were obtained in November 1944 when 500 per 15 minute tow were recorded.

Cyanea was taken in the surface and bottom hauls in May 1944 and in the surface sample for May 1945. These samples were collected in F. I. S.

SEASONAL VARIATIONS IN SIZE OF CENTROPAGES TYPICUS AND C. HAMATUS

Within a species, variations in size have been recorded for a number of copepods. These differences may be seasonal if more than one generation is produced per year, or geographical, or they may occur concurrently in one locality at the same or at different depths. Sewell (1948) has recently reviewed this subject. Most of these instances of size variations have been attributed to differences in the physical environment. Variations in temperature appear to be of considerable importance in causing the differences in size of broods produced during the year, but the general hydrological conditions of the water mass inhabited, the amount of available food, and the depth at which the organism lives may also influence the ultimate size of the individual. That the density may be of importance is exemplified by the range in size attained by *Acartia clausii* at different salinities, the brackish water forms always being smaller.

Calanus finmarchicus presents the best known example of seasonal variations in size. Investigations have shown that the size range of this species varies from generation to generation throughout the year and that it is probable that temperature and the amount of food available during development are important factors involved in causing these differences in size. By means of length measurements and wet and dry weight determinations, Bogorov (1934) found three size periods during the year; minimum size occurred during the autumn and winter, maximum size in the spring, while individuals maturing during the summer were of intermediate size. Variations in the wet and dry weight occurred coincidentally with the changes in length. According to Bogorov, these differences in size were correlated with the temperature at the time of spawning and development, the largest individuals being spawned at the lowest temperatures. Marshall, Nicholls, and Orr (1934) noted also that the three generations were recognizable by

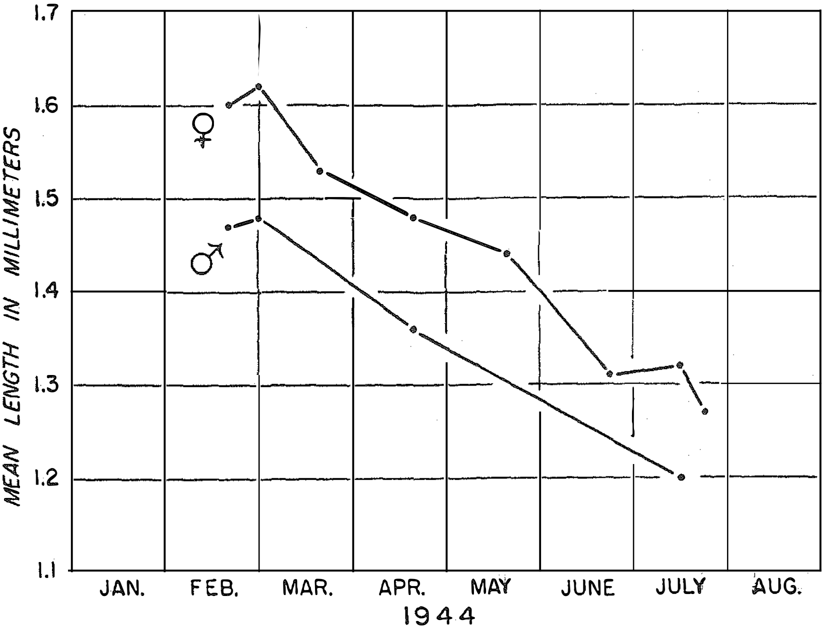


Figure 14. The variations in mean length in millimeters of male and female *Centropages hamatus* in 1944.

changes in the fat content but that there was less agreement between protein content and weight. They found that size maxima occurred shortly after diatom-rich periods.

Rather different results were obtained by Clarke and Zinn (1937) from material collected off Marthas Vineyard, Massachusetts. There the largest *Calanus* were those spawned in early summer that reached maturity during the winter. Accompanying phytoplankton studies by Lillick (1937) revealed a relatively small and early spring flowering, with little available phytoplankton during the remainder of the spring. There were tremendous summer and autumn flowerings coinciding with the period of development of the largest *Calanus* individuals. Thus in each region examined, the size of *Calanus* was correlated with abundance of food. In one case it occurred near the seasonal temperature minimum, in the other case near the maximum.

In studying the small copepods of Loch Striven, Marshall (1949) found, apart from sex differences, a seasonal change in the size of the copepods. In each species, maximum size was reached in April at the

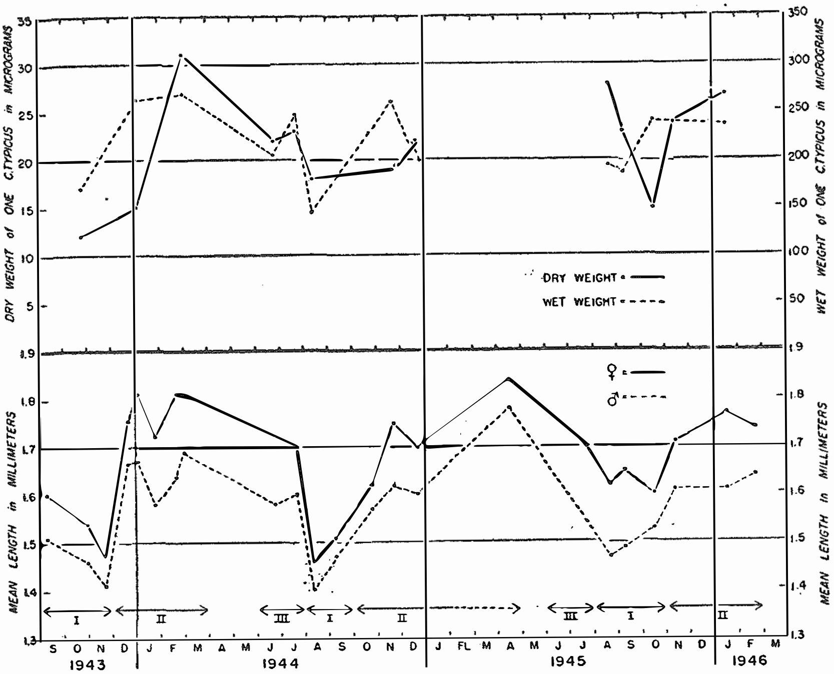
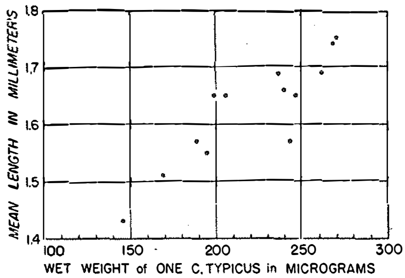


Figure 15. The variations in mean length in millimeters of male and female *Centropages typicus* during the three-year period and the variations in the wet and dry weights in micrograms of *Centropages typicus*. The three size periods are numbered and underlined with arrows.

time of appearance of the spring brood when temperatures were lowest and diatoms abundant. However, diatom increases during the summer were not correlated with significant changes in size; most of the species remained relatively small, although *Centropages hamatus* and *Temora longicornis* showed an increase in size at the end of the summer. Digby (1950) found a similar seasonal change in the size of the small copepods off Plymouth, where maximal size was attained in April or May by the different species. Here temperatures were minimal in February and March. *Centropages typicus*, for example, was small in January and February, reached maximal size in May, and then showed a decrease in size during the summer.

Measurements of *Centropages typicus* and *C. hamatus* from B. I. S. show that the size ranges of these species vary considerably during the year. Fig. 14 portrays the variations in mean length in millimeters of male and female *C. hamatus* in 1944, while Fig. 15 shows



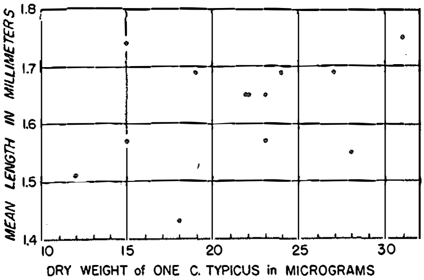


Figure 16 (Left). Dot diagram showing the wet weight in micrograms of one *Centropages typicus* plotted against the mean length in millimeters. Figure 17 (Right). Dot diagram showing the dry weight in micrograms of one *Centropages typicus* plotted against the mean length in millimeters.

similarly the variations in mean length of male and female *C. typicus* throughout the period studied as well as the variations in wet and dry weight. At least 25 individuals were measured from the head to the base of the caudal rami to obtain each mean. Only two generations have been observed for *C. hamatus,* which occurs primarily during the first half of the year; but *C. typicus* is present during the greater part of the year and the number of generations produced annually in this general region has not been determined thus far. However, an examination of the mean lengths given in Fig. 15 shows that, as in *Calanus,* three different size periods may be distinguished, and these are numbered and underlined with arrows. These size periods are especially apparent during the first half of the period studied, when *C. typicus* was most abundant. Individuals maturing in the winter attained maximum size, those maturing in June and July were of intermediate size, while the smallest individuals were found during the late summer and fall. Presumably these three size periods indicate three main generations during the year, the individuals maturing during the winter producing the generation of intermediate size which reached maturity in June and July, and these in turn spawning the smallest generation that matured in late summer and early fall. The occurrence in April 1945 of larger individuals than those measured at any other time of year (see Fig. 15) indicates the possibility that a fourth generation may occur, but since *C. typicus* did not appear regularly during the spring months no further data are available.

Wet and dry weight determinations were made on 13 samples of 300 or 400 adults, the sexes not being separated. These determinations are given in Fig. 15 as the weights of one *C. typicus* in micrograms.

When the wet weights are plotted against the mean lengths, as in Fig. 16, a fairly close correlation is apparent. On the other hand, as shown in Fig, 17, a considerable scattering of the points results when the dry weights are plotted against the mean lengths. Therefore, in some instances larger size simply meant a higher water content. Possibly some of the unevenness of these results is due to the fact that the sexes were not separated, since the water content is known to vary with the sex in *Calanus.*

The seasonal changes in mean length of the two species of *Centropages* indicate that the temperature exerts a constant effect during development, in that individuals of maximum length usually occurred when the temperature was minimal while minimal size coincided with maximal temperature. The time lag between size and temperature noted for *Calanus* is not as apparent for *C. typicus,* although it occurred occasionally. For example, in the fall of 1943 (see Fig. 15), minimal size was found in November at a temperature of 11° C, but during the following two years the smallest individuals occurred at times of maximal temperature. For female *C. typicus,* the correlation coefficient between mean length and temperature was −0.77 and for males −0.66. On the basis of 13 length determinations, the correlation coefficient for female *C. hamatus* was −0.92.

At this time it cannot be decided whether these correlations represent a direct temperature effect or some more complicated and indirect relationship. There is no information as to the abundance of phytoplankton food at the time the zooplankton collections were obtained. More recently a phytoplankton survey of B. I. S. has been made. The first half year resembled Lillick's (1937) data on the waters to the eastward, with a small late winter flowering and little phytoplankton during the spring. A smaller flowering occurred in late summer, no fall flowering was observed, and minimal amounts of phytoplankton were found in December. In general the quantity of phytoplankton in B. I. S. is intermediate between that found in Vineyard Sound and L. I. S. (Lillick, 1937; Riley, 1941, 1947) and it is more nearly uniform throughout the year than in either of these places. Judging from these scattered bits of information on the phytoplankton cycle, it seems probable that the periods of food abundance have little effect on the size of the *Centropages* population. The most that can be said is that the ratio of dry weight to wet weight was highest during the late winter and late summer. The absolute size, so far as is known, is correlated only with temperature.

DISCUSSION

B. I. S. is an area that acts as an intermediary between the neritic waters of the continental shelf and more sheltered littoral waters. It is only partially cut off from the open waters of the Atlantic on the southeast by Block Island and the eastern extremity of Long Island, and thus its waters are in a constant state of flux. To some extent the origin of the waters found within the Sound is indicated by their salinity, while organisms native to the various water masses aid in corroborating the salinity data. Since the copepods are the most important group of planktonic organisms in the surface layers of B. I. S., as our knowledge of their ecological and geographical distribution increases it will be possible to understand what species may be considered as indicators of the various water masses. Therefore a brief survey of the organisms known to occur in waters adjacent to B. I. S. is of value.

Over the continental shelf in these latitudes (Bigelow and Sears, 1939), the plankton is dominated by a small number of boreal species, the most important being *Calanus finmarchicus*, *Centropages typicus*, *Sagitta elegans*, *S. serratodentata*, and *Limacina retroversa.* The first three listed occurred in B. I. S., but the other two were not recorded. Euphausiids, *Euthemisto*, *Metridia lucens*, *Paracalanus parvus*, *Pseudocalanus minutus*, *Aglantha digitale*, ctenophores, and salps were also of importance in various parts of the region between Cape Cod and Chesapeake Bay, and of these only *P. minutus*, *P. parvus*, and tunicates were found within B. I. S., although the coelenterates were not identified and any ctenophores that may have been taken were completely fragmented. *Metridia lucens* was not recorded within B. I. S. during the period studied, but if it should occur there it would indicate the presence of offshore waters, since it has almost always been found abundant on the continental shelf more than 35 miles from land, rarely appearing near shore. Of the organisms that have been found most numerous over the continental shelf, only five or six were taken in the surface or trawl wing hauls in B. I. S.

North of Cape Cod, in the Gulf of Maine, a similar assemblage of organisms dominates the zooplankton. These include (Bigelow, 1928) *Calanus finmarchicus*, *Pseudocalanus minutus*, *Metridia lucens*, *Euchaeta norvegica*, *Sagitta elegans*, *Euthemisto*, euphausiids, *Limacina retroversa*, and *Pleurobrachia pileus.* The composition of the plankton communities in neritic areas northeast of B. I. S. thus shows many resemblances to that of the waters over the continental shelf immediately outside B. I. S.

In Narragansett Bay, directly east of B. I. S., a number of estuarine, littoral, and neritic species have been found (Williams, 1906, 1907). Most of these, such as *Calanus*, *Pseudocalanus minutus*, *Centropages hamatus*, *Temora longicornis*, *Acartia tonsa* and *A. clausii*, occurred regularly in B. I. S. Williams did not record *Centropages typicus* from the Bay although it may enter that area.

On the west the waters of B. I. S. merge with those of L. I. S. and F. I. S. (see Fig. 1). These are littoral areas where the salinity range, so far as is known, is usually in the upper twenties. No systematic investigation of the zooplankton of these regions has been made, but fragmentary data are available for a few organisms. The species of copepods known to occur in L. I. S. include those mentioned from Narragansett Bay and also *Labidocera aestiva*, *Paracalanus crassirostris*, and *Oithona brevicornis*. Besides these copepods, *Tortanus discaudatus* has been recorded in F. I. S., while *Centropages typicus* has been the dominant species on an occasion when the salinity was as high as 30°/₀₀. The estuarine forms, *Eurytemora hirundoides* and *E. americana*, are known from Narragansett Bay and F. I. S. while only the former has been recorded thus far from L. I. S.

The species listed from the littoral areas adjacent to B. I. S. may be divided into two groups: (1) those whose distribution extends out over the continental shelf and are therefore both littoral and neritic, and (2) those more or less confined to protected waters. In the latter group belong *Acartia clausii*, *A. tonsa*, *Labidocera aestiva*, *Tortanus discaudatus*, *Eurytemora hirundoides* and *E. americana*. The occurrence of these species in neritic areas would indicate the presence of inshore waters in these latitudes, although *Acartia clausii* is less littoral in distribution north of Cape Cod. *Paracalanus crassirostris*, called a "littoral-haunting species" by Sewell (1948: 327), undoubtedly should be included with this group of littoral species. The littoral-neritic species include *Centropages hamatus*, *Temora longicornis*, and *Pseudocalanus minutus;* these have the widest ecological distribution of the forms listed. *Calanus finmarchicus* and *Centropages typicus* are primarily neritic, although *Calanus* occurs in oceanic regions farther north and also may enter littoral areas, since its range of salinity tolerance is slightly wider than that of *Centropages*.

It is evident that the waters of B. I. S. act as a meeting ground for littoral, littoral-neritic, and neritic species, while the relative percentages of the various groups in any given area depend largely on the circulation of the different water masses. The copepods that occurred fairly regularly in B. I. S. (see Fig. 6) were boreal forms, common to the waters adjacent to and also north of the Sound. Therefore, although it is probable that the offshore waters that enter the Sound are mainly of northern origin, few northern species are so limited in distribution that their occurrence in B. I. S. may be considered proof of northern water. *Halithalestris croni*, recorded in March 1944 in the Sound, was the only northern copepod not hitherto noted south of Cape Cod. The presence of *Anomalocera patersonii* in the summer of 1944 and of the pteropods *Cliona limacina* and *Limacina retroversa* in May 1946 probably was indicative of northern waters, but these species also are found over the continental shelf in these latitudes. The occurrence of *Candacia armata* and *Rhincalanus nasutus* during the fall of 1944 shows at least that offshore waters had entered B. I. S. On the other hand, several species definitely of southern origin indicated the presence of Gulf Stream waters during the late summer and fall of 1943 in particular and of 1944 to a lesser extent. *Calanus minor*, *Corycaeus venustus*, *Eucalanus monachus*, *Temora turbinata*, *T. stylifera*, the doliolids, and the pteropod *Creseis virgula* are southern species alien to this region, so their presence was definitely indicative of the advent of southern water.

During the three-year period studied, the range of salinity noted for the surface waters of B. I. S. was not wide (see Fig. 2), from slightly less than $30^{\circ}/_{\circ\circ}$ to a little under $33^{\circ}/_{\circ\circ}$, and yet this relatively small degree of variation was sufficient to have important effects on the plankton community. During the period of higher salinity, *Centropages typicus* was unquestionably the dominant species for the greater part of the year. The occasional presence of the alien species already noted showed that offshore waters were moving into B. I. S., while the appearance of southern oceanic forms in the late summer and early fall of 1943 and 1944 provided evidence of indrafts of Gulf Stream water. From April 1945 onward the surface salinity varied usually around $30^{\circ}/_{\circ\circ}$, and this change was mirrored in the zooplankton which consisted almost entirely of littoral and littoral-neritic species. *Centropages typicus* was much less abundant, while *C. hamatus*, *Temora longicornis*, and *Acartia tonsa* made up higher percentages by count of the total samples than they previously had (see Fig. 5). During this later period there was little evidence of the presence of offshore water, but rather it appeared that, in the areas sampled by the net, water from less saline areas was entering B. I. S. This is borne out by the more frequent occurrence of the littoral species *Labidocera aestiva, Acartia tonsa,* and *Evadne nordmanni.* It must be remembered that these remarks apply only to the surface waters in the localities where the tows were made and that no general conclusions may be drawn concerning water movements throughout B. I. S. as a whole. These variations in the zooplankton which occurred coincidentally with the changes in salinity have been emphasized to demonstrate that the plankton from any given area in B. I. S. may aid in determining the origin of the waters sampled. In an area situated like B. I. S. it is probable that changes such as those mentioned in the composition of the zooplankton are a usual occurrence and that alternating periods of higher and lower salinity are normal consequences of the hydrographic system.

BIBLIOGRAPHY

Baker, H. M.
1938. Studies on the Cladocera of Monterey Bay. Proc. Calif. Acad. Sci., (4) *23:* 311–365.

Bigelow, H. B.
1928. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924), *40* (2): 1–509.

Bigelow, H. B. and Mary Sears
1939. Studies of the waters of the Continental Shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Harv. Mus. comp. Zool., *54* (4): 183–378.

Bigelow, R. P.
1894. Scientific Results of Explorations by the U. S. Fish Commission Steamer Albatross. No. XXXII. Report on the Crustacea of the Order Stomatopoda . . . Proc. U. S. nat. Mus., *17:* 489–550.

Bogorov, B. G.
1934. Seasonal changes in biomass of *Calanus finmarchicus* in the Plymouth area in 1930. J. Mar. biol. Ass. U. K., N. S. *19:* 585–612.

Calman, W. T.
1917. Crustacea. Part IV. Stomatopoda, Cumacea, Phyllocarida, and Cladocera. Rep. Brit. Antarct. ("Terra Nova") Exped., 1910, Zool. *3:* 137–162.

Cattley, J. G. and J. P. Harding
1949. *Penilia,* a cladoceran normally found off tropical and sub-tropical coasts, recorded in North Sea plankton. Nature, London, No. 4162: 238–239.

Clarke, G. L.
1940. Comparative richness of zooplankton in coastal and offshore areas of the Atlantic. Biol. Bull. Woods Hole, *78:* 226–255.

Clarke, G. L., E. L. Pierce, and D. F. Bumpus
1943. The distribution and reproduction of Sagitta elegans on Georges Bank in relation to the hydrographical conditions. Biol. Bull. Woods Hole, *85:* 201–226.

Clarke, G. L. and D. J. Zinn
1937. Seasonal production of zooplankton off Woods Hole with special reference to Calanus finmarchicus. Biol. Bull. Woods Hole, *73:* 464–487.

Davis, C. C.
1944. On four species of Copepoda new to Chesapeake Bay, with a description of a new variety of *Paracalanus crassirostris* Dahl. Publ. Ches. biol. Lab., No. 61: 1–11.

Deevey, G. B.
1948. The zooplankton of Tisbury Great Pond. Bull. Bingham oceanogr. Coll., *12* (1): 1–44.

Digby, P. S. B.
1950. The biology of the small planktonic copepods of Plymouth. J. Mar. biol. Ass. U. K., N. S. *29:* 393–438.

Essenberg, C. E.
1926. Copelata from the San Diego region. Univ. Calif. Publ. Zool., *28* (22): 399–521.

Fish, C. J.
1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. U. S. Bur. Fish., *41:* 91–179.
1936. The biology of Pseudocalanus minutus in the Gulf of Maine and Bay of Fundy. Biol. Bull. Woods Hole, *70:* 193–216.

Foster, E.
1904. Notes on the free-swimming copepods of the waters in the vicinity of the Gulf Biologic Station, Louisiana. Bull. Gulf Biol. Sta., No. 2: 69–79.

Garstang, Walter
1933. Report on the Tunicata. Part I. Doliolida. Rep. Brit. Antarct. ("Terra Nova") Exped., 1910., Zool. *4* (6): 195–251.

Gurney, Robert
1928–29. The fresh-water Crustacea of Norfolk. Trans. Norfolk Norw. Nat. Soc., *12:* 550–581.
1942. Larvae of Decapod Crustacea. Printed for the Ray Society. London. 306 pp.

Johnson, W. H. and J. E. G. Raymont
1939. The reactions of the planktonic copepod, Centropages typicus, to light and gravity. Biol. Bull. Woods Hole, *77:* 200–215.

Kemp, Stanley
1913. An account of the Crustacea Stomatopoda of the Indo-Pacific region based on the collection in the Indian Museum. Mem. Indian Mus., *4* (1): 1–217.

Lillick, L. C.
1937. Seasonal studies of the phytoplankton off Woods Hole, Massachusetts. Biol. Bull. Woods Hole, *73* (3): 488–503.

MARSHALL, S. M.
1949. On the biology of the small copepods in Loch Striven. J. Mar. biol. Ass. U. K., N. S. *28:* 45–122.

MARSHALL, S. M., A. G. NICHOLLS, AND A. P. ORR
1934. On the biology of *Calanus finmarchicus.* V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. J. Mar. biol. Ass. U. K., N. S. *19:* 793–827.

MERRIMAN, DANIEL AND RUTH C. SCLAR
1952. The fish eggs and larvae of Block Island Sound, 1943–1946. Bull. Bingham oceanogr. Coll., *13* (3): 165–219.

MERRIMAN, DANIEL AND H. E. WARFEL
1948. Studies on the marine resources of southern New England. VII. Analysis of a fish population. Bull. Bingham oceanogr. Coll., *11* (4): 131–164.

METCALF, M. M.
1918. Contributions to the biology of the Philippine Archipelago and adjacent regions. The Salpidae: a taxonomic study. Bull. U. S. nat. Mus., 100, *2*, Pt. 2: 1–193.

MOORE, EMMELINE
1947. Studies on the marine resources of southern New England. VI. The sand flounder, *Lophopsetta aquosa* (Mitchill); a general study of the species with special emphasis on age determination by means of scales and otoliths. Bull. Bingham oceanogr. Coll., *11* (3): 1–79.

RILEY, G. A.
1941. Plankton studies. III. Long Island Sound. Bull. Bingham oceanogr. Coll., *7* (3): 1–93.
1947. Seasonal fluctuations of the phytoplankton population in New England coastal waters. J. Mar. Res., *6* (2): 114–125.

SEARS, MARY AND G. L. CLARKE
1940. Annual fluctuations in the abundance of marine zooplankton. Biol. Bull. Woods Hole, *79:* 321–328.

SEWELL, R. B. S.
1948. The free-swimming planktonic Copepoda geographical distribution. Rep. 'John Murray' Exped., 1933–34, *8* (3): 317–592.

SHARPE, R. W.
1910. Notes on the marine Copepoda and Cladocera of Woods Hole and adjacent regions, including a synopsis of the genera of the Harpacticoida. Proc. U. S. nat. Mus., *38:* 405–436.

SUDLER, M. T.
1899. The development of *Penilia schmackeri* Richard. Proc. Boston Soc. nat. Hist., *29:* 109–131.

TESCH, J. J.
1946. The thecosomatous pteropods. I. The Atlantic. Dana Rep., No. 28: 1–82.

THOMPSON, HAROLD
1948. Pelagic Tunicates of Australia. Commonwealth Council for Scientific and Industrial Research, Australia. Melbourne. 196 pp.

WIBORG, K. F.
1940. The production of zooplankton in the Oslo Fjord in 1933–1934 with special reference to the copepods. Hvalråd. Skr., No. 21: 1–85.

WILLIAMS, L. W.
1906. Notes on marine Copepoda of Rhode Island. Amer. Nat., *40:* 639–660.
1907. List of the Rhode Island Copepoda, Phyllopoda, and Ostracoda, with new species of Copepoda. 37th Ann. Rep. R. I. Comm. inl. Fish., Spec. Paper No. 30: 69–79.

WILSON, C. B.
1932a. The copepods of the Woods Hole region Massachusetts. Bull. U. S. nat. Mus., 158: 1–635.
1932b. The copepod crustaceans of Chesapeake Bay. Proc. U. S. nat. Mus., *80* (15): 1–54.

APPENDIX

THE BOTTOM ORGANISMS

On eleven occasions during the three-year period studied, 14 trawl wing samples were obtained from the stramin net attached to the head line of the trawl. These hauls were collected on the following dates: May 18, July 23, August 13, September 10 and November 19, 1944, March 5, April 16, May 27, and October 15, 1945, January 14 and May 6, 1946. Two hauls were made in May 1944 and in March and October 1945. The localities where the samples were taken are listed with the dates in Table I. The duration of tow of the April 1945 sample is not known. Only those organisms which live primarily on or immediately above the bottom are included here; mention has already been made of the occurrence in the trawl wing samples of any planktonic forms that were taken.

Since the primary object in collecting these samples was to discover what organisms occurred above the bottom in the areas fished by the draggers, attention has been concentrated on the crustacea known to be of importance in the diet of various bottom living invertebrate-feeding fish. Obviously the mere presence or absence of the various organisms in the samples has no value other than to show what invertebrates were relatively abundant in the localities trawled on a certain date. No attempt has been made to identify all the forms, since, from the point of view of the present study, the results would not justify the time and effort necessary to accomplish this. Table II presents a checklist, giving the times of occurrence of the various bottom organisms in the trawl wing samples, while Table III shows semiquantitatively the relative numerical abundance of the more

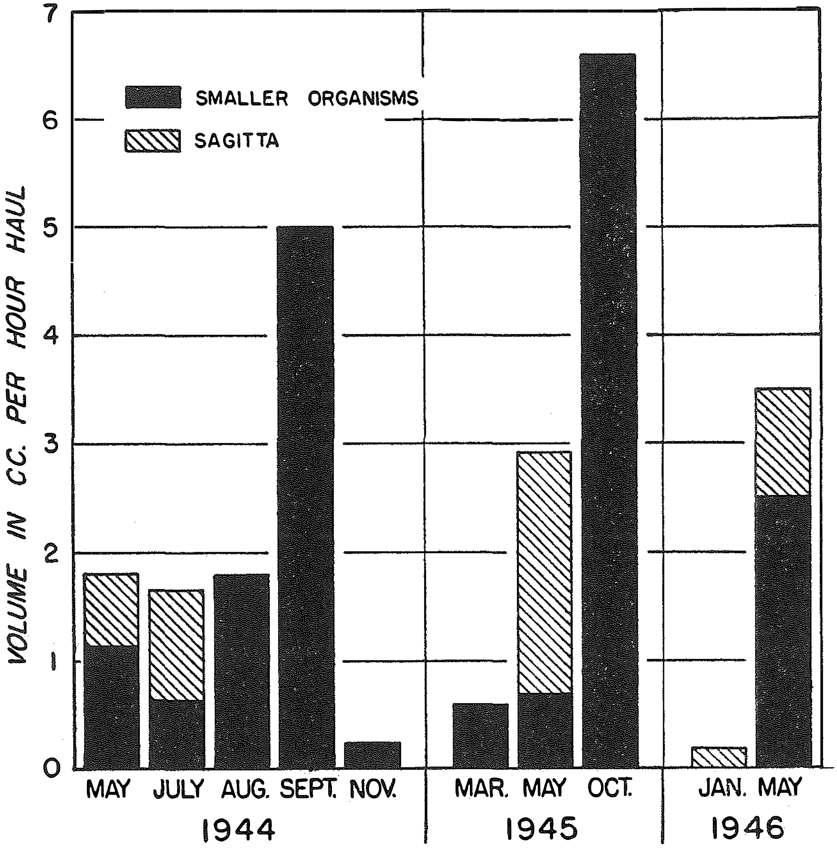


Figure 18. The volumes in cubic centimeters per hour haul of *Sagitta* and the smaller organisms taken in the trawl wing samples.

important forms. Fig. 18 gives the volumes of the organisms listed in Table III. These smaller organisms, especially the crustacea, represent the more edible part of the samples.

At various times *Sagitta elegans*, amphipods, mysids, and *Crago septemspinosus* occurred in greatest numbers. According to Merriman and Warfel (1948), the amphipod *Leptocheirus pinguis* is the dominant food of the winter flounder *Pseudopleuronectes americanus* and the little skate, *Raja erinacea*, the two species of fish taken in every sample haul during the three-year period. The winter flounder also ate two other amphipods, *Ampelisca* and *Unciola*, while the little skate consumed amphipods, *Cancer*, and *Crago*. Mysids formed the

TABLE II. Checklist. Times of Occurrence of Various Bottom Organisms in Trawl Wing Samples.

	1944					1945				1946	
	May	*July*	*Aug.*	*Sept.*	*Nov.*	*Mar.*	*Apr.*	*May*	*Oct.*	*Jan.*	*May*
S. elegans	x	x	–	–	x	x	x	x	–	x	x
Polychaetes	x	x	x	x	–	x	x	x	x	–	x
Gastropods	x	–	x	x	x	x	x	x	x	–	–
Nudibranchs	x	–	–	–	–	x	x	x	–	–	–
Cephalopods	–	x	x	–	–	–	–	–	x	–	–
Porifera	x	x	–	–	–	–	x	–	–	–	–
Hydroids	x	x	–	–	x	x	x	–	x	–	x
Nematodes	–	x	–	–	–	x	–	x	–	x	x
Echinoderms	–	x	x	x	x	x	x	–	x	–	x
Amaroucium	–	x	–	x	–	–	x	–	–	–	–
Neomysis	x	x	x	x	x	x	x	x	x	–	x
Cumacea	–	x	x	–	x	x	x	–	x	–	x
Isopods	x	–	–	–	–	–	x	–	x	–	–
Amphipods	x	x	x	x	x	x	x	x	x	–	x
Crago	–	–	x	x	–	x	x	x	x	–	x
Dichelopandalus	–	–	x	x	–	–	–	–	x	–	–
Pagurid larvae	–	x	–	–	x	–	–	–	x	–	–
Brachyuran larvae	–	x	x	x	x	–	–	x	x	–	x
Other Crustacean larvae	x	x	x	x	x	–	–	x	x	–	x
Brachyura	x	x	–	x	x	–	–	–	x	–	–
Acarina	–	–	–	–	–	x	–	–	–	x	–
Pycnogonida	–	x	–	–	–	–	–	–	–	–	–

main food of the windowpane flounder, *Lophopsetta aquosa,* which ranked second with the longhorn sculpin *Myoxocephalus octodecimspinosus* in frequency of occurrence. *Crago,* gammarids, and cumaceans have also been recorded (Moore, 1947) from the stomach contents of the windowpane flounder. Except for July 1944 and May 1945, when *Sagitta* was especially abundant, various of these crustaceans constituted the dominant elements, by count, in the trawl wing samples.

TABLE III. Bottom Organisms from Trawl Wing Samples. Semiquantitative as Number per Hour Haul. x: 10–100, xx: 101–1,000, xxx: 1,001–10,000.

	1944					1945			1946	
	May	*July*	*Aug.*	*Sept.*	*Nov.*	*Mar.*	*May*	*Oct.*	*Jan.*	*May*
S. elegans	x	xx	—	—	x	x	xx	—	xx	xx
Caprellids	x	x	x	x	—	—	—	x	—	xx
Other Amphipods	x	x	xx	xx	—	—	x	xxx	—	xx
Neomysis	x	x	xx	xxx	x	—	—	xx	—	—
Cumacea	—	—	x	—	—	—	—	—	—	x
Crago	x	—	x	xx	—	—	—	xx	—	—
Dichelopandalus	—	—	—	x	—	—	—	xx	—	—
Pagurid larvae	—	—	—	—	—	—	—	x	—	—
Brachyuran larvae	—	xx	x	x	—	—	x	—	—	—
Other Crustacean larvae	—	xx	x	x	x	—	x	xx	—	x
Polychaetes	—	—	—	x	—	—	—	xx	—	—
Gastropods	—	—	—	—	—	—	x	x	—	—
Post-larval Echinoderms	—	—	—	x	—	—	—	x	—	—

The Crustacea

The species of amphipods taken in the bottom hauls are listed in Table IV, together with the times of their occurrence. Ampeliscids were present more frequently than any of the other species except the caprellid *Aeginella longicornis*, which was noted on every occasion. Although gammarid amphipods were collected occasionally in the surface tows, *Gammarus annulatus* and *Calliopius laeviusculus* were the only species identified. *Hyperia galba* occurred in the surface tows (see Fig. 6) associated with *Cyanea*, and it was taken also in the bottom haul for May 1944. Two species not listed in Table IV were not identified; one of these was represented by a single specimen from the October 1945 sample, and the other was present in April and October 1945. Table IV shows that quite a number of amphipods not recorded in the fish stomach content analyses were available, while *Leptocheirus pinguis*, the most important food of the two dominant fishes, was noted on only four occasions.

Neomysis americana was taken in all but one of the bottom samples (see Table II). *Neomysis* was by far the dominant form in the August and September 1944 hauls, males and females with eggs being present. Maximum numbers were found in September 1944 when an estimated total of more than 1,100 mysids per hour haul was obtained, these crustacea constituting 67% of the total sample. The November 1944 sample contained small numbers of larval and post-larval mysids,

TABLE IV. SPECIES OF AMPHIPODS IN THE BOTTOM HAULS.

	1944				*1945*				*1946*
	May	*July*	*Aug.*	*Sept.*	*Mar.*	*Apr.*	*May*	*Oct.*	*May*
Ampelisca spinipes Boeck	x	x	x	x	x	x	x	x	x
A. macrocephala Lilljeborg (?)	–	–	–	–	–	–	–	x	–
Byblis serrata Smith	–	–	–	–	–	x	–	–	–
Calliopius laeviusculus (Krøyer)	–	–	–	–	–	–	x	x	–
Melita dentata (Krøyer)	–	–	–	–	–	–	–	x	–
Stenothoe cypris Holmes	–	x	–	–	–	–	–	–	–
Phoxocephalus holbölli (Krøyer)	–	–	–	–	x	–	–	–	–
Orthomenella pinguis (Boeck)	x	–	–	–	–	x	–	x	–
Leptocheirus pinguis (Stimpson)	x	–	x	–	–	x	–	x	–
Gammarus annulatus Smith	–	–	–	–	x	x	–	–	x
Monoculodes edwardsi Holmes	–	–	–	–	x	x	–	–	x
Photis sp.	–	x	x	x	–	x	x	–	–
Ericthonius brasiliensis (Dana)	–	–	x	x	–	–	–	x	–
E. rubricornis (Stimpson)	–	–	–	–	–	x	–	–	–
Jassa marmorata Holmes	–	x	x	–	x	x	–	–	x
Unciola irrorata Say	x	–	–	–	x	–	x	x	–
Corophium cylindricum (Say)	–	–	–	–	–	–	x	–	–
Dulichia monacantha (Metzger)	x	x	–	–	x	x	x	–	x
Aeginella longicornis (Krøyer)	x	x	x	x	x	x	x	x	x

while a few males and females were observed from March to May 1945.

Cumacea were found in seven of the trawl wing samples. These highly specialized forms were most numerous in the August 1944 sample when they constituted 9.6% of the total number.

Isopods were found infrequently in small numbers. *Edotea triloba* (Say) was present in May 1944 and in April and October 1945. *E. montosa* (Stimpson) was noted only from the surface tow for June 1945. *Idothea baltica* (Pallas) was taken in the bottom haul in March 1945 and in the surface sample for April 1945, while *I. phosphorea* (Harger) was present only in the bottom sample obtained in October 1945.

The decapods that were collected include *Crago septemspinosus, Dichelopandalus leptoceros* (Smith), pagurid Glaucothoë larvae, and brachyuran zoeae, megalopa, and post-larval stages. Unidentified decapod larvae were found in nearly all samples. *Crago septemspinosus* (see Tables II and III) was most abundant in October 1945 when it constituted 29% of the sample. Ovigerous females were noted in September 1944 and in May 1945 and 1946. The shrimp *Dichelopandalus leptoceros* and the pagurid Glaucothoë larvae were also most numerous in the October 1945 sample. Unidentified decapod larvae were most abundant in July 1944 and October 1945.

Several species of Brachyura were observed. Post-larval and early stages of *Cancer irroratus* Say were taken most frequently. They were noted in July and September 1944 and October 1945. The cancroid megalops larvae observed in August 1944 were probably also of this species. *Cancer borealis* Stimpson and *Libinia dubia* H. Milne Edwards were identified only from the October 1945 sample. One male *Pinnotheres maculatus* Say also occurred in the same sample, while in May 1944 another *Pinnotheres* was taken which could not be identified to species. Megalops larvae were never numerous, while zoeae occurred in greatest quantity in July 1944.

Other Organisms

Echinoderms were collected in most of the trawl wing samples (see Table II). *Leptasterias tenera* Stimpson was the commonest asteroid, *Asterias forbesi* (Desor) occurring only once in October 1945. *Echinarachnius parma* (Lamarck) was also recorded only from the October 1945 sample. Post-larval asteroids and ophiuroids were noted fairly frequently, both being present from July to September and in November 1944 and in April 1945, while asteroids were also taken in March 1945 and May 1946 and ophiuroids in October 1945.

Porifera were recorded on several occasions, *Halichondria* sp. being taken in May and July 1944, while *Haliclona oculata* (Bowerbank) and *Halichondria panicea* (Pall.) Flem. were found only in the July sample. *Esperiopsis quatsinoensis* Lambe was present in the April 1945 sample. The compound tunicate *Amaroucium,* probably *A. pellucidum,* occurred in several samples (see Table II). *Obelia articulata* A. Agassiz was the dominant hydroid in the March 1945 sample and probably in the majority of the others.

Polychaetes appeared in most of the bottom hauls, but they were usually represented by only a few individuals. They were most numerous in the October 1945 sample which contained *Harmothoë* primarily, although *Clymenella torquata* Leidy was also noted.

Gastropods occurred in the majority of the samples but were not identified, while nudibranchs were taken on several occasions (see Table II). Larval squid were observed in three samples. *Loligo* sp. appeared in July 1944 and October 1945, while *Ommastrephes* sp. was noted in August 1944.

Aside from the crustacea, the only other arthropods that were found were a few mites in the March 1945 and the May 1946 samples and one pycnogonid, *Nymphon grossipes* (Fabr.), in the July 1944 sample.

QUANTITY AND COMPOSITION OF THE ZOOPLANKTON OF BLOCK ISLAND SOUND, 1949

By Georgiana Baxter Deevey

Bingham Oceanographic Laboratory

CONTENTS

ABSTRACT

Oblique zooplankton hauls were obtained in Block Island Sound[1] during 1949, usually at monthly intervals, by means of a Clarke-Bumpus sampler, using both No. 2 and No. 10 silk nets. Displacement volumes were determined for the No. 10

---

[1] Hereafter Block Island Sound will be referred to as B. I. S., and Long Island Sound as L. I. S.

net samples, while measurements of displacement weight, dry weight, organic matter, and ash were made on the No. 2 net samples. Counts were made to obtain quantitative estimates of the number of various organisms per cubic meter. Both in numbers and volumes, the No. 10 net catch was considerably greater than that of the No. 2 net, indicating that a high proportion of the zooplankton population is too small to be retained by the No. 2 net. Maxima in total numbers of zooplankton occurred in midwinter, in late spring, and in late summer or early fall; the No. 2 net samples showed maxima in total volumes in midwinter and August, the No. 10 net samples in midwinter, May, and August. The mean annual displacement volume obtained for the No. 10 net samples was 0.68 cc/m^3, the estimated mean zooplankton crop being 20.4 cc/m^2 of sea surface; the figures obtained for the No. 2 net zooplankton were only about one third as great. The No. 2 net zooplankton yielded mean values of 19.34 mg/m^3 for the dry weight and 16.0 mg/m^3 of organic matter. These figures are low due to the virtual absence of zooplankton in the No. 2 net catches for April and May. Expressed as percentages of the displacement weight, the No. 2 net zooplankton gave mean averages of 11.5% dry weight, 8.9% organic matter, and 2.6% ash. The mean amount of organic matter in the No. 10 net samples, obtained by multiplying the displacement volume by the mean percent of organic matter, was 0.061 g/m^3 or 1.82 g/m^2 of sea surface.

The important categories of organisms included copepods, cladocera, pelagic tunicates, larval forms of bottom invertebrates, and coelenterates. Other groups recorded in smaller numbers or as occasional specimens were chaetognaths, heteropods, pteropods, ostracods, and fish eggs and larvae. In general, during the first half of the year the species present were the littoral and neritic forms native to this region, but from August to December the number of species was nearly doubled due to the influx of Atlantic waters containing many warm water organisms. The copepods that appeared seasonally in abundance included *Centropages typicus, Pseudocalanus minutus, Oithona similis, Acartia tonsa, Temora longicornis, Paracalanus parvus,* and *P. crassirostris. Oithona similis* was the dominant organism throughout the year from the point of view of numerical abundance.

Five species of cladocera were found: *Evadne nordmanni, E. spinifera, Podon leuckarti, P. intermedius,* and *Penilia avirostris.* The pelagic tunicates included *Fritillaria borealis* and *Oikopleura labradoriensis,* present from March to June, and the warm water forms: *Oikopleura dioica, O. longicauda, Doliolum nationalis, Dolioletta gegenbauri,* and *Thalia democratica.* Warm water forms recorded as occasional specimens were *Lucifer faxoni,* a few heteropods and pteropods, and the ostracod *Euconchoecia chierchiae.*

Sagitta elegans, not taken in abundance in 1949, occurred sporadically during the year. *Sagitta enflata* and *S. serratodentata* were present from August to December. Hydromedusae were found from March to December, with small maxima in May, August and October. *Muggiaea kochii* and other unidentified siphonophore fragments occurred from September to December.

The larval forms of a number of crustacean groups appeared in the plankton tows, including copepod nauplii, *Balanus* larvae, stomatopod larvae, porcellanid larvae, brachyuran larvae, and a few others. The larval forms of other bottom invertebrates that were fairly numerous were lamellibranch veligers, gastropod veligers, polychaete larvae and cyphonautes larvae.

The seasonal changes in the composition of the zooplankton population reflected the yearly salinity cycle which in turn was due to the relative rates of inflow of saline and littoral waters. Little relationship was noted between the periods of abundance of the phytoplankton and the zooplankton, presumably because the waters of B. I. S. are in a constant state of flux. The rate of production of the zooplankton was estimated to be about 17% per day.

INTRODUCTION

During 1949 a survey of the plankton, bottom invertebrates, and hydrography of B. I. S. was carried out by Gordon A. Riley and Frederick Smith. Riley (1952a, 1952b) has considered the hydrography and the phytoplankton, while this report is concerned solely with the zooplankton organisms.

Although a published survey of the zooplankton of B. I. S. (Deevey, 1952), based on a study of collections made from 1943–1946, appears herewith, the present report is of interest and of value for several reasons: (1) The zooplankton samples were obtained in combination with a more extensive survey of the phytoplankton and bottom invertebrates and of the chemical and physical factors of the environment. (2) By means of the Clarke-Bumpus sampler, quantitative data for volumes, displacement weight, dry weight, organic matter, and ash, as well as counts of the numbers of various organisms per cubic meter, have been obtained. Also, since a No. 10 net was used as well as a No. 2 net, a higher proportion of the total zooplankton was collected. (3) Oblique tows were made, so that at least the greater part of the water column was sampled.

The hydrography of B. I. S. has been studied by Riley (1952a), therefore little more need be mentioned here except to emphasize the origin of the different water masses that enter B. I. S. Saline Atlantic waters enter B. I. S. from the southeast, while the littoral waters of L. I. S. enter from the west and cross the western part of B. I. S. to Montauk Point. This constant inflow of saline and littoral waters results in the mixing of organisms of different origin; therefore the zooplankton picture in B. I. S. is more difficult to interpret than that from a relatively more circumscribed region. Offshore forms from the Atlantic as well as littoral species from L. I. S. may be obtained in a single oblique haul. Though many species live and complete their life histories in B. I. S. year after year, it is improbable that this body of water has a truly indigenous plankton fauna. The succession of organisms that has been found during the year may be due not only to seasonal variations in the species but to the fact that different water masses were sampled.

The data for temperatures and salinities recorded from various depths at the stations where samples were obtained during 1949 are given in Riley's (1952a) report on the hydrography. A seasonal variation in the salinity was noted. During the winter, primarily offshore waters entered B. I. S. and the salinity was over $31^{\circ}/_{oo}$. In April a drop in salinity occurred, especially in the surface waters, and the salinity was relatively low until July due to the influence of L. I. S. waters. In the late summer the salinity rose markedly to over $32^{\circ}/_{oo}$ as Atlantic waters again predominated, and it remained at this level until the end of the year. The zooplankton reflected the seasonal salinity cycle. The temperature cycle was normal, the lowest recorded temperature being 4.6° C in midwinter, the highest 20° C in July in the surface waters.

ACKNOWLEDGMENTS

I am deeply indebted to Gordon A. Riley who has generously assisted me in many ways. In particular, I am most grateful to him for his determinations of the displacement volumes, the displacement and dry weights, organic matter, and ash, and for contributing the paragraphs in the following section dealing with the methods used in obtaining these data. Also, I am especially indebted to him for the estimate of the rate of zooplankton productivity.

METHODS

The zooplankton samples were collected by means of oblique hauls with a Clarke-Bumpus sampler, using both a No. 2 and a No. 10 silk net. Although the samples were usually taken at monthly intervals, plankton hauls were made on two occasions in February and August, whereas none was collected during November. Table I lists the dates and the stations where the samples were collected, and it also shows how many samples were obtained.

The zooplankton samples were studied in the usual manner. Counts were made to obtain the percentage composition and estimates of the number of various organisms per cubic meter. The samples were also examined for the rarer species that might not have appeared in the counting chamber. Since both the percentage composition and the number of species per cubic meter varied in the samples taken with

TABLE I. DATES, LOCALITIES, AND NUMBER OF ZOOPLANKTON SAMPLES OBTAINED FROM B. I. S. IN 1949.

Date	Locality	Number and type of hauls	Net No.
I–11	2–3 mi. S. of Charleston, R. I.	1 horizontal	10
		1 oblique	2
II–3	Off Watch Hill, R. I.	1 oblique	10
		1 oblique	2
II–24	Hell Hole	1 oblique	10
		1 oblique	2
III–24	Hell Hole	1 oblique	10
		2 oblique	2
IV–9	Off Watch Hill, R. I.	1 oblique	10
		1 oblique	2
V–7	4 mi. SSE. of Watch Hill, R. I.	1 oblique	10
		1 oblique	2
VI–2	4 mi. S. to SSW. of Watch Hill, R. I.	1 oblique	10
		2 oblique	2
VII–21	4 mi. S. to SSW. of Watch Hill, R. I.	1 oblique	10
		1 oblique	2
VIII–9	4 mi. S. to SSW. of Watch Hill, R. I.	1 oblique	10
		1 oblique	2
VIII–28	3 mi. SE. of Watch Hill Pt., R. I.	1 oblique	10
		1 oblique	2
IX–17	Hell Hole	1 oblique	10
		1 oblique	2
		1 horizontal	2
X–6	Off Quonochontaug, R. I.	2 oblique	10
		1 oblique	2
XII–19	Off Quonochontaug, R. I.	1 oblique	10
		2 oblique	2

the No. 2 and the No. 10 nets, depending on the relative sizes of the organisms, it has been decided to use a "rule of thumb" in depicting the abundance of the various forms. Small organisms, such as copepod nauplii and the early copepodid stages, were retained only by the No. 10 net, while the No. 2 net caught adult forms and late developmental stages primarily. Due to the selectivity of the different mesh sizes of the nets, the figures used to show the relative abundance of the various forms will be the largest estimated numbers, unless stated otherwise. For example, if the No. 10 net retained a higher number of *Oikopleura dioica*, this figure will be given rather than the lower estimated number recorded on the same day for the No. 2 net sample. This method of simply choosing the larger figure is admittedly a compromise, but at least it is more objective than trying to decide arbitrarily which net retained the various species and developmental stages in more nearly their true proportion.

In estimating the percentage composition of females, males, and immature stages of *Centropages typicus* and *Pseudocalanus minutus*, the

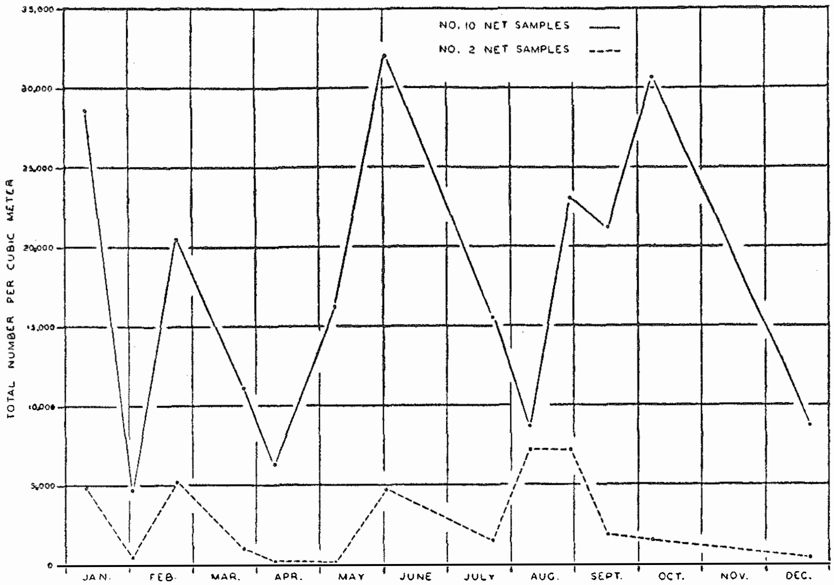


Figure 1. The total number per cubic meter of zooplankton organisms taken with the No. 2 and the No. 10 nets during 1949.

percentage compositions of the No. 2 and No. 10 net samples have simply been averaged. This seems reasonable, since the No. 2 net caught higher percentages of adults, while the No. 10 net retained the young stages primarily, although some adults were usually present.

After the counts were finished, some of the samples were destroyed in order to determine wet and dry weights, organic matter, and ash. The remaining samples were used for estimates of displacement volume and were then stored. In each case the preliminary treatment was the same, so that the wet weight in grams would be nearly comparable with the displacement volumes in milliliters.

The samples were strained on a filter of No. 20 bolting silk and were washed several times with tap water. The silk was put on a filter paper or some other absorbent surface and allowed to stand several minutes to remove excess water. The zooplankton was then scraped from the silk with a thin spatula and put into a measured volume of water for an estimate of displacement volume, or it was put into a crucible and weighed immediately. The weighed samples were dried at 100° C for two days, weighed, ignited, and weighed again.

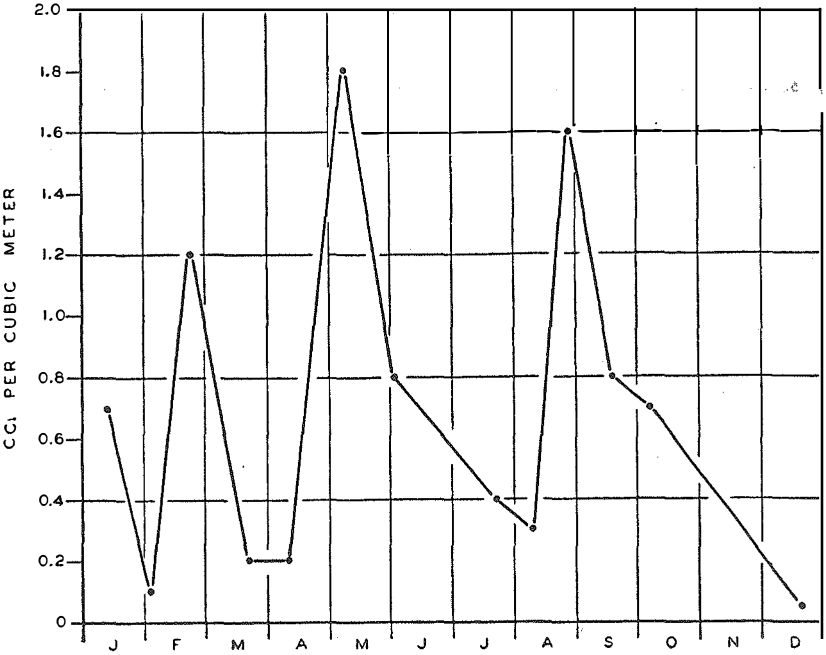


Figure 2. The total displacement volumes in cc/m³ of the zooplankton from the No. 10 net samples.

THE ZOOPLANKTON

The Total Zooplankton

The total numbers of zooplankton organisms per cubic meter taken with the No. 2 and No. 10 nets are shown in graphical form in Fig. 1. The difference in numbers of organisms retained by the two nets is evident. During the first half of the year maximal numbers were obtained in midwinter and in June by both nets. Minimal numbers were caught by the No. 2 net during the spring months, as was the case during the previous three-year study of No. 2 net samples (Deevey 1952). The organisms caught by the No. 10 net during this period were largely immature copepodids and copepod nauplii, forms too small to be retained by the No. 2 net. During the latter half of the year maximal numbers were obtained throughout August by the No. 2 net, and after this the numbers declined to a low in December. The No. 10 net samples, on the other hand, revealed a minimum in early

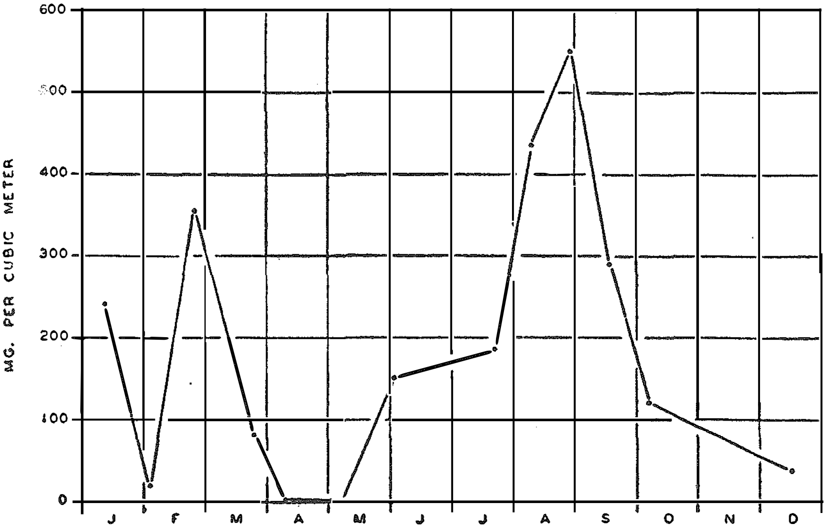


Figure 3. The total displacement weights in mg/m³ of the zooplankton from the No. 2 net samples.

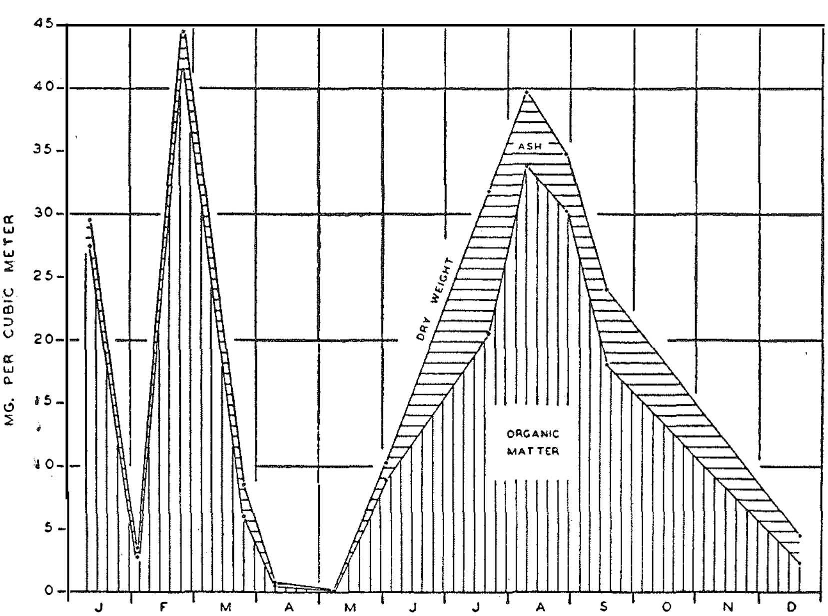


Figure 4. The dry weight, organic matter, and ash in mg/m³ of the zooplankton from the No. 2 net samples.

August followed by a rise to maximal numbers in October. The difference in numbers retained by the two nets was due largely to the presence of larval and immature copepods in the No. 10 net samples. Lamellibranch veligers were also taken in numbers by the No. 10 net. In general, the samples obtained with both nets showed maxima in midwinter, late spring, and in late summer or fall.

Total displacement volumes in cc/m^3 were determined for the No. 10 net samples except for January, while measurements of the displacement weight, dry weight, organic matter and ash in mg/m^3 were made on the No. 2 net samples, except for the October sample; in this latter instance the No. 10 net sample was analyzed. Figs. 2, 3, and 4 present these data in graphical form, while the figures obtained are given in Tables II and III.

The displacement volumes of the zooplankton from the No. 10 net (see Fig. 2) show some differences from the picture obtained from the numbers of organisms given in Fig. 1. These differences in the time of occurrence of maximal volumes and numbers may be attributed in part to the composition of the zooplankton. The midwinter maximum in both volume and numbers was caused by a high percentage of *Pseudocalanus* in this sample. The highest displacement volume was obtained in May, although the number of organisms was twice as great in June. The reason for this is by no means clear. It may be due, at least in part, to the presence of more hydromedusae in May and greater numbers of cladocera and lamellibranch veligers in June. On the other hand, the number of copepods was twice as high in June. The third maximum in volume occurred in late August, undoubtedly due to the high percentage of doliolids present, although the actual

TABLE II. TOTAL DISPLACEMENT VOLUMES IN CC/M^3

Date	*Net*	*Displacement Volume*	*Number of Organisms/M^3*
Feb. 3	10	0.1	4,680
Feb. 24	10	1.2	20,460
Mar. 24	10	0.2	11,050
Apr. 9	10	0.2	6,230
May 7	10	1.8	8,910
June 2	2	0.3	5,080
June 2	10	0.8	32,000
July 21	10	0.4	15,470
Aug. 9	10	0.3	8,650
Aug. 28	10	1.6	23,050
Sept. 17	2	0.2	580
Sept. 17	10	0.8	21,185
Oct. 6	2	0.2	1,475
Oct. 6	10	0.7	33,480
Dec. 19	10	0.05	8,625

TABLE III. DISPLACEMENT WEIGHTS, DRY WEIGHTS, ORGANIC MATTER AND ASH IN MG/M^3

Date	*Net*	*Displacement Weight*	*Dry Weight*	*Organic Matter*	*Ash*	*Number of Organisms/M*^{3}
Jan. 11	10	676.0	74.6	64.2	10.4	28,540
Jan. 11	2	242.0	29.6	27.4	2.2	4,800
Feb. 3	2	20.1	3.6	2.8	0.8	420
Feb. 24	2	354.0	44.6	41.4	3.2	5,140
Mar. 24	2	82.0	8.6	6.1	2.5	720
Apr. 9	2	2.7	0.7	0.6	0.1	840
May 7	2	0.1_6	0.0_4	0.0_4	—	100
June 2	2	151.0	10.2	8.8	1.4	4,300
July 21	2	187.0	31.8	20.5	11.3	1,480
Aug. 9	2	436.0	39.7	33.8	5.9	7,125
Aug. 28	2	549.0	34.8	30.2	4.6	7,115
Sept. 17	2	291.0	24.0	18.1	5.9	1,890
Oct. 6	10	424.0	62.9	44.1	18.8	27,800
Dec. 19	2	37.0	4.5	2.3	2.2	350

number of organisms was higher in October when the volume was relatively low. At this time the No. 10 net zooplankton consisted largely of small and larval copepods and lamellibranch veligers. The displacement volumes obtained for the No. 10 net samples yield a mean annual zooplankton concentration of 0.68 cc/m^3 of water. Since the average depth was 30 m, the estimated mean annual zooplankton crop was 20.4 cc/m^2 of sea surface.

The displacement weights of zooplankton in mg/m^3 from the No. 2 net samples are shown in graphical form in Fig. 3. In this instance the seasonal cycle follows more closely that of the numbers of organisms. The June maximum in numbers is not reflected in the weight curve, undoubtedly due to the fact that cladocera constituted 87% of this sample, while the July sample consisted largely of copepods which resulted in a higher displacement weight. The late August maximum may be attributed to the high percentage of doliolids present. The mean annual zooplankton concentration obtained for the No. 2 net samples is 213 mg/m^3 of water or 0.213 cc/m^3. These figures yield a volume of only 6.4 cc/m^2 of sea surface, an amount less than one third as great as that obtained from the No. 10 net samples. Obviously the No. 10 net retained a considerably higher proportion of the total zooplankton population. This discrepancy in the quantity of zooplankton obtained with the two nets shows clearly how the results may vary depending upon the size of net used, and it indicates also that a high proportion of the B. I. S. zooplankton organisms is too small to be retained by the No. 2 net.

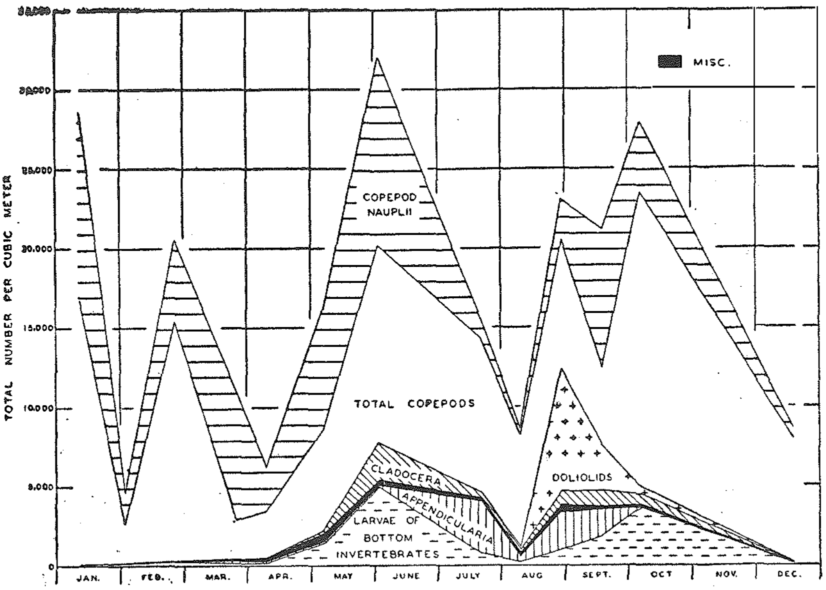


Figure 5. The number per cubic meter of the major groups of zooplankton organisms taken in the No. 10 net samples.

The data for the dry weight, organic matter, and ash in mg/m^3 obtained from the No. 2 net samples are presented in graphical form in Fig. 4. The No. 10 net zooplankton was analyzed for the October sample, and hence the data for October are omitted since they are not comparable to the other figures. From January to May the curve for dry weight corresponds to that for displacement weight and for the numbers of organisms. For the rest of the year the curve follows roughly that for total copepods, with a peak in early August. During the first half of the year the relative percentage of ash was low in proportion to the amount of total organic matter, while a relatively higher proportion of ash was found from July to October. The reason for this is not apparent. The No. 2 net samples yielded mean values of 19.34 mg/m^3 for the dry weight of the zooplankton and 16.0 mg/m^3 of organic matter. The No. 2 net figures are especially low due to the virtual absence of zooplankton in April and May. When these figures are converted to the amount present in the total water column, mean annual estimates of 0.580 g of zooplankton dry weight per square meter of sea surface and of 0.480 g of organic matter per square meter

TABLE IV. ZOOPLANKTON ORGANISMS. CHECKLIST AND PERIODS OF OCCURRENCE IN B. I. S. IN 1949.

Copepoda:	*J.*	*F.*	*M.*	*A.*	*M.*	*J.*	*J.*	*A.*	*S.*	*O.*	*N.*	*D.*
Centropages typicus	x	xx	x	x	x	x	x	xx	x	x	—	x
C. hamatus	x	xx	x	x	x	x	x	x	—	x	—	x
C. bradyi	—	—	—	—	—	—	—	—	—	x	—	x
Pseudocalanus minutus	x	xx	x	x	x	x	x	xx	x	x	—	x
Paracalanus parvus	x	—	x	—	—	—	x	xx	x	x	—	x
P. crassirostris	x	x	—	—	—	—	—	xx	x	x	—	x
Acartia tonsa	x	x	—	—	—	—	x	xx	x	x	—	x
A. clausii	—	x	x	x	—	—	—	—	—	—	—	—
A. longiremis	—	—	x	x	x	x	—	—	—	—	—	—
Temora longicornis	x	xx	x	x	x	x	x	x	—	x	—	x
T. turbinata	—	—	—	—	—	—	—	—	—	x	—	x
T. stylifera	—	—	—	—	—	—	—	xx	—	x	—	—
Tortanus discaudatus	x	—	x	—	x	x	—	—	—	x	—	—
Metridia lucens	—	—	—	—	x	—	x	x	—	x	—	—
Labidocera aestiva	—	—	—	—	—	—	—	xx	x	x	—	x
Calanus finmarchicus	—	—	x	x	x	x	x	xx	x	—	—	—
C. minor	—	—	—	—	—	—	—	x	x	x	—	x
Candacia armata	—	—	—	—	—	—	—	x	x	x	—	x
Eucalanus monachus	—	—	—	—	—	—	—	—	—	x	—	x
E. crassus	—	—	—	—	—	—	—	—	—	x	—	—
Rhincalanus nasutus	—	—	—	—	—	—	—	—	—	—	—	x
Mecynocera clausi	—	—	—	—	—	—	x	—	—	—	—	—
Eurytemora sp.	—	—	—	x	—	—	—	—	—	—	—	—
Oithona similis	x	xx	x	x	x	x	x	xx	x	x	—	x
O. brevicornis	—	—	—	—	—	—	x	x	x	x	—	—
O. spinirostris	x	x	—	—	x	x	—	—	—	x	—	x
Oncaea venusta	—	—	—	—	—	—	—	—	x	x	—	x
Corycaeus venustus	—	—	—	—	—	—	—	—	—	x	—	x
C. ovalis	—	—	—	—	—	—	—	—	—	x	—	—
C. speciosus	—	—	—	—	—	—	—	—	—	x	—	x
C. elongatus	—	—	—	—	—	—	—	—	—	x	—	—
Sapphirina auronitens	—	—	—	—	—	—	—	—	—	x	—	x?
Clytemnestra rostrata	—	—	—	—	—	—	—	—	—	x	—	—
Microsetella norvegica	—	—	—	—	—	—	—	—	—	x	—	x?
M. gracilis	—	—	—	—	—	—	—	—	x	—	—	—
Thalestris gibba	—	—	—	—	—	x	—	—	—	—	—	—
Alteutha depressa	—	—	—	—	—	—	—	—	—	x	—	—
Other harpacticoids	—	xx	—	x	x	x	—	—	—	—	—	x
Monstrilla anglica	—	—	—	x	—	—	—	—	—	—	—	—
Cladocera:												
Podon intermedius	—	—	—	—	—	—	x	xx	x	x	—	—
P. leuckarti	—	—	x	x	x	x	—	—	—	—	—	—
Evadne nordmanni	—	—	—	x	x	x	x	x	x	x	—	—
E. spinifera	—	—	—	—	—	—	—	—	x	x	—	—
Penilia avirostris	—	—	—	—	—	—	—	xx	x	x	—	—
Ostracoda:												
Euconchoecia chierchiae	—	—	—	—	—	—	—	—	—	x	—	x
Decapoda:												
Lucifer faxoni	—	—	—	—	—	—	—	x	x	x	—	—
Tunicata:												
Oikopleura dioica	—	—	—	—	—	—	x	xx	x	x	—	—
O. longicauda	—	—	—	—	—	—	—	—	x	—	—	—
O. labradoriensis	—	—	x	x	x	x	—	—	—	—	—	—
Fritillaria borealis	—	x	x	x	x	x	—	—	—	—	—	—
Doliolum nationalis	—	—	—	—	—	—	—	xx	x	x	—	—

TABLE IV. Zooplankton Organisms. Checklist and Periods of Occurrence in B. I. S. in 1949—(*Continued*)

Tunicata:	*J.*	*F.*	*M.*	*A.*	*M.*	*J.*	*J.*	*A.*	*S.*	*O.*	*N.*	*D.*
Dolioletta gegenbauri	—	—	—	—	—	—	—	xx	x	x	—	—
Thalia democratica	—	—	—	—	—	—	—	x	—	x	—	—
Chaetognatha:												
Sagitta elegans	—	x	x	x	x	x	—	x	—	—	—	—
S. serratodentata	—	—	—	—	—	—	—	x	—	x	—	x
S. enflata	—	—	—	—	—	—	—	x	x	x	—	x
Pteropoda:												
Limacina retroversa	x	—	—	—	—	—	—	—	—	—	—	—
Creseis virgula	—	—	—	—	—	—	—	xx	x	—	—	—
C. acicula	—	—	—	—	—	—	—	—	x	—	—	—
Heteropoda:												
Oxygyrus keraudreni	—	—	—	—	—	—	—	—	x	x	—	—
Firoloida desmaresti	—	—	—	—	—	—	—	—	x	—	—	—
Hydromedusae	—	—	x	x	x	x	x	xx	x	x	—	x
Siphonophores	—	—	—	—	—	—	—	—	x	x	—	x
Crustacean Larvae:												
Balanus nauplii	—	xx	x	x	x	x	—	—	—	—	—	—
Balanus cyprids	—	—	x	—	x	x	—	—	—	—	—	—
Stomatopod antizoeae	—	—	—	—	—	—	—	x	x	x	—	—
Zoeae	—	—	—	—	x	x	x	xx	x	x	—	—
Megalops larvae	—	—	—	—	—	—	x	xx	—	x	—	—
Porcellanid larvae	—	—	—	—	—	—	—	x	—	—	—	—
Larval Cumacea	—	—	—	—	—	x	—	—	—	—	—	—
Larval Hyperiids	—	—	—	—	—	—	—	—	x	x	—	—
Amphipods	—	—	—	—	x	—	—	x	x	—	—	—
Other crustacean larvae	—	—	x	x	x	x	x	xx	—	x	—	x
Molluscan Larvae:												
Gastropod eggs	—	—	—	—	x	—	—	—	—	—	—	—
Gastropod veligers	—	xx	x	x	x	x	x	xx	x	x	—	x
Lamellibranch veligers	—	x	x	x	x	x	—	xx	x	x	—	x
Loligo larvae	—	—	—	—	—	—	x	—	—	—	—	—
Polychaetes:												
Trochophores	—	—	x	—	x	—	—	x	—	x	—	x
Polychaete larvae	—	x	x	x	x	x	—	x	—	—	—	x
Autolytus sp.	—	x	—	—	—	x	—	x	—	—	—	—
Tomopteris sp.	—	—	—	—	—	—	—	x	—	x	—	—
Echinoderm Larvae	—	—	x	x	x	—	—	x	x	x	—	—
Cyphonautes Larvae	—	xx	x	x	x	x	x	x	x	x	—	—
Fish Eggs	—	—	x	x	x	x	—	x	x	—	—	x
Fish Larvae	—	—	—	—	—	—	x	x	x	x	—	—

xx = Samples obtained on two occasions in one month; see Table I.

are obtained. When the data for dry weight and organic matter are expressed as percentages of the displacement weight, the figures for April and May should probably be ignored, since too little zooplankton was obtained on these occasions to give reliable results. Including the April and May data, the dry weight averaged 13.3% of the displacement weight, organic matter 10.9%, and ash 2.4%. Excluding the questionable figures, the dry weight averaged 11.5% of the dis-

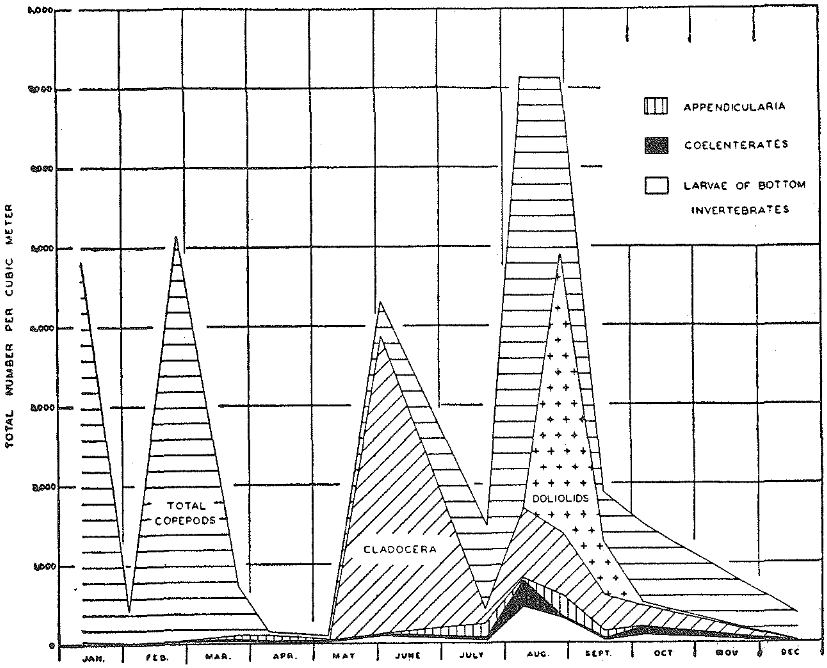


Figure 6. The number per cubic meter of the major groups of zooplankton organisms taken in the No. 2 net samples.

placement weight, organic matter 8.9%, and ash 2.6%. In a later section the figures of 8.9% organic matter will be used to obtain an estimate of the amount of organic matter in the No. 10 net samples.

THE COMPOSITION OF THE ZOOPLANKTON

The copepods were the dominant organisms taken in the zooplankton samples, although other important categories include the larval forms of bottom invertebrates, pelagic tunicates, cladocera, and coelenterates. Chaetognaths and fish eggs and larvae, though present, were never taken in any quantity. Several other groups were represented by occasional specimens during the year. These are pelagic ostracods, heteropods, pteropods, and the penaeid *Lucifer*. Table IV presents a checklist of the various recorded forms together with the time of their occurrence, while Figs. 5 and 6 give in graphical form the number per cubic meter of the major components of the zooplankton of the No. 10 and No. 2 net samples, which emphasize the differences

TABLE V. PERCENTAGE COMPOSITION ON THE NO. 10 NET SAMPLES.

	Jan.	*Feb.*		*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*		*Sept.*	*Oct.*	*Nov.*	*Dec.*
Pseudocalanus minutus	28.6	10.0	65.3	10.1	25.1	10.4	5.5	0	0	0	0	0	—	0
Centropages typicus	7.6	12.4	1.0	1.7	0	0	0	0	5.9	16.1	3.1	0	—	0
Centropages hamatus	0	0	0	0	0	0	0	9.7	0	0	0	0	—	0
Temora longicornis	0	0	0	0	0	10.0	18.5	0	0	0	0	0	—	0
Acartia tonsa	0	0	0	0	0	0	0	12.6	15.4	0	0	7.5	—	0
Paracalanus crassirostris	0	0	0	0	0	0	0	0	0	0	0	5.8	—	33.6
Oithona similis	19.9	31.0	7.3	11.0	9.8	16.3	11.4	35.4	57.0	10.6	16.5	21.5	—	48.8
Copepod Nauplii	41.3	42.5	25.1	74.1	47.1	48.0	37.1	8.0	4.6	11.3	41.4	21.7	—	7.3
Lamellibranch Veligers	0	0	0	0	0	5.4	12.4	0	0	0	8.5	22.0	—	0
Oikopleura dioica	0	0	0	0	0	0	0	21.4	3.7	10.2	8.1	0	—	0
Doliolum nationalis	0	0	0	0	0	0	0	0	0	31.3	4.6	0	—	0
D. gegenbauri	0	0	0	0	0	0	0	0	0	0	5.7	0	—	0
Microsetella norvegica	0	0	0	0	0	0	0	0	0	0	0	5.7	—	0
Miscellaneous	2.6	4.1	1.3	3.1	18.0	9.9	15.1	12.9	13.4	20.5	12.1	15.8	—	10.3

TABLE VI. PERCENTAGE COMPOSITION ON THE NO. 2 NET SAMPLES.

	Jan.	*Feb.*		*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*		*Sept.*	*Oct.*	*Nov.*	*Dec.*
Pseudocalanus minutus	68.0	72.0	94.3	73.5	6.9	28.4	5.2	0	3.2	1.0	0	0	—	0
Centropages typicus	33.5	26.0	2.0	4.1	3.0	0	0	17.0	6.3	6.3	20.9	7.6	—	38.2
C. hamatus	7.5	0	0	0	5.4	0	0	35.0	0	0	0	0	—	0
Acartia tonsa	7.4	0	0	0	0	0	0	12.4	47.2	19.7	0	32.8	—	4.0
Temora longicornis	0	0	0	0	7.8	19.3	19.2	2.5	0	0	0	0	—	4.0
Oithona similis	0	0	0	0	9.2	5.0	0	0	0	0	0	0	—	0
Paracalanus parvus	0	0	0	0	0	0	0	0	13.3	4.2	0	0	—	3.9
Oncaea venusta	0	0	0	0	0	0	0	0	0	0	4.2	8.1	—	0
Corycaeus speciosus	0	0	0	0	0	0	0	0	0	0	0	0	—	19.5
C. venustus	0	0	0	0	0	0	0	0	0	0	0	0	—	7.3
Cyphonautes larvae	0	0	0	0	0	7.2	0	0	0	0	0	0	—	0
Hydromedusae	0	0	0	5.8	3.5	14.3	0	0	4.4	0	0	0	—	0
Fritillaria borealis	0	0	0	6.7	54.0	0	0	0	0	0	0	0	—	0
Oikopleura dioica	0	0	0	0	0	0	0	11.4	0	0	4.4	0	—	0
Doliolum nationalis	0	0	0	0	0	0	0	0	0	45.7	18.9	0	—	0
Dolioletta gegenbauri	0	0	0	0	0	0	0	0	0	3.7	14.5	0	—	0
Podon leuckarti	0	0	0	0	0	6.9	20.3	0	0	0	0	0	—	0
P. intermedius	0	0	0	0	0	0	0	11.0	11.6	0	0	6.4	—	0
Evadne nordmanni	0	0	0	0	0	0	45.0	0	0	0	0	0	—	0
Penilia avirostris	0	0	0	0	0	0	0	0	0	9.1	20.3	9.1	—	0
Miscellaneous	3.6	2.0	3.7	9.9	10.2	18.9	10.3	10.7	14.0	10.3	16.8	36.0	—	23.1

in the catches obtained with the two net sizes. It is evident in Fig. 5 that copepods and copepod nauplii constituted the major proportion of the No. 10 net catch on nearly every occasion, while the larvae of bottom invertebrates were next by count. *Oithona similis* was the most numerous copepod taken by the No. 10 net during most of the year. Maxima of total copepods occurred in midwinter, in late spring, and in October. Cladocera, Appendicularia, and doliolids were the other groups of major numerical importance. Fig. 6, which gives in graphical form the number per cubic meter of the most important groups taken with the No. 2 net, presents a different picture. Total copepods appeared in maximal numbers in midwinter and in early August. The June maximum consisted almost entirely of cladocera, and these organisms continued in numbers into the fall months. Doliolids were of greatest importance in late August, while Appendicularia were present in smaller numbers during the greater part of the year. Coelenterates, crustacean larvae, and the larvae of other bottom invertebrates were taken in smaller numbers from late winter or early spring into the fall months.

Tables V and VI give, respectively, the percentage composition of the No. 10 and No. 2 net samples. The organisms included constituted 5% or more of one or more of the samples. It is evident that a greater variety of species was taken seasonally in appreciable numbers by the No. 2 net, while copepod nauplii and *Oithona similis* were responsible for a high percentage of the catch retained by the No. 10 net throughout the year.

It is of interest to compare the number of different organisms retained by the No. 2 and No. 10 nets, thereby ascertaining whether as great a variety of forms was caught by the No. 10 net. Fig. 7 presents the results, showing in graphical form the number of different organisms that appeared in the counting chamber per sample during the year. The upper curve gives the total number of species recorded per day from both net samples and includes the rarer forms that did not appear in the counting chamber. It is apparent that, for the greater part of the year, about the same number of species was caught by the No. 10 as by the No. 2 net. Whereas the bulk of the No. 10 net samples consisted of nauplii and *Oithona,* quite a number of species were none the less represented by at least a few individuals. For a good part of the year, therefore, the No. 10 net hauls sampled a high proportion of the species present. In October and December, during

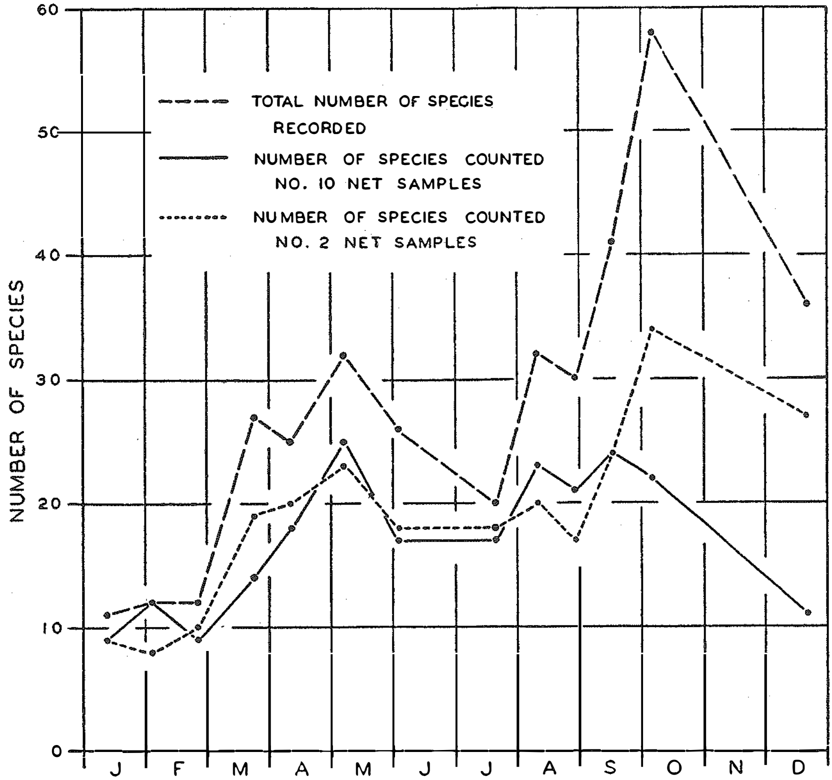


Figure 7. The number of different organisms counted in the No. 2 and No. 10 net samples and the total number of species recorded per day.

the period when Atlantic waters brought many offshore species into B. I. S., the number of these species retained by the No. 2 net was appreciably greater. In Fig. 7 the upper curve shows clearly the rise in number of species that began in late summer, due largely to the influx of offshore forms. The peak in the number of species in May was caused by the presence of a number of different groups: larval forms of bottom invertebrates, Cladocera, and Appendicularia, as well as a variety of copepods.

Due to the fact that oblique hauls were made and that a No. 10 net was used as well as a No. 2 net in 1949, there are several interesting differences between this study and the previous one on primarily surface samples collected from 1943 to 1946 (Deevey, 1952). The oblique tows caught some species in greater abundance and some in fewer numbers than the previous horizontal tows. *Pseudocalanus minutus*, for example, is probably most abundant at depths well below the surface, and this species was taken in considerably greater numbers in 1949. On the other hand, *Centropages typicus*, which was the dominant form during the greater part of the three-year study and which still remains one of the most important copepods, is apparently a surface species primarily and did not constitute as high a percentage of the total population in 1949 as was suggested previously. On the one occasion, in September, when both horizontal and oblique tows were made, *C. typicus* constituted 64% of the horizontal tow but only 21% of the oblique haul. The use of the more finely meshed net revealed the fact that, from the point of view of numerical abundance, *Oithona similis* should be considered the dominant year-round species in B. I. S.

Since the literature pertaining to the various species has been reviewed in the recent study of the zooplankton of B. I. S. (Deevey, 1952), it will not be necessary to repeat it in the following sections where the individual species are considered unless an organism was not treated previously. The words littoral, neritic, and oceanic, used to describe the various forms, will be employed as they were defined in the previous paper.

THE COPEPODS

Centropages typicus Krøyer

At least a few individuals of *C. typicus* were noted in every sample obtained throughout the year (see Table IV). The numbers recorded per cubic meter during 1949 are shown in Fig. 8. From this it is apparent that the highest numbers were obtained in January as well as from summer into the fall months. This species declined steadily in abundance from January to April. It was virtually absent during May and June, increased in numbers in July, and continued to be present for the rest of the year. This cycle in numbers follows the year's salinity cycle, the period during which extremely few specimens were taken coinciding with the months when the surface salinity was less than 30°/₀₀. During the periods of higher salinities, it was more abundant. As was previously noted, *C. typicus*, a neritic species with a fairly narrow salinity tolerance, does not appear in numbers at salinities of less than 30°/₀₀. This species must constantly enter B. I. S. with Atlantic waters.

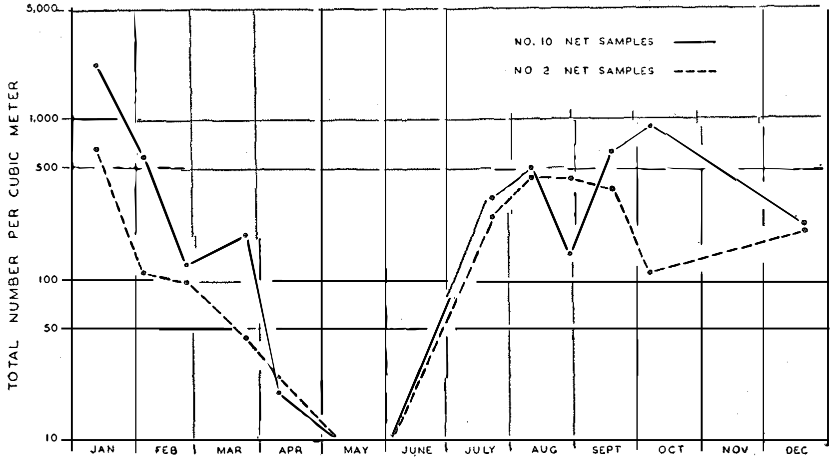


Figure 8. The total number per cubic meter, plotted on a logarithmic scale, of *Centropages typicus* in the No. 2 and No. 10 net samples.

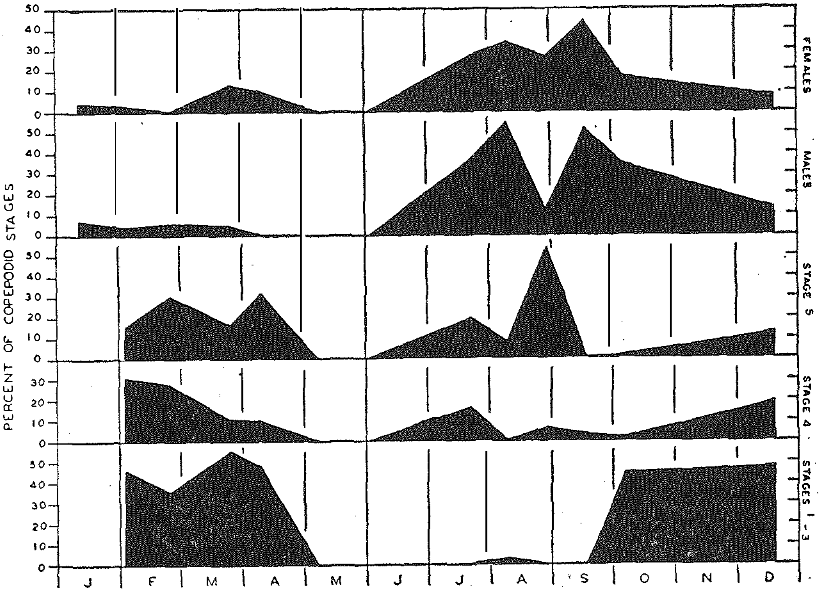


Figure 9. The percent of females, males, and the immature copepodid stages of *Centropages typicus*.

The variations in abundance of males, females, and immature stages indicate that adults were present in greatest quantities in January, in early August, and from September to early October. The earliest copepodid stages were collected in February and March, in early August, and from October to December. This constitutes evidence for three breeding periods during the year, as was previously suggested by the data collected from 1943–1946 (Deevey, 1952), largely on the basis of the variations in size of the adults. The relative percentages of the different stages of *C. typicus*, shown in graphical form in Fig. 9, also indicate three generations during the year, although the large numbers of adults previously recorded in midwinter were not found in 1949. It is highly probable that there is a midwinter breeding period in January or February, the individuals spawned at this time reaching maturity early in the summer. During the summer there is probably a rapidly developing generation spawned during July or early August which becomes mature in late August or September, and these individuals in turn produce the fall brood that matures by midwinter. The virtual absence of *C. typicus* in the samples collected during the spring months may be due to the fact that the waters sampled were predominantly of littoral origin. The variations in size previously recorded for *C. typicus* during the year indicated that there was a large-sized winter generation, a medium-sized early summer generation, and a small generation in the late summer or early fall. The corroborating evidence of the times of occurrence of the earliest copepodid stages bears out the data obtained from the seasonal variations in size of the adults.

Digby (1950) suggested the possibility of five generations per year for *C. typicus* off Plymouth, England. Adults in February and March produced nauplii that matured in May. Larger numbers of nauplii in June, August, and September were considered evidence for a total of five generations of adults between February and September. Off Plymouth, *C. typicus* showed a seasonal variation in size of small adults in January and February, maximal size in May, and adults of intermediate size for the rest of the year.

Pseudocalanus minutus (Krøyer)

This species is widespread in northern waters and is second in importance only to *Calanus finmarchicus* in the Gulf of Maine, where Fish (1936a) recorded three to four generations between March and

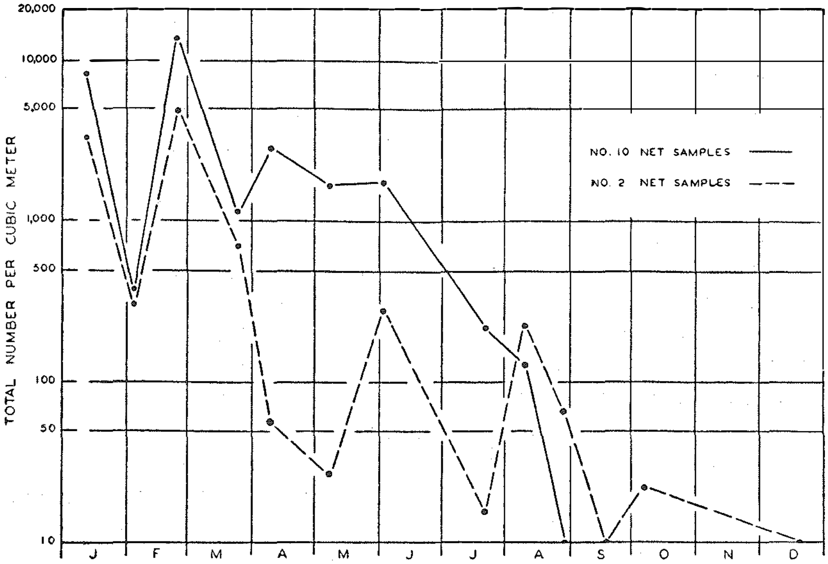


Figure 10. The total number per cubic meter, plotted on a logarithmic scale, of *Pseudocalanus minutus* taken in the No. 2 and the No. 10 net samples.

September, the developmental period being approximately two months. In Loch Striven, Marshall (1949) found that spawning occurred as follows: in late February, continuously from April until July with no clear-cut breeding periods, and in early August. Accord-

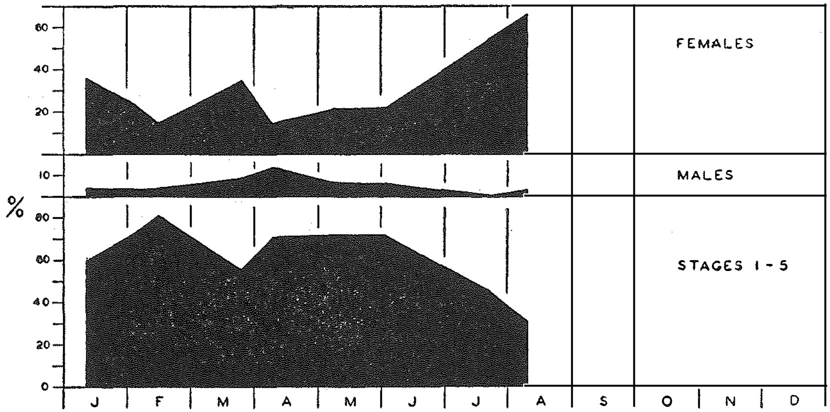


Figure 11. The percent of females, males, and the immature copepodid stages of *Pseudocalanus minutus.*

ing to Digby (1950), five generations were produced by this species during the year in the English Channel.

It occurred in considerably larger numbers in the oblique tows collected in B. I. S. in 1949 than it had in the horizontal tows from 1943–1946. It was recorded from every sample during the year (see Table IV) and was the dominant copepod during the winter to spring months, especially in the No. 2 net samples which contained little else in quantity during this period. Fig. 10 shows the number of *P. minutus* per cubic meter obtained during 1949. South of Cape Cod it is predominantly a winter to spring species and in 1949 it occurred in highest numbers from January to June, although it was present in smaller numbers in July and August. Throughout this period the immature stages were more abundant than the adults, and because of this it is difficult to determine definite spawning periods. Females carrying eggs were observed every month from January to June. Fig. 11, which depicts the relative percentages of females, males and immature copepodids, shows that the adults were relatively most numerous in January, in March and during the summer months. The highest number of immature stages was found in late February, with smaller peaks in January and April. The mean length of the females varied from 1.306 mm in January to 1.345 mm in March to 1.18 mm in July and August. Probably at least three generations were produced during the year.

Acartia tonsa Dana

Acartia tonsa is a littoral species which occurred almost entirely during the latter half of the year in B. I. S. (see Table IV). Fig. 12 shows the number per cubic meter of *A. tonsa* and of *Temora longicornis* during 1949. *A. tonsa* was present in January and from July to December, with peak numbers from July to October. Few individuals were recorded in September, but this is undoubtedly due to the fact that these samples were collected at the Hell Hole, a region of B. I. S. where this species would not be expected to occur in any numbers if Atlantic waters were predominating. Adults were found in highest numbers in early August, and on this occasion more males than females were present. During the rest of the period of occurrence, the major proportion of individuals recorded was immature.

In general *Acartia tonsa* was more abundant in 1949 than it was during the 1943–1946 survey. In the course of the previous study, it increased in numbers during the years coincident with a decrease in the salinity whereas in 1949 it appeared and increased in numbers during the period of rising salinity.

Temora longicornis (Müller)

This is a littoral and neritic species that was recorded from every sample except for those of late August and September (see Table IV). Fig. 12 shows the number per cubic meter obtained during the year. In this region, *T. longicornis* occurs primarily during the spring and early summer months. A few adults and immature copepodids were found from January to March, but in April the numbers began to increase, the maximum occurring in early June. Less were taken in July and August and none was present in September, but by December a few immature copepodids had appeared. Spawning occurred during the spring. From April until June, most of the specimens collected were immature. The percentage of adults rose from June to July, and after this it ceased to be of importance. However, it is presumed that there is a spawning period during the summer when the individuals that appear during the winter are produced.

In the English Channel, Digby (1950) found *Temora* abundant from April to September. He recorded five generations during the year, individuals maturing in February, late May and June, July, late August, and probably from October to December. In Loch Striven, Marshall (1949) noted two generations for this species. From January to mid-March nauplii predominated. Adults appeared in April and produced a brood which matured in May. No distinct August brood was observed. *Temora* nauplii were present for the greater part of the year in Oslo Fjord (Wiborg, 1940), but the main spawning occurred in April. In B. I. S. there must be at least two generations during the year.

T. longicornis is noted for its range of salinity tolerance, and in B. I. S. it was most numerous during the period of lowest salinity in 1949. Undoubtedly it is primarily a littoral species, although it has often been reported from neritic areas.

Paracalanus parvus (Claus)

Paracalanus parvus, a neritic and littoral species, was recorded on several occasions between 1943 and 1946, but in 1949 it was collected in greater numbers. Its period of occurrence is similar to that of

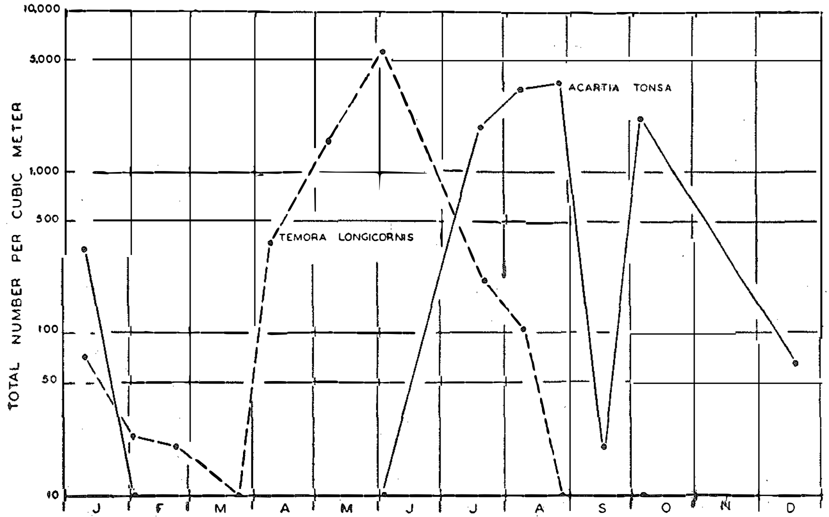


Figure 12. The total number per cubic meter, plotted on a logarithmic scale, of *Acartia tonsa* and *Temora longicornis*.

Acartia tonsa, since it was noted in January and March and from July to December. The numbers per cubic meter are shown in Fig. 13, which also shows the seasonal abundance of *P. crassirostris* and

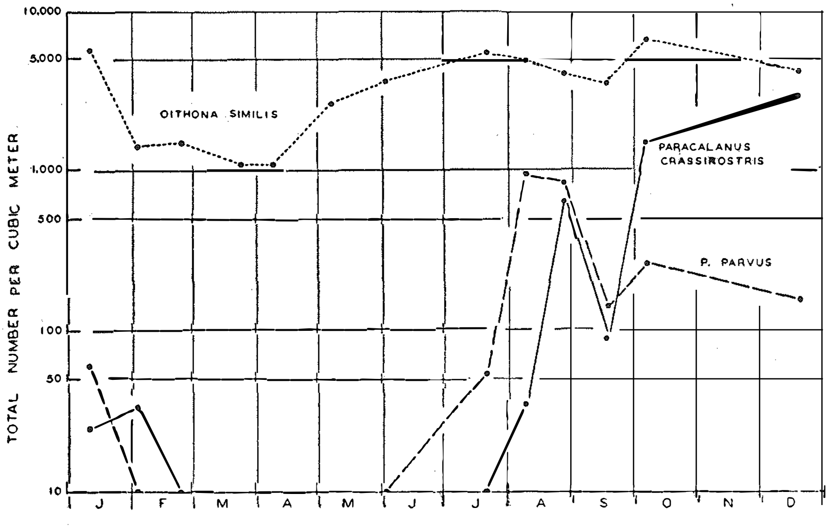


Figure 13. The total number per cubic meter, plotted on a logarithmic scale, of *Paracalanus parvus*, *P. crassirostris*, and *Oithona similis*.

Oithona similis. *P. parvus* occurred in highest numbers in August. Although no effort has been made to determine breeding periods, there are probably at least two of these, one in the summer and another in the late fall or winter.

P. parvus is a widely distributed species and is considered by Bigelow (1928) as probably cosmopolitan in temperate and tropical seas. He found it in the Gulf of Maine throughout the year; it has also been recorded throughout the year in Chesapeake Bay (Wilson, 1932b), where it was observed in greater numbers in the outer bay in the autumn. According to Bigelow its known salinity range is 19.3–40.0°/₀₀. Clarke and Zinn (1937) found it most abundant in August off Woods Hole, Massachusetts. In the English Channel (Digby, 1950) it occurred in numbers from the end of April to December, with maxima in May and June and from August to October. Digby noted five generations during the year, in rhythm with those of *Pseudocalanus*. In Loch Striven, Marshall (1949) was unable to distinguish distinct broods and believed breeding to be continuous.

Paracalanus crassirostris Dahl

So far as is known at present, *P. crassirostris* is a littoral species, but there are few records of its occurrence off the eastern coast of the United States. Due to its small size, only the finely meshed nets retain it. It has been recorded from Tisbury Great Pond on Marthas Vineyard, Massachusetts (Deevey, 1948), it was found in B. I. S. on quite a number of occasions from 1943–1946 (Deevey, 1952), and it is known to occur in L. I. S. (unpublished data). Davis (1944) has described a variety of this species from Chesapeake Bay.

Fig. 13 depicts the number of *P. crassirostris* during 1949. In B. I. S. small numbers were taken in January and February. Although none was recorded from March to July, it reappeared in August and increased in abundance during the fall, with a maximum in December, when it constituted nearly 34% of the No. 10 net sample. The seasonal cycle of this species therefore appears to be similar to that of its close relative, *Paracalanus parvus*. The number of breeding periods per year and the times of their occurrence have not been determined.

Oithona similis Claus

Judged by its continual presence and numerical abundance throughout the year, the dominant copepod in B. I. S. during 1949 was the small cyclopoid *Oithona similis,* which, like *Centropages typicus* and *Pseudocalanus minutus,* was recorded on every occasion (see Table IV). Although retained only occasionally by the No. 2 net, it constituted from 7–57% of the No. 10 net tows during the year. Fig. 13 gives the number per cubic meter in 1949. Females with eggs were recorded from March through June. Maximum numbers of *Oithona* were obtained in January, from July to August, and from October to December.

This species is of considerable importance in the Gulf of Maine (Fish, 1936b), where it reproduces from March to September. The western stock produced four broods during this period, in March, May, July, and September, while the eastern stock had three spawning periods, in April, June, and August. The developmental period varied from two months to six weeks. *O. similis* has also been found numerous in Chesapeake Bay (Wilson, 1932b), where it occurs in autumn and winter in the inner bay. In Oslo Fjord, where it is always abundant, Wiborg (1940) recorded two maxima, one in April to May and the other in July to August. In Loch Striven, Marshall (1949) noted that it was the most numerous of the small copepods and was present throughout the year. Breeding was continuous for most of the year, but the highest numbers were found during the summer. In the English Channel Digby (1950) noted that it was abundant from April to October, with maxima in early May, late July, and mid-September. He believed that five generations were probably produced during the year. In the colder waters where it occurs in abundance, *O. similis* is unquestionably an important member of the plankton fauna for the greater part of the year.

Other Copepods

The copepods which appeared seasonally but in small numbers, and the rare species which were brought into B. I. S., are all included under this heading. All of these are listed in Table IV. A number of species occurred fairly regularly but were never taken in abundance. *Centropages hamatus* (Lilljeborg), which was second in importance during the previous survey, was found only in small numbers in 1949. As in the case of *C. typicus,* possibly this may be due to a preference for surface waters. *C. hamatus* showed two maxima, one in January and one in July. It was present from January to early August and from October to December. Presumably there were two generations, one in the winter and one in July, as has been previously reported for this species. *Calanus finmarchicus* (Gunner) was also scarce and unimportant in 1949. It was recorded from March to September, but at no time was it collected in appreciable numbers. *Labidocera aestiva* Wheeler, a littoral species that normally occurs from late summer into the fall, was obtained in small numbers from August to December. Only immature copepodids appeared in the counting chamber. *Tortanus discaudatus* (Thompson and Scott), another littoral species, was recorded only in March, May, June, and October. *Eurytemora* sp., definitely a brackish water form although specific identification was not made, was taken only in April. *Acartia clausii* Giesbrecht and *A. longiremis* (Lilljeborg) were found during winter and spring, but they were considerably less abundant than *Acartia tonsa*. *A. clausii* was present from February to April, while *A. longiremis* occurred from March to June.

The cyclopoid *Oithona spinirostris* Claus appeared sporadically throughout the year in January and February, from April to June, and in October and December. Females with eggs were recorded in April and May. This may be an offshore species, but if so it was taken at the times of the lowest as well as highest salinities. *Oithona brevicornis* Giesbrecht, predominantly a littoral species, was present from July to October.

Several harpacticoids were also collected during the year. *Thalestris gibba* (Krøyer) was noted in June; according to Wilson (1932a), this is a boreal form that comes down from the north. *Macrosetella gracilis* (Dana), a tropical and warm temperate species, was found in September. *Clytemnestra rostrata* (Brady), a pelagic form, appeared in October, while *Alteutha depressa* Baird, according to Wilson (1932a) a littoral species, occurred at the same time. *Microsetella norvegica* (Boeck), a common pelagic harpacticoid, was found in both October and December.

The only indigenous parasitic species recorded during 1949 was *Monstrilla anglica* Lubbock, taken in April. The previous study had shown that this species might be expected to occur in the plankton from February to April.

Quite a number of offshore species were collected, especially during October and December. *Metridia lucens* Boeck was taken in several samples in May, July, August, and October. This is definitely an offshore species that has not been recorded hitherto from B. I. S.; its occurrence showed the presence of some Atlantic water in the Sound in May at a time of low salinity. *Mecynocera clausi* I. C. Thompson was noted in July. *Candacia armata* (Boeck) and *Calanus minor* (Claus) were found from late August to December. *Oncaea venusta* Philippi occurred from September to December. According to Digby (1950), *O. venusta* appears seasonally from September to December off Plymouth, England. *Corycaeus ovalis* Claus, *C. elongatus* Claus, *Eucalanus crassus* Giesbrecht, and *Euchaeta marina* (Prestandrea) were found only in October. *Temora stylifera* (Dana) appeared in August and October, while *Centropages bradyi* Wheeler, *Eucalanus monachus* Giesbrecht, *Sapphirina auronitens* Claus, *Corycaeus venustus* Dana, *C. speciosus* Dana, and *Temora turbinata* (Dana) were present in October and December. *Rhincalanus nasutus* Giesbrecht appeared only in December. *Oncaea venusta, Corycaeus speciosus,* and *C. venustus* occurred in sufficient numbers to constitute an appreciable percentage of the No. 2 net hauls. Female *Oncaea venusta* and *Corycaeus venustus* were observed with eggs in October, while *Corycaeus speciosus* females were carrying eggs in December.

CLADOCERA

Five species of Cladocera were found during 1949 (see Table IV). These were *Evadne nordmanni* Loven, *E. spinifera* Müller, *Podon leuckarti* Sars, *P. intermedius* Lilljeborg, and *Penilia avirostris* Dana. Four of these species were recorded in the previous study, the additional form being *Evadne spinifera* which appeared in small numbers in September and October. *E. spinifera* arrived with the influx of warm water species. According to Baker (1938), this species is found "as commonly if not more often as a pelagic form than as a coastal form." Figs. 14 and 15 give the numbers of the four important species. The few *Evadne spinifera* present were included in the counts for *E. nordmanni* for September and October.

Evadne nordmanni occurred in numbers in early June, with a smaller peak from August to October (see Fig. 15). Specimens of this species with resting eggs were noted in June and October, while some of the *E. spinifera* contained resting eggs in October. Occasional specimens of *Podon leuckarti* were observed in March and April, but this species was plentiful only in May and June, with maximal numbers in June (see Fig. 14). *P. leuckarti* also has been found in L. I. S. in June (unpublished data). Resting eggs were noted in June. *Podon inter-*

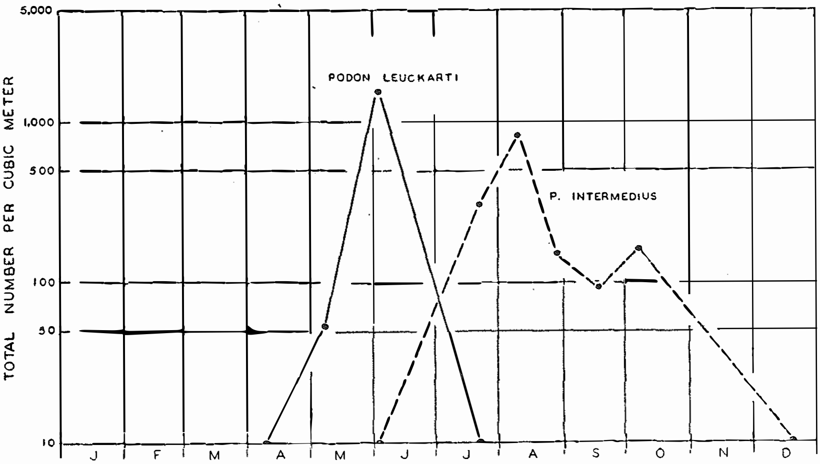


Figure 14. The total number per cubic meter, plotted on a logarithmic scale, of *Podon leuckarti* and *P. intermedius*.

medius occurred from July to October, with the highest numbers recorded in early August. *Penilia avirostris* was taken from August to October (see Fig. 15), the period of its occurrence as previously reported. Undoubtedly, this species occurs annually in this region. These four species of Cladocera, appearing seasonally, are an important part of the zooplankton community of B. I. S.

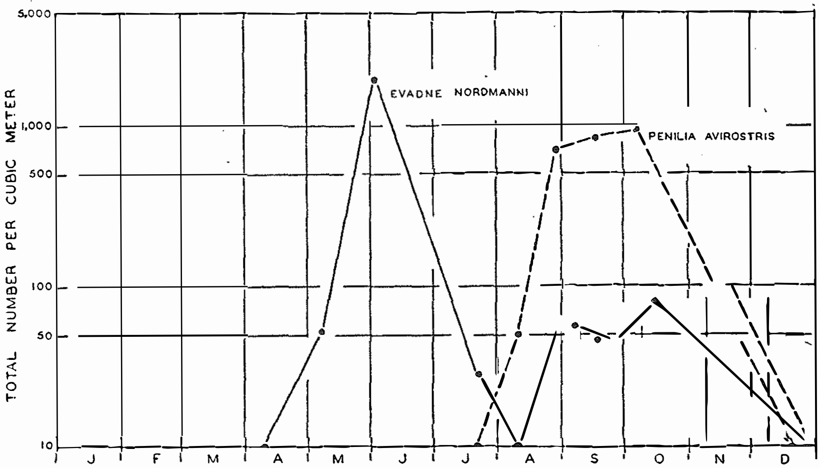


Figure 15. The total number per cubic meter, plotted on a logarithmic scale, of *Evadne nordmanni* and *Penilia avirostris*.

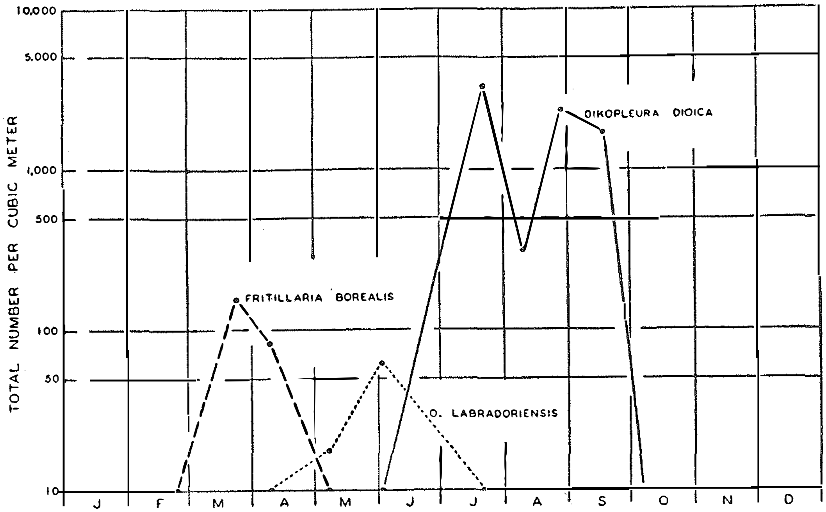


Figure 16. The total number per cubic meter, plotted on a logarithmic scale, of *Oikopleura labradoriensis, O. dioica,* and *Fritillaria borealis.*

TUNICATES

A greater number of pelagic tunicates was found during 1949 than during the previous three-year study (see Table IV). The Appen-

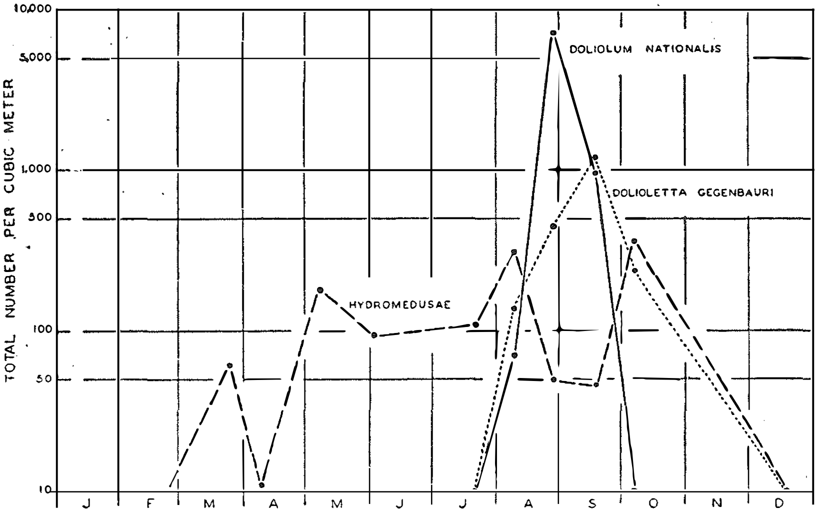


Figure 17. The total number per cubic meter, plotted on a logarithmic scale, of *Doliolum nationalis, Dolioletta gegenbauri,* and of hydromedusae.

dicularia were represented by *Fritillaria borealis acuta* Lohmann, *Oikopleura labradoriensis* Lohmann, and *O. dioica* Fol. A few specimens of *O. longicauda* Vogt were also noted in the September samples. The doliolids present were the two species already recorded, *Doliolum nationalis* Borgert and *Dolioletta gegenbauri* (Uljanin). *Thalia democratica* (Forskål), the only salp taken, was found only in late August and October. Figs. 16 and 17 give the numbers per cubic meter of most of these species.

Fritillaria borealis was present from February to June, with highest numbers in March, while *Oikopleura labradoriensis* occurred from March to June with a small peak in early June (see Fig. 16). These are both cold water species; the temperature ranged between 5 and 13° C during the period of their occurrence. As in previous years, *O. dioica* was taken from July to October, with maximal numbers in July and from late August to September.

Both species of doliolids were present from early August to October (see Fig. 17), but *Doliolum nationalis* occurred in maximal numbers in late August, while *Dolioletta gegenbauri* reached a peak in September. The total number of doliolids present, however, was a little greater than the sum of the two species, since larval forms and "old nurses" were taken that could not be identified to species. The larval doliolids occurred in greatest number in September but were also present in October. The phorozooids of *D. nationalis* were most numerous, but gonozooids were also observed. Gonozooids, phorozooids, oozooids, and gastrozooids of *D. gegenbauri* were obtained.

All of these pelagic tunicates are offshore species. *Fritillaria borealis* and *Oikopleura labradoriensis* provide evidence for the presence of more northern Atlantic water in B. I. S. during winter and spring. The species collected during the summer and fall are warm water forms. Of these only *Oikopleura longicauda* has not been recorded hitherto from B. I. S.

COELENTERATES

The coelenterates taken in the zooplankton tows included hydromedusae and siphonophores, although the latter were in most instances merely fragments of colonies, floats or bells or gonophores or bracts. Hydromedusae were present from March to December. Most of the forms collected are listed in Table VII. *Hybocodon prolifer, Rathkea octopunctata* and *Obelia* sp. were observed most frequently. The total number of hydromedusae per cubic meter during the year is shown in

Fig. 17. The numbers collected were never high, but small peaks of abundance were obtained in May, August, and October.

TABLE VII. CHECKLIST OF OCCURRENCE OF HYDROMEDUSAE IN B. I. S. IN 1949.

	Mar. 24	*Apr. 9*	*May 7*	*June 2*	*July 21*	*Aug. 9*	*Aug. 28*	*Sept. 17*	*Oct. 6*
Hybocodon prolifer	x	x	x	x	x	—	—	—	—
Rathkea octopunctata	x	x	x	x	—	—	—	—	—
Actinuli	x	x	—	—	—	—	—	—	—
Obelia sp.	x	x	x	x	x	x	x	x	x
Podocoryne carnea	—	—	—	—	—	x	—	—	—
Liriope sp.	—	—	—	—	—	—	x	—	—
Aglantha digitale	—	—	—	x	—	—	—	—	—
Bougainvillea autumnalis	—	—	—	—	—	—	x	—	—

In large part, the siphonophore fragments were not definitely identified. These were collected from September to December and were obviously warm water forms brought north by the Gulf Stream. The diphyid siphonophore *Muggiaea kochii* was present from September to December, though never in appreciable numbers. Diphyid bells, doubtless fragments of *Muggiaea* cormidia, were recorded in September and October. Fragments of agalmid siphonophores were also obtained from September to December.

CHAETOGNATHS

Sagitta elegans is the only chaetognath that occurs in B. I. S. in any quantity, but in 1949 this species was not obtained in numbers in the oblique tows. It was found in the samples from February to June, in August, and in December (see Table IV). The highest numbers were recorded in May and June. The specimens collected were almost all immature. The reason for the scarcity of *S. elegans* during this year is not apparent, especially since this species is in all probability a regular inhabitant of B. I. S. and since most of the water column must have been sampled by the nets.

Sagitta serratodentata and *S. enflata* were found from late August to December. Both of these forms are warm water species that appeared in B. I. S. during the fall, apparently due to the influx of Gulf Stream water. Another species was present in December, but only immature specimens were obtained and so specific identification was not made.

CRUSTACEAN LARVAE

Quite a number of crustacean groups were represented in the plankton by larval forms (see Table IV), although only copepod nauplii were abundant throughout the year. These nauplii, not identified, undoubtedly belonged to a variety of species. Fig. 5 shows the total number of copepod nauplii per cubic meter. Peak numbers were obtained in January, March, June, and September. Copepod nauplii constituted 7–74% of the No. 10 net samples.

Table VIII lists most of the crustacean larvae that were obtained in the zooplankton hauls, and it shows also the periods of their occurrence. A number of brachyuran species were represented. As was the case during the three-year survey, the only stomatopod larvae that were collected were the early antizoeae of *Lysiosquilla*. Specimens of larval *Crago septemspinosus* appeared more frequently than any other form. *Balanus balanoides* larvae were found from February to June, while *B. crenatus* nauplii were taken only in May and June. Brachyuran zoeae, collected in greater quantity than any of the other crustacean groups, occurred in highest numbers in July and August. Three different types of megalops larvae were present but were not identified. Total crustacean larvae constituted an appreciable proportion of the No. 2 net samples.

TABLE VIII. CHECKLIST OF OCCURRENCE OF CRUSTACEAN LARVAE IN B. I. S. IN 1949.

	F.	*M.*	*A.*	*M.*	*J.*	*J.*	*A.*	*S.*	*O.*	*N.*	*D.*
Zoeae:											
Cancer irroratus	—	—	x	x	x	—	—	—	—	—	—
Callinectes sapidus	—	—	—	—	x	x	xx	x	x	—	—
Carcinides maenas	—	—	—	x	x	x	—	—	—	—	—
Pinnotheres maculatus	—	—	—	—	—	x	xx	—	x	—	—
Libinia sp.	—	—	—	—	—	x	xx	—	x	—	—
Neopanope texana sayi	—	—	—	—	—	—	x	—	—	—	—
Pelia mutica	—	—	—	—	—	—	x	—	—	—	—
Megalops larvae	—	—	—	—	—	x	xx	—	x	—	—
Larval mysids	—	—	x	—	x	—	x	—	—	—	—
Larval cumaceans	—	—	—	—	x	—	—	—	—	—	—
Lysiosquilla antizoeae	—	—	—	—	—	—	x	x	x	—	—
Crago septemspinosus	—	—	x	x	x	x	xx	x	x	—	x
Hippolyte zostericola (?)	—	x	x	x	x	—	—	—	x	—	—
Eupagurus sp.	—	—	—	—	—	x	x	—	x	—	—
Glaucothöe larvae	—	—	—	—	—	—	—	—	x	—	—
Upogebia sp.	—	—	—	—	—	x	x	—	x	—	—
Porcellanid larvae	—	—	—	—	—	—	x	—	—	—	—
Balanus balanoides nauplii	xx	x	x	x	x	—	—	—	—	—	—
B. balanoides cyprids	—	x	—	x	x	—	—	—	—	—	—
B. crenatus nauplii	—	—	—	x	x	—	—	—	—	—	—

OTHER LARVAL FORMS

The larval forms of a number of bottom invertebrates were taken in greater quantity than during the previous study, largely due to the use

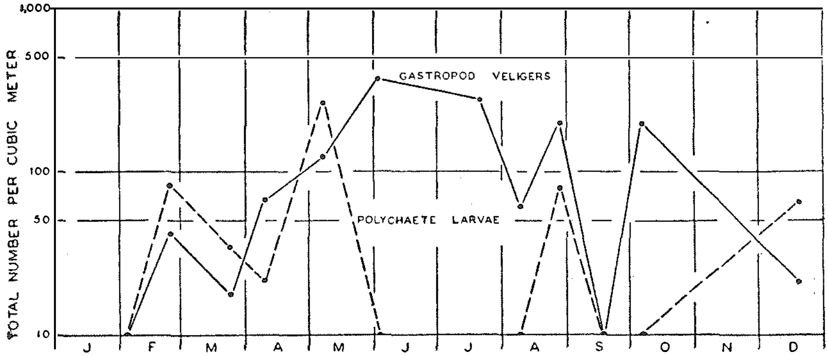


Figure 18. The total number per cubic meter, plotted on a logarithmic scale, of gastropod veligers and polychaete larvae.

of the No. 10 net. These include lamellibranch veligers, gastropod veligers, polychaete larvae, and cyphonautes larvae in particular. Few echinoderm larvae were collected, although a number of echinoderms are common in the bottom fauna of B. I. S. The seasonal abundance in numbers per cubic meter of the more important forms is shown in Figs. 18 and 19, while the periods of their occurrence are indicated in Table IV. Only the lamellibranch veligers were taken in sufficient quantity to constitute an appreciable part of the total samples. Figs. 5 and 6 show that the larvae of bottom invertebrates were of considerable numerical importance in the No. 10 and No. 2 net samples. Larval crustacea were also included in this category.

Lamellibranch veligers were present in the samples for the greater part of the year, but due to the uncertainty attendant on their identification, no effort has been made to identify them. Veligers were obtained in every month except January and July, and in November when no samples were collected. The greatest numbers were found in early June and in October (see Fig. 19).

Gastropod veligers occurred from early February to December, although, as previously noted, no samples were obtained in November. They were never present in as great abundance as the lamellibranch veligers, but, as shown in Fig. 18, small maxima were found in June to July, in late August and October. Gastropod eggs were observed only in May.

A larval squid, *Loligo* sp., 3 mm in length, was taken in July.

The cyphonautes larvae of Bryozoa, not previously recorded from the zooplankton samples of B. I. S. due to their small size, were found

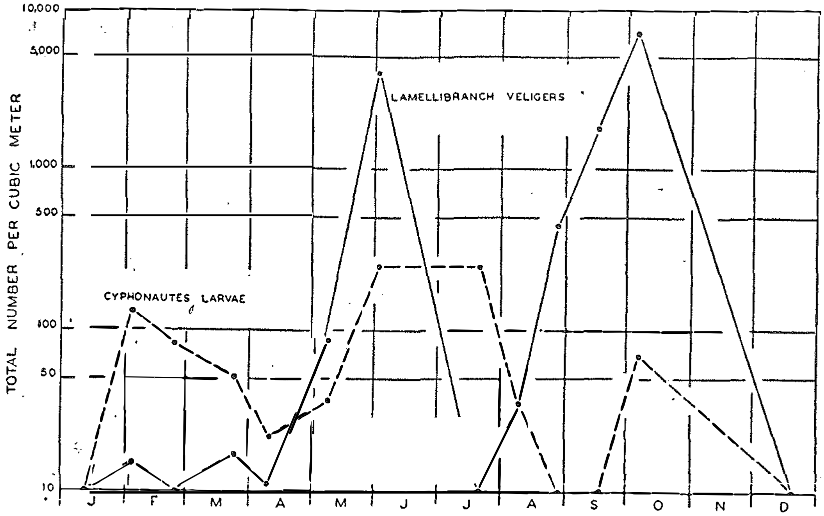


Figure 19. The total number per cubic meter, plotted on a logarithmic scale, of lamellibranch veligers and cyphonautes larvae.

continuously from early February to October. They were most abundant from June to July, but smaller peaks were noted in February and October (see Fig. 19).

Aside from the occurrence of *Autolytus* sp. in February, June and late August, and of *Tomopteris* sp. in late August and October, the polychaetes were represented only by trochophores and larvae. Larval polychaetes were taken from February to June, and in August, October, and December. The total number of polychaete larvae per cubic meter is shown in Fig. 18.

Echinoderm larvae were noted only on occasion and were never numerous. Echinoplutei were found from March to May, while ophioplutei were recorded in September and October. Late larval stages, possibly of asteroids, were observed in July and late August.

OTHER SPECIES

Aside from the forms already mentioned, there remain a few rare species which do not fit into the groups treated. These include the penaeid *Lucifer*, ostracods, heteropods, and pteropods. A few specimens of *Lucifer faxoni* Borradaile were present from late August to October. This species was also collected in the open waters immediately outside B. I. S. during the previous survey. The related species, *L. typus*, recorded by Bigelow and Sears (1939) over the continental shelf in these latitudes, has not yet appeared in samples from B. I. S.

During October and December, a few male, female and immature specimens of the pelagic ostracod *Euconchoecia chierchiae* Müller were obtained in B. I. S. This is an oceanic warm water species first described from the coast of Brazil. According to Skogsberg (1920), specimens from the North Atlantic in the region of the Gulf Stream, described by Cleve under a different name, also belong to this species. This ostracod is of interest since it is the only marine form in which the females carry eggs for a while between the back of the body and the shell, and females with eggs are included in the material from B. I. S. *E. chierchiae* may be commoner along the east coast of the United States than has been realized hitherto, since a plankton tow collected by H. T. Odum off the coast of North Carolina late in the fall of 1949 contained a higher percentage of this species than of any other form.

The pteropods that were found in 1949 were *Creseis virgula*, *C. acicula*, and *Limacina retroversa*. *C. virgula*, previously reported from B. I. S., appeared throughout August and in September, while *C. acicula* was found only in September. Both of these species have been recorded from the waters over the continental shelf southward from Atlantic City, New Jersey (Bigelow and Sears, 1939). The common northern pteropod *Cliona limacina* was not found in 1949, although a few young specimens of *Limacina retroversa* (Fleming) appeared in January.

Two species of heteropods were collected during the fall. One of these was the relatively large species *Firoloida desmarestia* Lesueur which was found in September. The other was the tiny atlantid, *Oxygyrus keraudreni* Rang, which appeared in September and October. According to Bigelow and Sears, *Firoloida* has been collected over the continental shelf from Atlantic City southwards, so this may be the most northern record for this species on this coast.

Except for *Limacina retroversa*, all of these are warm water forms and, as in the case of many of the other warm water species, they were brought north by the Gulf Stream, which apparently exerts a tremendous influence on the zooplankton populations of coastal areas such as B. I. S. during the late summer and fall months.

DISCUSSION

QUALITATIVE CONSIDERATIONS

In general the zooplankton picture obtained during 1949 agrees with that found from 1943–1946. More or less the same species were of importance during both periods studied. As previously stated, the oblique tows revealed the fact that *Pseudocalanus minutus* occurs in numbers for a greater part of the year and is more abundant than was indicated by the horizontal tows. Because of its preference for deeper waters and presumably for lower temperatures, *P. minutus* was obtained only during the colder months in the surface tows. *Centropages typicus,* still one of the most important copepods in B. I. S., is probably most abundant only in the surface waters. Other species which were not found to be as abundant as they were during the previous study included *Centropages hamatus, Labidocera aestiva,* and *Calanus finmarchicus.* On the other hand, *Paracalanus parvus* and *P. crassirostris* were considerably more numerous than they were from 1943–1946. The use of the No. 10 net showed that the dominant copepod throughout the year, from the point of view of numerical abundance, was the small cyclopoid *Oithona similis.*

The copepods that constitute the bulk of the zooplankton population of B. I. S. are all littoral or neritic species. *Centropages typicus* and *Calanus finmarchicus* are strictly neritic forms in these latitudes, while *Acartia tonsa, Labidocera aestiva, Paracalanus crassirostris, Temora longicornis,* and *Centropages hamatus* are predominantly littoral species, although all of these except *L. aestiva* and *P. crassirostris* are common not far from shore in neritic areas. *Pseudocalanus minutus* and *Paracalanus parvus* appear to be equally littoral and neritic organisms, and this applies also to *Oithona similis.* Other species which occurred briefly or sporadically, such as *Acartia clausii* and *Tortanus discaudatus,* are littoral forms that have never been found in abundance in B. I. S.

In contrast with the large number of warm water species that entered B. I. S. during the late summer and fall, few offshore forms were found during winter and spring. *Metridia lucens,* taken in May as well as later in the year, must have entered from the Atlantic. The presence of *Limacina retroversa* in January, of *Oikopleura labradoriensis* and *Fritillaria borealis* during the winter and spring months, and of *Thalestris gibba* in June may be considered evidence of the advent of more northern Atlantic waters. *Rhincalanus nasutus* is an offshore species, but this was found only in December.

Many warm water species appeared during the late summer and fall. These include the copepods *Candacia armata, Calanus minor, Mecynocera clausi, Oncaea venusta, Eucalanus monachus, E. crassus, Sapphirina auronitens, Corycaeus venustus, C. ovalis, C. speciosus, C. elongatus, Temora stylifera, T. turbinata, Euchaeta marina,* and *Centropages bradyi,* the penaeid *Lucifer faxoni,* the ostracod *Euconchoecia chierchiae,* the chaetognaths *Sagitta serratodentata* and *S. enflata,* the heteropods and pteropods, the tunicates *Doliolum nationalis, Doliolетta gegenbauri, Thalia democratica, Oikopleura dioica* and *O. longicauda,* the siphonophores, and the cladoceran *Penilia avirostris.* Nine of these species of copepods have not been recorded previously from B. I. S., while four offshore species collected during the three-year survey did not appear in the 1949 samples. Possibly because the more saline Atlantic waters enter B. I. S. primarily in the bottom layers, a somewhat larger number of offshore species was collected by oblique hauls than had been obtained previously by horizontal tows.

During the first half of the year the zooplankton population was made up of the littoral and neritic species that would be expected to occur in this region, but during the second half of the year so many alien species entered the Sound that the entire picture was changed. Fig. 7 shows clearly the rise in the number of species that occurred during the fall. This is apparently the normal pattern of events in B. I. S. The influence of the offshore waters from the north is not as detectable during the winter months, since the species brought into the Sound are similar to the ones normally present at that time. During the spring, littoral waters from L. I. S. predominate; hence minimal numbers of neritic species are found and the zooplankton population consists largely of littoral species and the larval forms of bottom invertebrates. It is during late summer and fall, when the offshore waters are mainly of southern origin, that the changes in the composition of the zooplankton population are particularly striking. Similarly, most of the phytoplankton species were littoral or neritic forms, while offshore species were found mainly from August to December (Riley, 1952b).

Because the waters of B. I. S. are in a constant state of change due to the admixture of waters of different origin, the zooplankton and phytoplankton samples collected at a given station and throughout the year showed little relationship to one another. The phytoplankton has been analyzed by Riley (1952b) as Harvey units of plant pigments per cubic meter. A peak of phytoplankton occurred in late February, little was present from March to May, then there was a gradual rise to a smaller peak in late August, and finally there was a decrease to a low in December. In the fall a zooplankton maximum followed a phytoplankton bloom, but during the spring months, when little phytoplankton was present, a zooplankton maximum occurred in early June, while a peak of zooplankton in January preceded the late February phytoplankton maximum. Presumably this lack of relationship is due to the mixture of populations of different origin.

COMPARISON OF TOTAL ZOOPLANKTON WITH OTHER COASTAL AREAS

Though not thoroughly satisfactory, one means of obtaining an estimate of the total quantity of zooplankton in a given locality is to measure the mean annual zooplankton concentration as cc of displacement volume per cubic meter of water. Due to the great variation in size of the individuals, this method is more reliable than the use of estimates of the numbers of organisms per cubic meter. In most instances the volumetric data available for other coastal waters are not strictly comparable to the B. I. S. data, since different methods and net sizes were employed to strain the zooplankton. The different results obtained with the No. 2 and No. 10 nets emphasize this. As previously noted, the displacement volumes measured for the No. 10 net samples yielded an annual mean concentration of 0.68 cc/m^3 of water, a figure more than three times the mean of 0.21 cc/m^3 obtained from the No. 2 net samples. In this instance the figure for the No. 10 net samples obviously represents a higher proportion of the total zooplankton population.

Volumetric measurements of the total zooplankton studied in various regions have been summarized by Bigelow and Sears (1939) and by Riley, Stommel, and Bumpus (1949); these authors have noted and commented upon the various methods used. Many of the data reviewed by Bigelow and Sears are given as settlement volumes. Redfield (1941) has reported that volumetric determinations made by this method vary from 3.3 to 7 and average 4.9 times greater than displacement volumes.

For comparison with the data from B. I. S., there are seasonal data from the Gulf of Maine (Redfield, 1941), Georges Bank (Riley and

Bumpus, 1946), off Marthas Vineyard, Massachusetts (Clarke and Zinn, 1937), and from the coastal waters of the continental shelf from Cape Cod to Chesapeake Bay (Bigelow and Sears, 1939), In general the estimated mean annual volumes of zooplankton obtained by these investigators are of the same order of magnitude. For the waters over the continental shelf south of Cape Cod, Bigelow and Sears obtained mean displacement volumes of 0.4–0.8 cc/m^3. Redfield's mean annual volumes ranged from 0.3–0.53 cc/m^3 for the various sectors of the Gulf of Maine. The Georges Bank zooplankton yielded an estimated mean annual concentration of 0.72 cc/m^3. Clarke and Zinn's data for their station off Marthas Vineyard were measured as settling volumes from oblique hauls made with a scrim net. When their figures are converted to volumes per cubic meter and divided by 4.9, which is Redfield's average for the difference between settlement and displacement volumes, a mean annual concentration of 0.3 cc/m^3 is obtained. If these estimates of the mean annual zooplankton concentrations are accepted without concern for the methods used to obtain them, it appears that B. I. S. produces as high a volume of zooplankton as the other coastal areas. Actually, of the volumes listed, only the Georges Bank figure is strictly comparable, the zooplankton samples having been obtained in oblique hauls by using a Clarke-Bumpus sampler with a No. 2 net. If this volume, 0.72 cc/m^3, is compared with the No. 2 net figure of 0.21 cc/m^3 obtained for B. I. S., it would seem that Georges Bank has three to four times as much volume of zooplankton per cubic meter as B. I. S., although the actual numbers of organisms per cubic meter taken with the No. 2 net were higher for B. I. S. than for Georges Bank. Of course it is impossible to know at present whether the No. 2 net caught a higher proportion of the total population of Georges Bank than was obtained by this net in B. I. S., but it is probable that this was so. Similarly, Redfield's Gulf of Maine samples were taken with a No. 0 net and must therefore have missed the smaller organisms. Although the present volumetric data suggest that a similar total quantity of zooplankton per unit volume of water is present in the coastal waters of the northeastern United States, it is conceivable that, in comparison with the Gulf of Maine and Georges Bank, B. I. S. may prove to be relatively poor in zooplankton.

To obtain an estimate of the total volume of zooplankton maintained in a given area, the volume per cubic meter is multiplied by the mean depth in meters, the product being the amount of zooplankton beneath a square meter of sea surface. When the available volumetric data are thus converted, an entirely different picture of the total zooplankton results (see Riley, Stommel, and Bumpus, 1949: fig. 10). The B. I. S. No. 10 net samples yielded an annual mean zooplankton crop of 20.4 cc/m^2 of sea surface, while the No. 2 net samples gave a mere 6.4 cc/m^2. When these figures are compared with the 40 cc/m^2 reported as the mean average for the Gulf of Maine and the 48 cc/m^2 for Georges Bank, it is apparent that at most B. I. S. maintains only half as much zooplankton as these other areas. Clarke and Zinn's data for their station off Marthas Vineyard at a depth of 30 m yielded an estimated mean annual crop of 9 cc/m^2 for their scrim net samples. Therefore, while the volume of zooplankton per cubic meter may be of the same order of magnitude throughout the coastal areas studied, the total population underlying a square meter of sea surface is of necessity less in the shallower waters.

There are virtually no data on mean annual quantity of total zooplankton measured as dry weight or organic matter available for comparison with the B. I. S. data. Harvey (1950) estimated 1.5 g/m^2 of sea surface as the mean annual quantity of zooplankton organic matter present in the waters off Plymouth, England, the average depth being 70 m. Riley and Gorgy (1948) have given data for one coastal station obtained in August 1947 outside B. I. S. and Riley (unpublished data) made analyses of samples collected with a Clarke-Bumpus sampler and a No. 10 net in March and December 1947 at depths up to 50 m in this general region. The March and December displacement weights were low, 0.077 g/m^3, when compared with the 0.840 g/m^3 obtained from the August sample. The total organic matter for these three samples averaged 0.0485 g/m^3 and 1.73 g/m^2 of sea surface. The No. 2 net samples were used for the dry weight and organic content determinations of the B. I. S. zooplankton; the mean annual estimates obtained are about one third to one fourth as high as those just noted. The total mean organic content of the No. 2 net zooplankton was 0.0160 g/m^3 or 0.480 g/m^2 of sea surface. It is unfortunate that the No. 2 net samples were used for these determinations, since it is obvious that the No. 10 net sampled a higher proportion of the total zooplankton. However, it is possible to estimate the amount of organic matter in the No. 10 net samples by multiplying the mean displacement volume (0.68) by the mean per cent of the displacement weight of organic matter (.089). This gives an estimated mean of 0.0605 g/m^3 of organic matter, or 1.82 g of organic matter per square meter of sea surface. This is probably a valid estimate, since the displacement volumes of the No. 10 net samples were two to four times higher in all instances than those for the No. 2 net samples, while the percentage content of organic matter appears to be similar for both.

Differences in the percentage content of organic matter, estimated as per cent of the displacement weight, have been noted between coastal and offshore waters. Riley and Gorgy (1948) found that the coastal water zooplankton was considerably richer in organic content than the zooplankton of offshore waters. According to Riley, Stommel, and Bumpus (1949), the average for all offshore waters investigated is 4.8% of the displacement weight, while the coastal water zooplankton probably averages around 10%. Presumably the Sargasso Sea zooplankton is relatively poor in organic content due to the absence of fatty reserves (Riley and Gorgy). The mean per cent of organic matter for the B. I. S. zooplankton was 8.9%, the dry weight averaged 11.5%, and the ash 2.6% of the displacement weight. The mean water content was therefore 88.5%, somewhat higher than the 83% estimated by Harvey for Plymouth zooplankton. In general, therefore, the per cent of organic content of the B. I. S. zooplankton is similar to that of the coastal water plankton and averages around twice that of the zooplankton of offshore waters. This would be expected, since the amount of phytoplankton available was more than adequate for the quantity of zooplankton.

Zooplankton Productivity

It is possible to make an estimate of the mean rate of production of the zooplankton from the ratio of the total zooplankton carbon over the amount of carbon consumed per day minus the amount required. The carbon content of the zooplankton is assumed to be one half of the total organic matter. The mean displacement volume of the No. 10 net samples was 20.4 cc/m^2 of sea surface. According to Riley, Stommel, and Bumpus (1949: 67), an average zooplankton population filters about 63 cc/mg of displacement weight per day. Thus the zooplankton population of B. I. S. filtered $20.4 \times 1000 \times 63 = 1285$ l/day, or 4.3% of the total water column. Since the average phytoplankton production in the upper 20 m is estimated to be 25–30% per day, or 20% per day on the basis of a 30 m column, apparently the zooplankton eats only about one fifth of the phytoplankton that is produced.

As previously noted, the amount of total organic matter in the No. 10 net samples is obtained by multiplying the displacement volume by 8.9%, the mean per cent of the displacement weight of organic matter. The total carbon is one half of the result, 910 mg. The amount of carbon consumed per day is computed by multiplying the number of liters filtered by the mean number of Harvey units of phytoplankton by a conversion factor for the carbon content in mg per pigment unit (see Riley, Stommel, and Bumpus, 1949: 27) $= 1285 \times 11.2 \times 0.017 =$ 245 mg of carbon consumed per day. The estimated mean consumption is therefore $245/910 \times 100 = 27\%$ of the weight of the zooplankton carbon. The carbon requirement for respiration is 0.45% of the displacement weight per day. This figure is the mean of experiments by Riley on natural zooplankton populations collected in August and December 1947 from coastal waters outside B. I. S. (see Riley, Stommel, and Bumpus, 1949: 60). Thus the amount of carbon used in respiration is 92 mg/day or 37% of the carbon consumed. According to these figures, the zooplankton productivity could be 245 minus $92 = 153$ mg of carbon per day, or $153/910 \times 100 = 16.8\%$ per day. A similar answer is obtained, of course, if the data for the No. 2 net samples are used, but the questionable April and May figures must be excluded since they were not included in obtaining the mean per cent of organic matter. The No. 2 net zooplankton filtered 403 l of water per day. The mean carbon content determined from the analyses was 287 mg/m^2 of sea surface, 77 mg of carbon were consumed per day, 29 mg were used in respiration, leaving 48 mg of carbon as the net increase per day. The rate of production was therefore $48/287 \times 100 = 16.7\%$ per day. Harvey (1950) estimated a production rate of 10% per day for English Channel zooplankton, but this was based solely on the daily growth of *Calanus* from egg to adult and does not include the total population.

There is no assurance that the actual reproductive rate of the zooplankton is as high as is indicated by these theoretical estimates. The latter are intended to show only that the amount of phytoplankton in B. I. S. is sufficient to maintain rapid growth provided it is consumed and utilized at a normal rate. It does not appear that lack of food is responsible for the fact that the total quantity of zooplankton in B. I. S. is small when compared with such areas as Georges Bank and the Gulf of Maine.

The explanation probably lies in physical oceanographic circumstances. It has been shown that the zooplankton is not indigenous, but rather it is continually renewed by admixture with adjacent littoral and oceanic waters. Possibly some of the species that are introduced do not find the physical environment conducive to rapid growth and reproduction. Possibly others multiply rapidly, as indicated by the abundance of nauplii in the samples, but the same processes that bring zooplankton into the area quickly sweep them away before the zooplankton crop achieves large proportions. There is no way of knowing which of these two phenomena is quantitatively more significant; however, it is reasonable to suppose that the total crop would be larger if the circulation pattern permitted the maintenance of an indigenous population.

BIBLIOGRAPHY

Baker, H. M.

1938. Studies on the Cladocera of Monterey Bay. Proc. Calif. Acad. Sci., (4) *23:* 311–365.

Bigelow, H. B.

1928. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924), *40* (2): 1–509.

Bigelow, H. B. and Mary Sears

1939. Studies of the waters of the Continental Shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Harv. Mus. comp. Zool., *54* (4): 183–378.

Clarke, G. L. and D. J. Zinn

1937. Seasonal production of zooplankton off Woods Hole with special reference to Calanus finmarchicus. Biol. Bull. Woods Hole, *73:* 464–487.

Davis, C. C.

1944. On four species of Copepoda new to Chesapeake Bay, with a description of a new variety of *Paracalanus crassirostris* Dahl. Publ. Ches. biol. Lab., No. 61: 1–11.

Deevey, G. B.

1948. The zooplankton of Tisbury Great Pond. Bull. Bingham oceanogr. Coll., *12* (1): 1–44.

1952. A survey of the zooplankton of Block Island Sound, 1943 to 1946. Bull. Bingham oceanogr. Coll., *13* (3): 65–119.

Digby, P. S. B.

1950. The biology of the small planktonic copepods of Plymouth. J. Mar. biol. Ass. U. K., N. S. *29:* 393–438.

FISH, C. J.

1936a. The biology of Pseudocalanus minutus in the Gulf of Maine and Bay of Fundy. Biol. Bull. Woods Hole, *70:* 193–216.

1936b. The biology of Oithona similis in the Gulf of Maine and Bay of Fundy. Biol. Bull. Woods Hole, *71:* 168–187.

HARVEY, H. W.

1950. On the production of living matter in the sea off Plymouth. J. Mar. biol. Ass. U. K., N. S. *29:* 97–137.

MARSHALL, S. M.

1949. On the biology of the small copepods in Loch Striven. J. Mar. biol. Ass. U. K., N. S. *28:* 45–122.

REDFIELD, A. C.

1941. The effect of the circulation of water on the distribution of the calanoid community in the Gulf of Maine. Biol. Bull. Woods Hole, *80:* 86–110.

RILEY, G. A.

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

1952b. Phytoplankton of Block Island Sound, 1949. Bull. Bingham oceanogr. Coll., *13* (3): 40–64.

RILEY, G. A. AND D. F. BUMPUS

1946. Phytoplankton-zooplankton relationships on Georges Bank. J. Mar. Res., *6:* 33–47.

RILEY, G. A. AND SAMMY GORGY

1948. Quantitative studies of summer plankton populations of the western North Atlantic. J. Mar. Res., *7:* 100–121.

RILEY, G. A., HENRY STOMMEL AND D. F. BUMPUS

1949. Quantitative ecology of the plankton of the western North Atlantic. Bull. Bingham oceanogr. Coll., *12* (3): 1–169.

SKOGSBERG, TAGE

1920. Studies on marine ostracods. Pt. I. Zool. Bidr. Uppsala. Suppl.-Bd. I. 784 pp.

WIBORG, K. F.

1940. The production of zooplankton in the Oslo Fjord in 1933–1934 with special reference to the copepods. Hvalråd. Skr., No. 21: 1–85.

WILSON, C. B.

1932a. The copepods of the Woods Hole region Massachusetts. Bull. U. S. nat. Mus., No. 158: 1–635.

1932b. The copepod crustaceans of Chesapeake Bay. Proc. U. S. nat. Mus., *80* (15): 1–54.

THE PELAGIC FISH EGGS AND LARVAE OF BLOCK ISLAND SOUND

BY DANIEL MERRIMAN AND RUTH C. SCLAR

Bingham Oceanographic Laboratory

TABLE OF CONTENTS

ABSTRACT

This paper presents an account of the pelagic fish eggs and larvae taken in surface and bottom tows over a three-year period (1943–1946) in Block Island Sound. The surface tows were taken monthly; the bottom tows were taken at irregular intervals. Each species is discussed separately, with comments on methods of identification, abundance, spawning period, general life history, distribution, etc. A key to the fish eggs and larvae of the area by months is included. The data indicate that dominant year-classes of butterfish, weakfish and cunner originated in June–July 1944, and that successful spawning by these three species is correlated with high surface salinity. Catch records and available meteorological data from 1930 to 1948 support, though they do not establish as fact, the validity of these hypotheses.

INTRODUCTION

In August 1943 the staff of the Bingham Oceanographic Laboratory began an intensive study of the fish populations of the Block Island Sound area (hereafter referred to as B. I. S.). About 30 species of fish are caught with considerable regularity in the course of each annual cycle by commerical draggers operating in the region, and another 15 species are taken on occasion but are no more than casual members of the catch. Of this total only eight are important as regularly marketed forms: butterfish, scup, whiting, cod, hake, fluke or summer flounder, yellowtail or dab, and winter flounder; the last is the dominant element in the catch and the chief object of the relatively small draggers which work this area.

The present work on the fish eggs and larvae of B. I. S. is a part of the oceanographic survey of the general region. As described by Merriman and Warfel (1948), samples of fish caught by commercial fishermen operating modified otter trawls from one to 15 miles off eastern Connecticut and western Rhode Island were studied each month from August 1943 to July 1946, except on five occasions when weather, tie-ups, or illness caused a break in continuity. Surface plankton hauls and full field observations were taken as a matter of routine by staff members over this three-year period; on certain occasions more than one plankton haul was made at a station, or during the day, or in the course of a particular month. This paper deals with the fish eggs and larvae of some 40 surface tows. Also, from time to time during the 36-month span a stramin net was attached to the head-rope or door of the otter trawl in an effort to sample the plankton near the bottom; the fish eggs and larvae from these 13 hauls are also reported here. Table I lists the fish eggs and larvae taken in the surface and bottom hauls. The invertebrate zooplankton of these surface and bottom collections are discussed by Deevey in this issue (pp. 65–119), and reference should be made to table I and fig. 1 of her paper for the dates and localities of the hauls.

The general region of B. I. S. was originally chosen because of its accessibility and because its contained fishery is relatively small and rather clearly circumscribed. Obviously the problems of sampling, so critical to studies in marine biology, are far less complicated under these conditions than in larger fisheries extending over great areas. Even here, however, there are innumerable difficulties in collecting the basic material in sufficient quantities to give an adequate picture of the structure of the vertebrate and invertebrate populations. Hauls not only have to be taken at sufficiently frequent intervals to detect seasonal and other changes, but they must be of a size that is not

TABLE I. Scientific and Common Names of the Fish Whose Eggs and Larvae Were Taken in the 1943–1946 B. I. S. Plankton and Stramin-net Hauls. The Table Shows Whether the Eggs, the Larvae, or Both Eggs and Larvae Were Taken in Surface Hauls (S), Bottom Hauls (B), or at Both the Surface and the Bottom (SB). See Text Under Each Species.

	Eggs	*Larvae*
Clupea harengus: herring	....	S
Syngnathus peckianus: pipefish	....	S
Hippocampus hudsonius: seahorse	....	S
Scomber scombrus: mackerel	SB	S
Poronotus triacanthus: butterfish	SB	S
Stenotomus chrysops: scup, porgy	....	S
Cynoscion regalis: weakfish, squeteague, sea trout	SB	S
Tautogolabrus adspersus: cunner	S	SB
Tautoga onitis: tautog, blackfish	....	S
Myoxocephalus aeneus: brassy sculpin	....	B
Myoxocephalus octodecimspinosus: longhorn sculpin	....	S
Cyclopterus lumpus: lumpfish	....	B
Cryptocanthodes maculatus: wrymouth	....	S
Merluccius bilinearis: whiting, silver hake	....	B
Gadus morhua: cod	SB	SB
Urophycis spp.: hakes	....	S
Paralichthys dentatus: summer flounder, fluke	....	B
Limanda ferruginea: dab, yellowtail	....	SB
Lophopsetta aquosa: sand flounder, windowpane	....	B
Lophius americanus: angler, goosefish, monkfish	S	......

impractical, whether they be for fish, plankton, or bottom organisms. In order to gain a proper understanding of the marine biology of such a region, all parts of the population must be studied continuously over long periods of time. It is not enough to study a single fish, which perhaps shows signs of decline at the time. The interrelationships of all the component parts of the population as well as the basic physical and chemical oceanography of the area must be known. The paucity of such long term studies accounts in part for the lack of progress in marine fisheries work in this country in the past quarter of a century or more. There are no short cuts in this field. It is impossible to arrive at broad conclusions and sound generalizations until the fundamental information is at hand. The present paper represents a contribution to our knowledge of the vertebrate zooplankton of the B. I. S. region, and as such it provides a small step towards an understanding of the biological productivity of the area.

ACKNOWLEDGMENTS

The great majority of our plankton hauls were made from Ellery Thompson's dragger "Eleanor" out of Stonington, Connecticut. The staff members and graduate students in the Bingham Laboratory have been more than fortunate in their association with Captain Thompson; they have been blessed with his constant cooperation and interest, with an unfailing and generous hospitality and with a close and lasting friendship. We are also grateful to Captain Harold McLaughlin, from whose dragger "Marise" a number of plankton collections were made, and to Captain A. L. Roderick of the "Rita." We here record our indebtedness to J. B. Bindloss of Stonington, who gave much assistance in the initial phases of our study of B. I. S. by providing us with basic information on the fishery and by introducing us to the above-mentioned skippers. Herbert E. Warfel, now Headmaster of the American School at Manila, participated in all the field trips and, together with the senior author, made the collections.

Gordon A. Riley and Sarah B. Wheatland both gave generously of their time and advice in the preparation of the Discussion. We are also indebted to William F. Royce and Edgar L. Arnold, Jr., U. S. Fish and Wildlife Service, for the loan of many specimens of fish eggs and larvae from the Woods Hole collections for comparative purposes. In connection with the confusing problem of distinguishing between the eggs and early larvae of the butterfish, *Poronotus triacanthus*, and the squirrel hake, *Urophycis chuss* (see pp. 183–185), we record with gratitude the assistance of Miss Louella E. Cable, U. S. Fish and Wildlife Service, and Dr. Charles J. Fish, Director of the Narragansett Marine Laboratory (University of Rhode Island), Kingston, R. I. The Connecticut State Board of Fisheries and Game, through annual grants, helped to support the field work on which this and other studies of the B. I. S. area are based. Reference to Deevey (1952) provides further acknowledgment in which we also share.

MATERIALS AND METHODS

The surface plankton tows which yielded the eggs and larvae for this study were taken at least once a month over a period of three years (1943–1946), with the exception of January, February and December 1945, and April and July 1946 (see Deevey, 1952; table I and fig. 1). As already stated by Deevey, all surface samples were collected with a No. 2 silk net measuring one foot in diameter and approximately two feet in length. This net was towed 75–100 feet directly behind the stern of a commercial vessel dragging a large otter trawl over the sea bottom at approximately two miles an hour. Under these circumstances the relatively high speed of the engine caused a turbulent wake through which the plankton net was towed, with the probable result that the organisms throughout the upper 10 or 15 feet of water were sampled rather than only those in strictly surface layers. The wake of the vessel in these circumstances is often highly irregular, depending on weather and water conditions, and it is certain that the plankton net did not strain all the water through which it passed at a constant rate. Indeed, under the worst conditions it appeared that occasional violent swirls of water actually washed some of the plankton out of the net. Similarly, in rough weather, particularly with a following swell, the pull on the towing line varied from a heavy strain to a total slack, probably giving rise to the conditions which Barnes (1949) has pictured to show the ejection of water from a plankton net when the forward speed is reduced materially. Deevey (1952: 70–73) has further emphasized the shortcomings of the methods of sampling the plankton population used in this study, and we concur with her comments.

Yet there is considerable evidence from the numbers of fish eggs and larvae of different species in successive hauls at the same station on the same date that the sampling was surprisingly satisfactory at times.

Treating the pelagic eggs first, on November 21, 1943, two 10-minute hauls were taken; there were 77 cod eggs in the first and 47 in the second. On July 16, 1944, both hauls contained eggs which were identified as butterfish, weakfish, and cunner; the numbers of eggs with which each species was represented in each haul were as follows:

	Haul 1 (16 mins.)	*Haul 2 (17 mins.)*
Butterfish	312	296
Weakfish	369	344
Cunner	155	164

Three hauls on March 5, 1945, 20, 10 and 15 minutes long respectively, produced a total of 11 cod eggs—four from the first haul, four from the second, and three from the third. Turning to the fish larvae, the herring taken on November 21, 1943 were divided equally between the two hauls (four and four). On July 16, 1944, the larval hake were divided four and two, weakfish 11 and 83, cunner 51 and 10, and tautog three and zero between the first and second hauls. On March 5, 1945, the two larval longhorn sculpins were both taken in the first haul. It appears from the above that a one-foot plankton net, as towed under the conditions outlined, is capable of sampling the surface fish eggs and larvae with fair consistency, especially where large numbers are involved; it is also clear that much more refined methods are necessary to achieve a uniformly accurate sampling of the numbers and distribution of the eggs and larvae by months. However, even the most careful and precise methods might not produce significantly better results in B. I. S., for as Riley (1952) shows, the water of the whole area is subject to such constant exchange with Atlantic water on the one hand and with Long Island Sound water on the other that it is in a constant state of flux.

Most of the surface tows were 15 minutes in length. When the haul was for a shorter or longer time we have not adjusted the actual number of eggs or larvae to a 15-minute period, as did Deevey (1952); rather, the true figures and the length of the tow are recorded (Tables II and IV). On dates when two or more hauls were taken at one station, the counts as well as the towing periods are listed in the tables as one.

Tables III and V show the results of the bottom stramin-net hauls. This net, one foot in diameter, was attached to the head rope or door of the commercial trawl in an attempt to sample the water two to five feet off the bottom. The duration of the tow was of course governed by the length of the commercial haul, and the contents of the stramin net were not necessarily restricted to the near-bottom fauna, since it unquestionably fished effectively during both the descent and ascent of the trawl. Thus, at both ends of the operation of setting and hauling the commercial gear, the stramin net fished the surface waters for at least several minutes on every occasion. As with the surface hauls, the tables show the actual number of eggs and larvae taken as well as the length of each tow in minutes; similarly, when more than one haul was made at one station the numbers of eggs or larvae are combined as are also the towing times. Such duplicate hauls were made only twice with the bottom stramin net, on May 18, 1944 and October 15, 1945; neither haul on the latter date yielded any eggs or larvae. The yield on the fomer date from the first and second hauls respectively was: mackerel eggs, three and one; brassy sculpin larvae, three and zero; lumpfish larvae, seven and zero; cod larvae, three and zero. All the species of eggs taken in bottom hauls (Table III) were also represented in the much shorter surface hauls (Table II) at the same station on the same date. In four out of five of these cases the number of eggs was greater in the surface hauls, and we assume that these eggs were taken in the stramin net during the descent or ascent of the trawl. On November 19, 1944, the stramin net took 45 cod eggs whereas the matching surface haul yielded only 10; even here there is no clear evidence that any of these eggs were actually taken in bottom waters. However, of the eight species of fish larvae taken in the bottom hauls, only three were also represented in surface tows, and it seems probable that the stramin net took at least five species which are normally found only in the region of the bottom at this stage of development—the brassy sculpin, lumpfish, whiting, fluke and sand flounder (Tables I and V).

Of the 40 surface plankton hauls made in the course of this study, one (August 29, 1943) was discarded because the net tore, and six contained no fish eggs—Oct. 31, 1943, March 19, 1944, October 15 and November 11, 1945, and March 24 and May 6, 1946 (Table II). Fish larvae were taken in 26 of the 39 surface hauls (Table IV). Eggs were taken in only five of the 13 bottom stramin-net hauls (Table III); larvae were present in six of the 13 hauls (Table V).

In the laboratory the fish eggs and larvae were sorted from the rest of the zooplankton by detailed examination of each entire haul under the dissecting microscope. The fish eggs and larvae in each sample were then separated into the constituent species. Preliminary sorting was accomplished on the basis of general appearance, diameter measurements of the eggs, presence or absence of oil globules, size and number of such globules if present, pigment pattern and color, fin-ray counts, etc. Identification to genus and species then followed on the basis of such key references as Bigelow and Welsh (1925), Dannevig (1919), Hildebrand and Cable (1934, 1938), and Kuntz and Radcliffe (1917). General information on the fishes of the region, their development, relative abundance, spawning seasons, etc., in such works as Bigelow and Welsh (1925), Breder (1929), Hildebrand and Schroeder (1928), Merriman and Warfel (1948), Nichols and Breder (1926), Perlmutter (1939), and Warfel and Merriman (1944), plus our own local knowledge, often provided the clues by which certain species were eliminated and others were finally identified. Discussion under each species indicates where there was an element of doubt in the identification.

In all of the samples all larvae and, with the exception of one pair of hauls, all fish eggs were used for analysis. Only 10% of the total number of eggs were examined in detail from the two surface hauls on June 23, 1944. Of approximately 19,000 eggs contained in this sample (the two hauls were preserved as one), a representative tenth was obtained by conventional methods involving a grid technique. Thus the total numbers given for the different species of fish eggs in this haul in Table II were derived by multiplying by ten the portion of the sample examined. This entire haul was scanned for larvae so that the actual number of newly hatched fish taken on this date is listed in Table IV.

The numbers of eggs and larvae listed in Tables II–V are true counts for each species whenever the total number in a single haul was under 500. When the number of eggs was over 500 the counts are accurate to within at least 5%, as indicated by the plus and minus signs in Table II.

The diameters of the eggs and the oil globules, as mentioned in the discussion of the different species, were measured with an ocular micrometer and are accurate to the nearest one hundredth of a millimeter. Checks on the accuracy were made by measuring a sample on two successive days and comparing the results. In small samples all the eggs were measured; at least 25% were measured in samples up to 250 in number, and a minimum of 10% of the largest samples was measured. Measurements of the smaller larvae were made with the ocular micrometer; the larger individuals (over 15 mm) were measured on a millimeter scale. Accurate length measurements were often impossible owing to distortion or curling of the specimens (for example, see discussion of butterfish, weakfish and cunner larvae), but unless otherwise stated the lengths given are accurate to the nearest 0.2 mm.

The preservation of samples in formalin on board ship was not performed in a uniform manner in that the strength of the solution varied from 5–10%. This strength, which is greater than that which should be used for plankton samples, almost certainly accounts for the distortion of certain larvae. We also mention the method of preservation here since reference to the account by species will show that we have extended the known diameter range of certain fish eggs (see under mackerel, weakfish, and cunner) both below and above the previously recorded limits.

THE INDIVIDUAL SPECIES

Clupea harengus

EGGS: The eggs are demersal, as described by Bigelow and Welsh, and appeared in none of the plankton hauls.

LARVAE: Herring larvae were taken only in surface hauls (Tables I and V). One taken on September 12, 1943 was 11 mm long, eight taken on November 21, 1943 were 12–26 mm, six taken on December 18, 1944 were 14–27 mm, and one taken on January 14, 1946 was 30 mm long. These measurements are only approximate since most of the specimens were curled or otherwise distorted.

In discussing the spawning period of the herring, Bigelow and Welsh state: "In Machias Bay [Maine] . . . herring spawn . . . from mid-July until the end of September. Passing thence westward we find the breeding period progressively later and shorter—mid-August until October about Petit Manan and near Mount Desert; mid-September until the end of October near Casco Bay and off Wood Island; September 20 until about November 1 in Ipswich Bay; the month of October in Massachusetts Bay; while west of Cape Cod the herring do not begin to spawn until mid or late October, with the major production of eggs about the 1st of November." Breder (1929) says: "They spawn in the fall, in the latitude of New York in November." It would appear from the length of herring larvae taken in our collections in September and November that some spawning occurs in southern New

TABLE II. FISH EGGS TAKEN IN SURFACE PLANKTON HAULS

Date	*Length of haul in minutes*	*Scomber scombrus*	*Poronotus triacanthus*	*Cynoscion regalis*	*Tautogolabrus adspersus*	*Gadus morhua*	*Lophius americanus*
1943–1944							
Aug. 29	Sample discarded—net tore						
Sept. 12	20	—	54	43	—	—	—
Oct. 31	10	—	—	—	—	—	—
Nov. 21	20*	—	—	—	—	124	—
Dec. 19	15	—	—	—	—	310	—
Jan. 2	15	—	—	—	—	28	—
Jan. 23	15	—	—	—	—	74	—
Feb. 20	15	—	—	—	—	7	—
Feb. 29	15	—	—	—	—	24	—
Mar. 19	15	—	—	—	—	—	—
Apr. 19	15	3	—	—	—	—	—
May 18	15	10	—	—	—	—	—
June 23†	30*	—	3,360 ±	10,270 ±	5,210 ±	—	10?
July 16	33*	—	608	713	319	—	—
July 23	15	—	188	1,000 ±	865 ±	—	—
1944–1945							
Aug. 13	20	—	87	89	17	—	—
Sept. 10	15	—	4	83	—	—	—
Oct. 26	15	—	—	4	—	—	—
Nov. 19	16	—	—	—	—	10	—
Dec. 18	25	—	—	—	—	133	—
Jan.	No haul taken						
Feb.	No haul taken						
Mar. 5	45*	—	—	—	—	11	—
Apr. 16	15	40	—	—	—	—	—
May 27	15	207	—	—	—	—	—
June 18	15	47	—	17	290	—	—
July 17	15	—	4	135	2,025 ±	—	—
1945–1946							
Aug. 21	10	—	2	5	1	—	—
Sept. 9	15	—	6	80	—	—	—
Oct. 15	15	—	—	—	—	—	—
Nov. 11	15	—	—	—	—	—	—
Dec.	No haul taken						
Jan. 14	15?	—	—	—	—	10	—
Feb. 19	15	—	—	—	—	1	—
Mar. 24	15	—	—	—	—	—	—
Apr.	No haul taken						
May 6	30*	—	—	—	—	—	—
June 9	15	24	46	2	114	—	—
July	No haul taken						
Totals		331	4,359	12,441	8,841	732	10

* More than one haul; Nov. 21, '43, two 10 min. tows; June 23, '44, two 15 min. tows; July 16, '44, one 16 min. and one 17 min. tow; Mar. 5, '45, one 20 min., one 10, and one 15 min. tow; May 6, '46, two 15 min. tows. Counts are totals of all hauls on any one day.

† One-tenth of sample examined; counts multiplied by 10 throughout.

TABLE III.—FISH EGGS TAKEN IN BOTTOM STRAMIN-NET HAULS

Date	*Length of haul in minutes*	*Scomber scombrus*	*Poronotus triacanthus*	*Cynoscion regalis*	*Gadus morhua*
1943–1944					
Aug. 29	Sample discarded—net tore				
Sept. 12	No bottom haul taken				
Oct. 31	No bottom haul taken				
Nov. 21	No bottom haul taken				
Dec. 19	No bottom haul taken				
Jan. 2	No bottom haul taken				
Jan. 23	No bottom haul taken				
Feb. 20	No bottom haul taken				
Feb. 29	No bottom haul taken				
Mar. 19	No bottom haul taken				
Apr. 19	No bottom haul taken				
May 18	145*	4	—	—	—
June 23	No bottom haul taken				
July 16	No bottom haul taken				
July 23	90	—	27	8	—
1944–1945					
Aug. 13	65	—	—	—	—
Sept. 10	60	—	—	—	—
Oct. 26	No bottom haul taken				
Nov. 19	75	—	—	—	45
Dec. 18	No bottom haul taken				
Jan.	No haul taken				
Feb.	No haul taken				
Mar. 5	90	—	—	—	1
Apr. 16	45?	—	—	—	—
May 27	70	—	—	—	—
June 18	No bottom haul taken				
July 17	No bottom haul taken				
1945–1946					
Aug. 21	No bottom haul taken				
Sept. 9	No bottom haul taken				
Oct. 15	145*	—	—	—	—
Nov. 11	No bottom haul taken				
Dec.	No haul taken				
Jan. 14	60	—	—	—	—
Feb. 19	No bottom haul taken				
Mar. 24	No bottom haul taken				
Apr.	No haul taken				
May 6	90	—	—	—	—
June 9	No bottom haul taken				
July	No haul taken				
Totals		4	27	8	46

* Two hauls; May 18, '44, one 60 and one 85 mins.; Oct. 15, '45, one 70 and one 75 mins.

England waters in the late summer and early fall. Further evidence of this comes from observations by Perlmutter (1939) who took hatched

TABLE IV.—FISH LARVAE TAKEN IN SURFACE PLANKTON HAULS

Date	*Length of haul in minutes*	*Clupea harengus*	*Syngnathus peckianus*	*Hippocampus hudsonius*	*Scomber scombrus*	*Poronotus triacanthus*	*Stenotomus chrysops*	*Cynoscion regalis*	*Tautogolabrus adspersus*	*Tautoga onitis*	*Myoxocephalus octodecimspinosus*	*Cryptocanthodes maculatus*	*Gadus morhua*	*Urophycis* spp.	*Limanda ferruginea*
1943–1944															
Aug. 29	Sample discarded—net tore														
Sept. 12	20	1	—	—	—	1	—	—	—	—	—	—	—	28	—
Oct. 31	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nov. 21	20*	8	—	—	—	—	—	—	—	—	—	—	—	2	—
Dec. 19	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jan. 2	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jan. 23	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feb. 20	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Feb. 29	15	—	—	—	—	—	—	—	—	—	14	—	—	—	—
Mar. 19	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apr. 19	15	—	—	—	—	—	—	—	—	—	1	2	—	—	—
May 18	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
June 23	30*	—	—	—	7	—	—	—	19	—	—	—	—	6	—
July 16	33*	—	1	—	—	—	1	94	61	3	—	—	—	6	—
July 23	15	—	—	—	—	—	—	3	10	—	—	—	—	5	—
1944–1945															
Aug. 13	20	—	—	—	—	—	—	—	—	—	—	—	—	6	3
Sept. 10	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oct. 26	15	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Nov. 19	16	—	—	—	—	—	—	—	—	—	—	—	—	4	—
Dec. 18	25	6	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE IV—*Continued*

Date	*Length of haul in minutes*	*Clupea harengus*	*Syngnathus peckianus*	*Hippocampus hudsonius*	*Scomber scombrus*	*Poronotus triacanthus*	*Stenotomus chrysops*	*Cynoscion regalis*	*Tautogolabrus adspersus*	*Tautoga onitis*	*Myoxocephalus octodecimspinosus*	*Cryptocanthodes maculatus*	*Gadus morhua*	*Urophycis* spp.	*Limanda ferruginea*
1944–1945—*Cont.*															
Jan.	No haul taken														
Feb.	No haul taken														
Mar. 5	45*	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Apr. 16	15	—	—	—	—	—	—	—	—	—	—	—	1	—	—
May 27	15	—	—	—	—	1	—	—	—	—	—	—	—	1	—
June 18	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
July 17	15	—	—	1	—	—	—	—	—	—	—	—	—	1	—
1945–1946															
Aug. 21	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sept. 9	15	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Oct. 15	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nov. 11	15	—	—	—	—	—	—	—	—	—	—	—	—	10	—
Dec.	No haul taken														
Jan. 14	15?	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Feb. 19	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mar. 24	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Apr.	No haul taken														
May 6	30*	—	—	—	—	—	—	—	—	—	—	—	1	—	—
June 9	15	—	—	—	—	—	—	—	—	—	—	—	—	2	—
July	No haul taken														
Totals		16	1	1	7	2	1	97	90	3	17	2	2	73	3

* See footnote to Table II.

TABLE V.—FISH LARVAE TAKEN IN BOTTOM STRAMIN-NET HAULS

Date	*Length of haul in minutes*	*Tautogolabrus adspersus*	*Myoxocephalus aeneus*	*Cyclopterus lumpus*	*Merluccius bilinearis*	*Gadus morhua*	*Paralichthys dentatus*	*Limanda ferruginea*	*Lophopsetta aquosa*
1943–1944									
Aug. 29	No bottom haul taken								
Sept. 12	No bottom haul taken								
Oct. 31	No bottom haul taken								
Nov. 21	No bottom haul taken								
Dec. 19	No bottom haul taken								
Jan. 2	No bottom haul taken								
Jan. 23	No bottom haul taken								
Feb. 20	No bottom haul taken								
Feb. 29	No bottom haul taken								
Mar. 19	No bottom haul taken								
Apr. 19	No bottom haul taken								
May 18	145*	—	3	7	—	3	—	—	—
June 23	No bottom haul taken								
July 16	No bottom haul taken								
July 23	90	2	—	—	11	—	—	1	4
1944–1945									
Aug. 13	65	—	—	—	—	—	—	—	—
Sept. 10	60	—	—	—	—	—	—	—	—
Oct. 26	No bottom haul taken								
Nov. 19	75	—	—	—	5	—	4	—	—
Dec. 18	No bottom haul taken								
Jan.	No haul taken								
Feb.	No haul taken								
Mar. 5	90	—	—	—	—	—	—	—	—
Apr. 16	45?	—	—	—	—	—	—	—	—
May 27	70	—	—	4	—	2	—	40	—
June 18	No bottom haul taken								
July 17	No bottom haul taken								
1945–1946									
Aug. 21	No bottom haul taken								
Sept. 9	No bottom haul taken								
Oct. 15	145*	—	—	—	—	—	—	—	—
Nov. 11	No bottom haul taken								
Dec.	No haul taken								
Jan. 14	60	—	—	—	—	—	—	—	—
Feb. 19	No bottom haul taken								
Mar. 24	No bottom haul taken								
Apr.	No haul taken								
May 6	90	—	4	5	—	—	—	—	—
June 9	No bottom haul taken								
July	No haul taken								
Totals	—	2	7	16	16	5	4	41	4

* See footnote to Table III.

herring larvae on the western south shore of Long Island, New York, during October.

The distinction of these larvae from those of the menhaden (*Brevoortia tyrannus*) and the three species of anchovies (*Anchoa hepsetus hepsetus*, *Anchoa mitchilli mitchilli* and *Anchoviella eurystole*) listed by Hildebrand (1943) as occurring in these waters is likely to present certain difficulties. The spawning periods are similar, and the long slender body, general arrangement of fins, convoluted intestine, and superficial appearance are characters common to all five of these larval forms. On closer examination the two *Anchoa* species are eliminated by the fact that the anal fin originates anterior to a vertical line from the base of the last dorsal fin ray. In the herring, menhaden and *Anchoviella eurystole* the whole anal fin is distinctly posterior to the dorsal; however, over the range of lengths here considered there is a much larger gap between the anal and dorsal in the herring than in the menhaden and silvery anchovy. This fact, combined with the slightly more slender body form of the herring, its sharply delineated myotomes, absence of pigment pattern, relative size of eye, and general shape of head, made identification of these larvae fairly positive. Additional evidence was derived from the respective lengths at which the dorsal and anal fins are formed in the larvae of these three species; Bigelow and Welsh, and Kuntz and Radcliffe (1917) show that in the herring these fins, particularly the anal, are first formed at greater lengths than in the menhaden or silvery anchovy. Final evidence came from dorsal and anal fin-ray counts—herring: D. 18, A. 17 (Jordan and Evermann, 1896); menhaden: D. 19, A. 20 (Jordan and Evermann, 1896); *A. eurystole:* D. 13–16, A. 15–18 (Hildebrand, 1943); our counts on the three largest larvae fitted the requirements for the herring.

Syngnathus peckianus

EGGS: The male of this species carries the developing eggs in a "marsupial" pouch, and according to Bigelow and Welsh the young are retained in the brood pouch until they are 8 or 9 mm long.

LARVAE: Only one specimen 46 mm in length was taken, that on July 16, 1944 (Table IV). This fish was either the product of early spawning that year or of late reproduction in the summer of 1943; its size agrees well with large numbers of individuals taken in shore hauls in July 1942 by Warfel and Merriman (1944), who include a discussion of the length of the spawning period, rate of growth, etc. This species is a shallow water form, and we would not expect its larvae to be taken far offshore in any abundance; the station where this specimen was taken was only 1½ miles from the Rhode Island Coast.

Obviously the identification of this species presents no difficulties whatsoever.

Reference to the Key (p. 204) shows that this species is listed for only the month of July. Actually the pelagic larvae, though few in offshore waters, probably occur from June (see Nichols and Breder, 1926) through August and perhaps September and even October (see Warfel and Merriman, 1944). Perlmutter (1939) reported taking postlarvae and juveniles in Long Island waters from May through October.

Hippocampus hudsonius

EGGS: The breeding habits of this species are similar to those of the pipefish, and the young apparently do not become pelagic until they are approximately 10 mm long (Bigelow and Welsh).

LARVAE: A single specimen, 28 mm in length, was taken on July 17, 1945. Bigelow and Welsh state that it breeds in the summer; from the length of our specimen we suspect that it was liberated from the paternal pouch in June, thus indicating a late spring mating in these waters. Here again this species appears to be a shallow water form, and we would not expect to find the larvae far offshore; this specimen was taken 1½ miles S.E. of Watch Hill, Rhode Island (at Station 10; see Deevey, 1952: fig. 1).

The identification of larval sea horses of this size presents no difficulties, the angle of the head serving to distinguish this species from pipefish at a glance.

The Key (p. 204) shows that it is listed for only the month of July. Pelagic larvae probably occur in southern New England waters from June to August.

Scomber scombrus

EGGS: Mackerel eggs were taken in both surface and bottom hauls (Table I). However, the fact that only four mackerel eggs were taken in the stramin net over the three-year period—as opposed to 331 in the surface plankton hauls (Tables II and III)—would seem to indicate that the eggs of this species are not abundant in deeper waters; indeed it is more likely that the few eggs recorded in the bottom hauls were actually taken as the net was being lowered or hauled in. This is in agreement with Sette (1943), who found that the number of mackerel eggs decrease rapidly with depth.

Mackerel eggs were taken in surface plankton hauls in small numbers in April and May 1944 and June 1946, and in considerable amounts in April, May and June 1945 (Table II). According to Bigelow and Welsh the height of the spawning season in Massachusetts Bay is the last half of May and the month of June. Sette (1943), who states that spawning takes place during the month of May off the New Jersey Coast, says, "So far as is now known, no spawning takes place in the enclosed waters of the bays and sounds west and south of Block Island." If our identification of the eggs is correct, spawning may begin in southern New England waters as early as mid-April. Sette (1943) found mackerel eggs in water as cool as 7.3° C. The surface temperature on April 19, 1944 was 4.3° C and on April 16, 1945 6.4° C at the stations where mackerel eggs were taken. It is possible that these eggs may have been brought into the area from warmer water further offshore, but it seems more likely that a limited amount of spawning does take place in B. I. S. (though ". . . negligible in quantity compared with the spawning in open waters") and that reproduction early in the season may occur at temperatures only slightly above 4.0° C.

We have not been able to check on the degree of ripeness of mature mackerel in this region in April, since the adult of this species was taken on only one occasion in the 3-year sample trawl hauls (Merriman and Warfel, 1948); this is not surprising since the mackerel is a pelagic form which would only be taken by such gear on occasion.

The positive identification of mackerel eggs caused us some difficulty. On the basis of spawning season and egg diameter, the only other species in this area with which the mackerel egg might be confused are the sea robin (*Prionotus carolinus*) and the weakfish. The sea robin is practically eliminated from consideration because its spawning season overlaps only the latter part of that of the mackerel; Kuntz and Radcliffe (1917) say it spawns in June, July and early August, and this is confirmed by the more recent work of Marshall (1946) who, however, suggests ". . . an even longer period with possible variations as the seasons vary." Furthermore, the large number of oil globules characteristic of this species would serve to distinguish its eggs from those of mackerel or weakfish had they been present in the sample.

We are therefore left with the distinction between mackerel and weakfish. In the course of the original sorting of the egg samples, one of us (R. S.) at first placed in the same category all the eggs which we subsequently divided into mackerel and weakfish. On more careful inspection she divided them between these two species almost exactly as shown in Table II, but she was dubious about the basis of separation. At that stage she made length-frequency curves of the egg diameters of the samples tentatively assigned to these two species; the other author (D. M.) then made tentative identification of the samples on the basis of the shape of these curves. According to Hildebrand and Cable (1934) the diameter of weakfish eggs ranges from 0.7 to 1.3 mm; Bigelow and Welsh give a range for mackerel eggs of from 0.97 to 1.38 mm, in which Sette (1943) concurs. The length frequencies of the diameters of the egg samples eventually identified as weakfish quite consistently showed a bimodal distribution, with peaks at the lower and near the upper ends of the range (see p. 188); the samples assigned to the mackerel category showed a more restricted unimodal distribution, the peaks falling at 1.2 mm. These characteristic differences in the shape of the curves, in conjunction with the dates at which the various samples were collected (compare mackerel and weakfish in Table II) and their known spawning periods enabled D. M. to separate mackerel and weakfish eggs on a tentative basis without examining them under the microscope. Subsequently he separated these samples into two categories by microscopic examination without reference to the conclusions obtained from the length-frequency analyses or to earlier conclusions reached by R. S. Identifications from these three independent sources were in excellent agreement. The eggs identified as belonging to the mackerel usually had a degree of opacity which was not apparent in weakfish samples, and the diameter of the weakfish oil globules did not reach the lower end of the known range of diameter for mackerel oil globules (see Key, p. 203). In both weakfish and mackerel eggs a high percentage was in an early stage of development. If our identification of mackerel is correct, the lower limit of the egg diameter has to be extended to 0.88 mm.

LARVAE: Mackerel larvae were taken only in the surface plankton hauls and on only one occasion, June 23, 1944, when seven specimens were present. This was the one date on which adult mackerel were taken in the 3-year sample hauls (Merriman and Warfel, 1948), and this date also follows the two months in which mackerel eggs were taken in that year. The larvae, identified from illustrations in Bigelow and Welsh, measured respectively 5.0 (2 individuals), 6.0, 7.0, 9.5 (2 individuals), and 24.0 mm. The large specimen was easily recognized, since dorsal and anal finlets were already developed; this individual also gives credence to the belief that spawning occurs as early as April in this latitude, since Sette (1943) found that mackerel hatched in early May were 22.0 mm long by July 1.

Poronotus triacanthus

The identification of eggs and larvae of *Poronotus triacanthus* presents certain difficulties owing to confusion between this species and the squirrel hake, *Urophycis chuss*. Kuntz and Radcliffe (1917) described and illustrated what they believed to be the eggs and larvae of butterfish, and Bigelow and Welsh used some of their illustrations in "Fishes of the Gulf of Maine." However, Perlmutter (1939) states: "In the process of identifying butterfish eggs and larvae, the author discovered that the development of the squirrel ling, *Urophycis chuss*, had been erroneously described by Kuntz and Radcliffe . . . as the development of the butterfish, *Poronotus triacanthus*. The author was informed later that Sette, Pearson, Hildebrand and Cable had also recognized this error." Hildebrand and Cable (1938), in their description of the eggs and young of *Urophycis chuss*, make no reference to Kuntz and Radcliffe (1917) in this connection, but if we assume that Kuntz and Radcliffe's illustrations really are of squirrel hake they should at least bear reasonable similarity to the drawings of the same species in Hildebrand and Cable. Comparison of Kuntz and Radcliffe's figs. 60–62 with Hildebrand and Cable's figs. 124–127 illustrate nicely some of the difficulties which beset the ichthyologist who tries to make positive identification of pelagic fish eggs and larvae from published descriptions. These difficulties are even better illustrated by the sketches of Perlmutter (1939), especially with regard to differentiating between the butterfish and squirrel hake egg. In all events, assuming that Perlmutter (1939) and Pearson (1941) are correct in stating that Kuntz and Radcliffe's *P. triacanthus* is actually *U. chuss*, the only illustration of the butterfish egg in the literature is that by Perlmutter, and since this is not adequate by itself, we must turn to other means of identification. Although Perlmutter does not give any measurements, we assume that butterfish and squirrel hake eggs have similar diameters, a fact which Dr. Charles J. Fish has confirmed in a personal communication to us. The diameters of the eggs in our samples ranged from 0.7 to 0.8 mm; a single oil globule was generally present, but not infrequently there were a number of what appeared to be smaller oil globules[1] in the advanced developmental stages, the diameter range (including the smaller globules) being from 0.10 to 0.25 mm.

Our samples, which, by their similarity throughout, are almost certainly composed of eggs of the same species, were compared with the illustrations of Kuntz and Radcliffe (1917), Hildebrand and Cable (1938) and Perlmutter (1939). There are significant differences from the eggs of *U. chuss.* 1) The pigmentation of the dorsal surface of the embryos at different stages is less dense—in distribution and actual numbers and sizes of chromatophores. 2) There are no chromatophores on the ventral surface of the embryo as shown in Hildebrand and Cable's fig. 125. 3) The oil globule is rarely pigmented, which is in contrast to the condition shown in both Kuntz and Radcliffe and in Hildebrand and Cable (Perlmutter's drawings do not show the oil globule). 4) The oil globule in our samples never lies under the abdomen as described by Hildebrand and Cable; most commonly it is close to or associated with the caudal end of the embryo. 5) The yolk varies from being completely unpigmented to having the sparse pigmentation shown by Perlmutter; chromatophores are never as abundant as indicated for *U. chuss* by Kuntz and Radcliffe, Hildebrand and Cable, or Perlmutter. 6) The diameter of the true oil globule (excluding the smaller oil droplets mentioned previously) is indicative of *Poronotus* rather than *Urophycis* according to measurements on specimens taken in the Woods Hole region (Dr. Fish, personal communication). In general, the range for *Poronotus* is 0.17–0.2 mm and that for *Urophycis* 0.15–0.17 mm; our own specimens show a clear peak in diameters of the large central oil globule at 0.2 mm, apparently somewhat above the top limit for *Urophycis*.

In view of these differences, even though most of the criteria are relative and although positively identified eggs of *U. chuss* were not

---

[1] In connection with these smaller oil globules, Dr. Fish (personal communication, V/15/'51), who kindly examined our eggs, writes: "In other eggs oil had separated out in small yellowish droplets on and in the yolk, and in some cases even within the large oil globule. I first took these to be small oil globules, but the occurrence in only a portion of the eggs in certain vials in which all were obviously of the same species, the difference in color and appearance of the droplets as compared with the single large globule, and their similarity to the oil which often settles out in plankton samples containing a high proportion of *Calanus finmarchicus*, makes me certain that they were formed after the preservation of the samples."

available for direct comparison, it seems quite certain that our eggs are truly those of the butterfish, *Poronotus triacanthus*. However, in all fairness to the argument we must point out certain contrary bits of evidence. First, despite the abundance of eggs identified as butterfish (Table II), relatively few butterfish larvae were taken (Table IV); and conversely, although the number of larvae identified as *Urophycis* spp. was many times greater than those identified as butterfish, no hake eggs appeared in the plankton catches. Second, some of the reasons for believing that these eggs are those of *Poronotus triacanthus*, as indicated above, are based on the degree of pigmentation—or rather, the lack of pigmentation compared with that in *Urophycis*. The possibility that chromatophores may have disappeared during the storage period has to be considered. Had any of the eggs contained late embryos about to hatch, this problem could have been clarified with certainty, but unfortunately such was not the case. Dr. Fish (personal communication, V/31/1951) wrote, "If it can be assumed that chromatophores would not have disappeared in preservation then I would say that all of your samples are apparently butterfish, because Bigelow's records of *Urophycis* egg development were undoubtedly made with known eggs." Third, Miss Cable, who also examined our samples, wrote us (personal communication, III/28/1950), "I . . . find some differences between them and the published drawings of *Urophycis chuss* (Hildebrand and Cable, 1938: 615–16) but think they may be, nevertheless, eggs of that species." However, she went on to say that the eggs of neither *U. chuss* nor *P. triacanthus* were available to Hildebrand and Cable, who worked from the drawings of *U. chuss* by W. W. Welsh, who, in turn, had obtained the eggs directly from the fish and had fertilized and hatched them at the Gloucester hatchery in the summer of 1912; she ended her letter by saying, "You still have to make the final decision."

It seems to us that the preponderance of evidence clearly favors the assignment of these eggs to the butterfish, *Poronotus triacanthus;* further indication that this view is probably correct is to be found in the following discussion on spawning.

EGGS: The eggs of the butterfish were taken in a number of surface plankton hauls (Table II) and also in one bottom stramin-net haul; the latter, made on July 23, 1944, contained 27 eggs. In view of the large numbers of eggs of this species in the June and July 1944 surface hauls it seems reasonable to assume that the few eggs in this bottom haul were actually taken in the upper water layers as the net was being set or brought back to the boat. It is clear that the eggs of this species are characteristic of the near-surface waters.

Our samples of eggs were taken over the three-year period in June, July, August and September, with the great majority in June and July. Bigelow and Welsh state that the spawning season in the Gulf of Maine is from June through August, and Nichols and Breder (1926) name June as the month in which butterfish spawn in southern New England waters. Our own observations on ripe fish in B. I. S. in recent years place the peak of spawning in late June and July, a fact which provides added evidence that these eggs are those of the butterfish. However, during these months the fish does not seem to be as abundant in this area as in the late summer and fall (Merriman and Warfel, 1948), and it seems probable that spawning may take place further offshore and that the eggs are carried into the Sound with surface Atlantic water. Thus Kuntz and Radcliffe (1917) found that in the Woods Hole region there is a run of butterfish of short duration in June, that there are relatively few individuals in inshore waters during the summer months, and that they become abundant again in September.

Table II shows that large numbers of eggs were taken in June and July 1944 as compared with other years; see DISCUSSION.

LARVAE: The young of this species were taken only in surface hauls on September 12, 1943 and on May 27, 1945. The first of these was 19 mm in length, and because of its size it presented no difficulty in identification; presumably this fish was the product of an earlier spawning, in June or July. The other was 3.5 mm and closely resembled Perlmutter's (1939) fig. 2D, but it differed in a number of respects from Hildebrand and Cable's (1938) figs. 129 and 131 of *U. chuss* and from larvae in our own collections which we have assigned to the squirrel hake. This individual, quite newly hatched, must have resulted from an early spawning of this species.

Stenotomus chrysops

EGGS: No eggs of the scup were taken in either surface or bottom hauls in the course of this study.

Bigelow and Welsh state that the scup spawns in southern New England waters from May to August, chiefly in June. The buoyant eggs range from 0.85 to 0.90 mm in diameter according to Kuntz and

Radcliffe (1917). These facts plus the presence of a single oil globule (measurements not given by Kuntz and Radcliffe or by Bigelow and Welsh) are compatible with weakfish and mackerel eggs (see p. 203). However, it seems highly improbable that any of the eggs identified as mackerel or weakfish in this work could have been scup, since our length-frequency curves of the egg diameters assigned to mackerel and weakfish show low points in the range from 0.85 to 0.90 mm. Furthermore, microscopic examination of all the samples of eggs which we have divided into mackerel and weakfish showed no eggs sufficiently distinct from these two forms to give any indication of a third category. As a general rule, adult scup were not taken in great quantity in the three-year sample trawl hauls (Merriman and Warfel, 1948). This, however, does not indicate that the scup is not abundant in the area, for other trawlers frequently catch this species in great quantities by "ballooning" the head rope of the net so that fishing is effective at a greater distance above the bottom. It seems peculiar, therefore, that the eggs and larvae should not have been taken in greater numbers, but our findings are similar in this respect to Kuntz and Radcliffe (1917) who say that "eggs were not abundant in the plankton at any time . . ."

LARVAE: A single larval specimen was taken on July 16, 1944 in a surface haul. It was 4.5 mm long and was identified from illustrations in Kuntz and Radcliffe, where it fit between their figs. 33 and 34. The general outline and relatively small mouth distinguish it from weakfish larvae.

Cynoscion regalis

EGGS: The eggs of the weakfish were taken in both surface and bottom hauls (Tables II and III). However, only eight of these eggs were taken in the bottom hauls, and these were all the result of a single tow on July 23, 1944. This was a time when the eggs of this species were particularly abundant in the surface hauls, and we believe that these eight eggs were taken as the net passed through surface layers. The eggs are clearly characteristic of near-surface waters.

Weakfish eggs were taken from June to October. According to Bigelow and Welsh this species spawns from May to October, with the major production of eggs falling in the June–July period. Our samples show a high peak of abundance at precisely this time (Table II), and they indicate that spawning does not begin as early as May in these waters. The weakfish, like the mackerel, was not common in the three-year sample trawl hauls, but it is primarily a pelagic species whose abundance in this general region is well known.

The identification of these eggs and their distinction from other forms, notably mackerel and scup, has already been discussed in the sections dealing with these two species. Welsh and Breder (1923) describe the eggs and larvae of this species, and Hildebrand and Cable (1934) give a further account. We have already indicated (p. 182) that length frequencies of the diameters of the eggs assigned to the weakfish gave a bimodal curve with peaks at approximately 0.75 and 1.00 mm. This corresponds with the experience of Pearson (Hildebrand and Cable, 1934) and of Welsh and Breder (1923) on small samples of weakfish eggs. Hildebrand and Cable (1934) give the range of diameter of the egg of this species as 0.7 to 1.13 mm. In the present work we have found a few eggs whose diameter was 0.68 mm and several which measured 1.18 mm. Welsh and Breder (1923) state that the yolk usually contains one to four oil globules, and that, when only one is present, it ranges from 0.18 to 0.27 mm; mackerel eggs contain a single oil globule 0.28–0.35 mm in diameter according to Sette (1943). We should also record that a large majority of the eggs examined by us were in an early stage of development before the embryo had taken form.

LARVAE: The young of this species were taken on only two occasions, 94 on July 16, 1944 and three on July 23, 1944. This was the year in which large quantities of the eggs were taken during June and July; in other years in the same period the numbers of eggs were relatively small and no larvae appeared in our collections. The average length of these 97 specimens was from 3.0 to 5.5 mm, obviously individuals which were the product of recent spawning activity. The larvae were almost always distorted or otherwise damaged, particularly in the head region, thus making accurate measurement difficult.

Tautogolabrus adspersus

EGGS: Cunner eggs were taken only in the surface plankton hauls and in considerable abundance in June, July and August 1944 and 1945, as well as in June 1946 (no haul was made in July 1946). Bigelow and Welsh state that the spawning season occurs in June, July and August in the Gulf of Maine, and Kuntz and Radcliffe (1917) write, "This species spawns in June and July." Evidence from our collections indicates that spawning occurs as late as August in B. I. S., although it is clear from the numbers shown in Table II that the peak of spawning occurs in June and July.

When we take into consideration the season, egg diameter, and lack of oil globules, the only species whose eggs can be confused with those of the cunner is *Tautoga onitis,* the blackfish or tautog. Bigelow and Welsh state that the diameter of the egg of the cunner is from 0.75 to 0.85 mm, that of the tautog 0.9 to 1.0 mm. At least 85% of all eggs classed by us as cunner are 0.85 mm or less in diameter. Kuntz and Radcliffe (1917) also state that these two species can be distinguished only by the slight difference in size. A small proportion of our eggs exceeded 0.85 mm in diameter, a number being 0.90 to 0.95 mm; one egg in this category was 1.30 mm in diameter. Working on the basis of diameter alone, these larger eggs would be classed as those of the tautog. However, in our larger samples, where the egg diameter exceeded that given by previous workers for the cunner, the eggs were in identically the same stage of development, *i. e.,* the embryos were well developed and pigmentation was present. If these samples contained a mixture of both species it would be highly unlikely that all the eggs would be in the same stage of development; therefore we have placed these eggs in the cunner category and have provisionally enlarged the egg diameter range of this species. The fact that relatively large numbers of cunner larvae and very few tautog larvae turned up in the surface plankton hauls lends strength to the assignment of these eggs to the cunner category. Further evidence on this score is provided by the number of adult cunners and tautog in the three-year sample trawl hauls (Merriman and Warfel, 1948) which show that only one specimen of *Tautoga onitis* was taken in this period while 79 adult cunners were present.

LARVAE: Young *Tautogolabrus adspersus* were taken on June 23, July 16 and 23, 1944. The vast majority of the June specimens ranged between 2.75 and 2.85 mm in length, although there were several at 4.0 mm, one at 6.0 mm, and one at 7.0 mm; these larger individuals suggest the possibility of spawning as early as May in these waters. The July 16 specimens ranged from 2.65 to 5.25 mm in length, with the average size falling near the lower limit of these measurements. The July 23rd sample contained ten larvae from 2.5 to 4.1 mm in length, the product of recent spawning, as well as one larva 8.7 mm and another 11.0 mm in length, these latter apparently the product of June spawning.

There is no possibility of confusing the larvae of this species with those of the blackfish. The pigment pattern in the cunner immediately separates it from the tautog of similar size (see Kuntz and Radcliffe, 1917). Our own specimens were also checked against collections obtained from the U. S. Fish and Wildlife Service and from specimens identified by A. E. Parr in the Bingham collections. The two larger specimens, taken on July 23, 1944 in bottom stramin-net hauls, perhaps give some indication as to the size at which the larvae of this species undertake a demersal or semidemersal existence.

Tautoga onitis

EGGS: If our identification of cunner (*vide supra*) is correct, no eggs of the tautog were taken in the course of this study.

LARVAE: Larvae were obtained on one occasion—three on July 16, 1944, in a surface plankton haul. These specimens ranged from 3.0 to 3.5 mm in length and are clearly referable to this species as described and illustrated by Kuntz and Radcliffe (1917). In the Key which follows (p. 204), the larvae are restricted to the month of July, the only occasion on which they were taken in this work; more adequate sampling would probably yield specimens in both June and August, for Kuntz and Radcliffe (*loc. cit.*), speaking of the Woods Hole region, state that the principal spawning month is June and that eggs are abundant in the plankton as late as July 15th. Bigelow and Welsh say, "We have found no tautog eggs nor larvae in our towings in the Gulf of Maine, but being comparatively so scarce a fish and breeding close to the coast, we may simply have missed them."

Myoxocephalus aeneus

EGGS: The eggs of this species are demersal and accordingly none were taken in the surface or bottom plankton hauls.

LARVAE: According to Bigelow and Welsh, the spawning season lasts all winter off southern New England. Three larvae were taken on May 18, 1944 and four on May 6, 1946, both lots in bottom stramin-net hauls (Table V). The length of these specimens was between 8 and 10 mm, accurate measurements being impossible because of the curled condition of the larvae. We cannot be certain of the distinction between this species and the succeeding one, *Myoxocephalus octodecimspinosus*, but the more stubby and well rounded bodies of these were quite different in appearance from the relatively thin bodies of the larvae which we have assigned to the longhorn category. It may be no more than chance, but we call attention to the fact that these seven larvae were taken only in bottom hauls, while those specimens which we have identified as *M. octodecimspinosus* were taken only in surface hauls.

Myoxocephalus octodecimspinosus

EGGS: Like the preceding species, the eggs are demersal. They were taken frequently in December and January in the three-year sample trawl hauls (Morrow, 1951).

LARVAE: The young of the longhorn sculpin were taken in February, March and April in surface hauls (Table IV). As indicated in the discussion for the preceding species, they were distinguished from the little sculpin by the shape of their body. They ranged in length from 7 to 10 mm, precise measurements being impossible because of the curled condition of the larvae. Further indication that these specimens belong to this species and not with *aeneus* is derived from their size. If the specimens here identified as *M. aeneus* were actually *octodecimspinosus,* we should have expected them to be somewhat larger in May when they were taken.

Cyclopterus lumpus

EGGS: This species produces large spongy masses of eggs which sink to the bottom (Bigelow and Welsh).

LARVAE: Some 16 larvae, assigned to this species, were taken in the bottom stramin-net hauls—seven on May 18, 1944, four on May 27, 1945 and five on May 6, 1946 (Table V). Bigelow and Welsh indicate that the spawning season is a protracted one from February until near the end of May. This is borne out by the size of the specimens taken in our hauls, the majority of which fell between 4.0 and 6.0 mm, with three specimens at 7.0, 8.5, and 10.0 mm respectively. Presumably these larger specimens were the product of a midwinter spawning, while the smaller individuals may have been hatched in March or April. However, we call attention to the fact that larvae were taken in our bottom hauls in three successive years only in the month of May. In 1944 no hauls were made in the preceding months, but in 1945 hauls in March and April failed to yield any larvae of this species.

Identification was made possible by the fact that the ventral fins had already become modified to form the characteristic six pairs of fleshy knobs in the center of the sucking disc. These knobs are equidistantly spaced over the posterior 75% of the circumference of the disc.

Cryptocanthodes maculatus

EGGS: Bigelow and Welsh state that neither the eggs nor early larval stages are known, but there is every reason to believe that this species lays demersal eggs and that, like other close relatives such as *Macrozoarces americanus,* it guards them (*cf.* Olsen and Merriman, 1946).

LARVAE: Two larvae were taken in a surface plankton haul on April 19, 1944. These specimens were 22 and 29 mm long respectively, apparently the product of an early winter spawning; they were identified by their shape and general appearance, by fin-ray counts, and by comparison with the excellent illustration in Dannevig (1919).

Merluccius bilinearis

EGGS: The eggs of the silver hake are pelagic, and Bigelow and Welsh state that this species is ". . . the most important summer spawner among Gulf of Maine fishes." They also state that Sable Island is probably its eastern breeding limit and that their most westerly egg record was off Nantucket Shoals. They conclude that it is not likely that this fish spawns inshore far west of Cape Cod. In keeping with these observations we did not obtain any eggs of this species in the course of this work—this despite the fact that *bilinearis* is one of the most abundant fish in the area (Merriman and Warfel, 1948).

LARVAE: Silver hake larvae were taken on two occasions in the bottom stramin-net hauls, 11 on July 23 and five on November 19, 1944. Those in the July 23rd sample ranged from 4 to 7.5 mm, the majority being 6 mm or less in length. The five larvae taken on November 19th measured from 5.5 to 9.0 mm. This haul also contained a specimen of *Merluccius bilinearis* which was 9 cm in length. The total absence of eggs of this species in our collection and the presence of these larvae in bottom samples give some indication that the larvae may have been brought in by currents from waters outside B. I. S.

Identification of these larvae was made from the drawings of Kuntz and Radcliffe (1917) (reproduced in Bigelow and Welsh). Their pigmentation differed somewhat from that shown in the cited illustrations, but the general morphology and the graded series of specimens permitted positive identification. The larvae of *Centropristes striatus,* the sea bass (specimens loaned to us by the U. S. Fish and Wildlife Service), are very similar to the whiting in body form, and since the chromatophores on the body in early stages are found in groups of three in both species there is opportunity for confusion. This is especially true when examining larvae which are lying on their sides. However, it is easy to separate these two species by looking at the pigment patches from the dorsal surface; in the sea bass the three patches of pigment are located directly on the mid-dorsal line and extend down onto the lateral surfaces; in the whiting the pigmented areas do not merge across the midline, so that in dorsal view they give the appearance of three *pairs* of pigmented areas.

Gadus morhua

EGGS: The eggs of the cod were taken in both surface and bottom hauls (Tables II and III). This species was most abundant in the three-year sample trawl hauls during the fall and early winter months; it was entirely absent from the catches from May through September (Merriman and Warfel, 1948). It appears that large numbers of these fish congregate in the shallow waters of B. I. S. during the spawning season, which apparently reaches its peak in these waters in December. Table II shows that eggs were taken in the surface hauls in November, December, January and February, 1943–1944, with the peak of abundance falling on December 19th. Similarly in 1944–1945 the peak fell on December 18th and eggs were taken as late as March 5, 1945; note, however, that no hauls were taken in January and February 1945. The bottom stramin-net hauls yielded cod eggs twice only, 45 on November 19, 1944, and one on March 5, 1945. Whether or not the 45 eggs on November 19 were taken in the bottom waters or during the passage of the net to the surface is a matter of conjecture. This sample contained eggs in two distinct stages of development; the majority were in an early stage, but in some the embryo was relatively well developed. Despite the fact that the surface plankton net took only ten eggs on the same date, we are inclined to think that the bottom stramin net took the majority of this sample on its way to the surface. Surface samples taken as early as November contained quite well advanced embryos as well as early stages, *i. e.*, their composition in terms of stage of development was in general similar to that of the sample taken in the bottom stramin net. Later in January, February and March, eggs in advanced stages of development tend to dominate the catch, although occasional eggs show only a germinal disc, thus indicating that scattered spawning continues up to the latter part of February or the early part of March. Unfortunately bottom hauls were made on only three of the 11 occasions when cod eggs might reasonably be expected to be present as judged from the results of the surface hauls.

The identification of cod eggs presented no great difficulty. According to Bigelow and Welsh, they range from 1.16 to 1.82 mm in diameter and lack an oil globule. The only possible species with an overlapping spawning season which might present difficulties in this region are the pollack, *Pollachius virens*, and the haddock, *Melanogrammus aeglifinus*. The pollack is practically eliminated from consideration by the fact that it is extremely rare in B. I. S. trawl-net catches and was never taken during this season in the three-year sample trawl hauls (Merriman and Warfel, 1948); further, its eggs average 1.15 mm in diameter (Bigelow and Welsh), and only five of the 778 eggs identified by us as cod were this small. The haddock was also rare in these waters and is a later spawner whose reproductive period only overlaps the latter part of that of the cod. Although the diameters of cod and haddock eggs are similar, there is no evidence that leads us to believe that the few eggs identified as cod taken in March represented anything but the end of the cod spawning season. Further evidence that haddock eggs did not enter into the picture is provided by the fact that haddock larvae, which are clearly distinguishable from those of the cod, were not taken in any of our samples.

LARVAE: Cod larvae were taken in small numbers in both surface and bottom hauls. Those from the surface, one on April 16, 1945 and one on May 6, 1946, measured 19 and 16 mm respectively. Those taken in the bottom sample measured 11, 21 and 22 mm respectively on May 18, 1944, and 10 and 11 mm on May 27, 1945. With reference to the bottom hauls, here again we cannot state with certainty that the specimens were actually taken in deeper waters rather than at or near the surface. Despite the small numbers, however, the larger quantity in the bottom net hauls gives some indication that these larvae may have been taken near the bottom. As indicated previously, the positive identification of these larvae represented no difficulty (see Bigelow and Welsh).

Urophycis spp.

EGGS: Assuming the validity of our identification of the eggs of the butterfish, *Poronotus triacanthus* (see pp. 183–185), no eggs referable to hake species appeared in either the surface or bottom samples.

LARVAE: A sum total of 73 larvae referable to this genus were taken on 13 occasions in the surface plankton hauls (Table IV), but no representatives of this genus were taken in the bottom hauls. Merriman and Warfel (1948) show that three species of *Urophycis* are taken in trawl hauls from this general region. *U. regius*, the spotted hake, is so rare that we exclude it from consideration in the present analysis. *U. tenuis*, the white hake, and *U. chuss*, the squirrel hake, are both abundant in the summer and early fall, with the latter showing a tendency to appear somewhat earlier in the spring. According to Bigelow and Welsh practically nothing is known of the breeding habits of the white hake, although there is some evidence that it is a fall and winter spawner whose active reproductive season may extend into April. The squirrel hake apparently spawns in June and July. Table VI gives the lengths of the hake larvae taken at various dates in the surface plankton hauls and gives also a provisional division of these specimens into the *chuss* and *tenuis* categories. This separation is based on 1) the description of the former by Hildebrand and Cable (1938), who state that "the interradial membranes of the ventrals are black distally" in specimens about 5 mm in length, 2) the length measurements and the seasons at which the specimens were caught, 3) examination of the larger specimens which yielded certain diagnostic characters discussed below, and 4) the comparison of the smaller specimens on the basis of the characters which are more readily apparent in individuals more than 20 mm in length. Examination of the three large individuals in the collection of June 23, 1944 indicated that two species were represented. It is known from Bigelow and Welsh that in adult *U. chuss* the ventral fins overlap the vent as a rule, although not invariably; however, when they do the character is diagnostic in differentiating *chuss* from *tenuis*. The other means of separating these adults is by means of the number of scales in the lateral line—roughly 140 in *U. tenuis* and 110 in *U. chuss;* this latter character is obviously of no use in the identification of larvae of the sizes here represented. In one of the three large specimens taken on June 23 the ventrals extended well beyond the vent (*U. chuss*). We also noted in this individual that the dorsal fin originated well posterior to the origin of

TABLE VI.—Lengths (in mm) of *Urophycis* spp. Larvae Taken on Different Dates in Surface Plankton Hauls. Provisional Division into *U. chuss* and *tenuis* Described in Text.

Date	*chuss?*	*tenuis?*
May 27, 1945	1 at 5.0	—
June 9, 1946	1 at 7.0	—
	1 at 9.0	—
June 23, 1944	1 at 5.0	—
	1 at 6.5	—
	1 at 8.0	—
	—	1 at 23.5
	1 at 24.5	—
	—	1 at 27.0
July 16, 1944	1 at 3.0	—
	1 at 3.5	—
	4 at 5.0	—
July 17, 1945	1 at 5.0	—
July 23, 1944	3 at 2.0	—
	1 at 2.5	—
	1 at 3.0	—
Aug. 13, 1944	1 at 4.5	—
	4 at 5.0	—
	1 at 5.5	—
Sept. 9, 1945	1 at 10.5	—
Sept. 12, 1943	—	9 at 3.0
	—	7 at 3.5
	—	6 at 4.0
	—	4 at 4.5
	—	2 at 5.0
Oct. 26, 1944	—	1 at 33.0
Nov. 11, 1945	—	1 at 4.0
	—	2 at 5.0
	—	2 at 5.5
	—	1 at 6.0
	—	1 at 6.5
	—	1 at 7.5
	1 at 11.0	—
	1 at 12.0	—
Nov. 19, 1944	—	1 at 4.0
	—	3 at 5.0
Nov. 21, 1943	—	1 at 3.5
	—	1 at 5.0
Totals	28	45

the pectorals (as viewed from the dorsal surface) and that each anterior nasal aperture was characterized by a distinct fleshy collar. In the other two individuals the ventrals did not reach the vent, the dorsal fin originated at the level of the insertion of the pectorals, and the collar around the anterior nasal aperture was replaced by a posteriorly directed flap of skin which extended to the posterior nasal aperture; these specimens were identified as *U. tenuis.* The use of these distinguishing characters on smaller larvae, in conjunction with the other criteria listed above, enabled us to make provisional separation of all 73 specimens as shown in Table VI.

If this separation is valid, the small specimens of *chuss* taken from May through September and in November would of course be young of the year. Bigelow and Welsh state that this species spawns ". . . at least as early as June south of Cape Cod." Our data (Table VI) would indicate that spawning in this region begins in May and perhaps reaches its peak in June and July. The two larger specimens of *chuss* taken on November 11, 1945 would appear to be the product of the latter part of the spawning period, *i. e.*, July or possibly August. The large specimen taken on June 23, 1944 (24.5 mm) must have been the product of either extremely late spawning the preceding year or early May reproduction in 1944—probably the latter. Turning to the specimens identified as *U. tenuis,* the small larvae taken in September and November (3.0 –7.5mm) must have been the product of early spawning. If these identifications are correct, the spawning season probably begins earlier than is indicated by Bigelow and Welsh, who state that ". . . spawning takes place in fall and winter and occasionally as late as April." The average length of the *tenuis* larvae taken in September is 3.7 mm while the average length of those taken in November is 5.6 mm. The larger specimens of *U. tenuis* taken on June 23, 1944 must have been the product of the previous fall or winter spawning, and the 33 mm individual taken October 26, 1944 would have to be the result of spawning in the early spring.

If our identifications are correct, it would appear that neither of these species spawn in any great abundance in B. I. S., since no eggs were taken, and that the larvae are carried into the area following spawning to the east.

Paralichthys dentatus

EGGS: No eggs of the summer flounder were taken in our tows. Bigelow and Welsh state: "Practically nothing is known of its breeding habits. Presumably its eggs are buoyant like those of its close relative, the four-spotted flounder, and since the ovaries of fish caught are small or immature it is supposed to spawn in autumn or winter, perhaps moving out into deep water for the purpose." Hildebrand and Cable (1930) mention the fact that a few *P. dentatus* with large roes were seen in November at Beaufort, North Carolina, and that the eggs have apparently never been taken; they conclude from all the available evidence ". . . that the eggs quite certainly are cast during the winter."

LARVAE: Four fluke larvae were taken in the bottom stramin net on November 19, 1944. Three of these were 6 mm and one was 8 mm long. It was possible to make fin ray counts on the largest specimen and these fell within the known range for this species (Norman, 1934). All other local flounders are excluded from consideration on the basis of either their known spawning periods or the fin ray counts. Verification of this identification was made from the description and illustrations by Hildebrand and Cable (1930).

Limanda ferruginea

EGGS: No eggs of the dab or yellowtail were taken in our tows. Bigelow and Welsh state that spawning begins in the early spring and lasts all summer in the Gulf of Maine; Nichols and Breder (1926) say, "Spawns in spring and summer . . ." for the southern New England area.

LARVAE: Young were taken on three occasions: May 27, 1945, when 40 larvae ranging from 4.0–12.5 mm were taken in a bottom stramin-net haul, July 23, 1944, when one larva 10 mm in length was taken in a bottom haul, and August 13, 1944 when three larvae 2.5–3.0 mm in length appeared in the surface plankton haul. This species is taken in rather limited abundance in B. I. S. (Merriman and Warfel, 1948), and it would appear from the absence of eggs in our collections that spawning must take place to the eastward. It is also interesting that the larger larvae were taken in the bottom hauls, a fact which supports the contention of Bigelow and Welsh that ". . . the dab is not as long subject to involuntary migrations with the current as are some other flounders."

In the early larval stages this species is probably indistinguishable from the winter flounder, *Pseudopleuronectes americanus.* However, the spawning season of the latter reaches a peak in February and

March in these waters. Also, the eggs are demersal and spawning takes place in the region of shallow bays and estuaries in waters of low salinity; hence the larvae and young apparently do not get into deeper waters of the sort where these studies were made until at least their second year. Fin-ray counts of the larger specimens in our samples made the assignment of these specimens to *Limanda ferruginea* certain, and there is every reason to believe that the small individuals in these collections are also dabs.

Lophopsetta aquosa

EGGS: No eggs of the windowpane or sand flounder were obtained. Perlmutter (1939) and Moore (1947) agree that the spawning period of this species extends from May into August.

LARVAE: Four specimens of the young of this species, ranging from 4.0–8.0 mm, were taken in a bottom stramin-net haul on July 23, 1944. The identification of these larvae caused no difficulties whatsoever owing to the excellent illustrations in Bigelow and Welsh and in Moore (1947). These fish were obviously the product of relatively recent spawning.

Perlmutter (1939) took the eggs and larvae of this species in great abundance in the course of the survey of the salt waters of Long Island. However, examination of his table 22 shows that the vast majority of his specimens were taken in the Peconic and Gardiner's bays in relatively shallow water. It seems clear from the absence of eggs and the paucity of larvae in our collections that B. I. S. is not an area where this species spawns very successfully—this despite the fact that the windowpane or sand flounder is abundant on a year-round basis (Merriman and Warfel, 1948). However, better sampling in the inshore and bay areas would probably have produced more specimens; we note, in this connection, that the majority of the hauls comprising our samples in the late spring and summer (when this species spawns) were taken relatively far offshore.

Lophius americanus

EGGS: Table II indicates that 10 (?) eggs of the goosefish were taken on June 23, 1944 in a surface plankton haul. As stated in the section on Material and Methods, the numbers of eggs taken on this date were so great that only one-tenth of the sample was examined to determine the relative proportions of the different species of fish eggs present in it. However, the entire sample was scanned with great care in the initial separation of fish eggs and larvae from the other plankton. In the process of scanning, only one egg referable to *Lophius americanus* was seen, and it is almost certain that this was the only one present. However, we have indicated 10 (?) in Table II in order to be consistent with the procedure for other fish eggs in the haul, where the number for each species has been multiplied by 10.

It is well known that the eggs of the goosefish are shed in ribbon-shaped veils or sheets which float on the surface. However, Bigelow and Welsh point out that the eggs occasionally become isolated and that ". . . when this occurs they float like any buoyant fish eggs." The diameter of our egg was 1.88 mm and that of its contained oil globule .55 mm. The only other egg of this size among the species of fish in these waters at this season is that of the menhaden, which is immediately eliminated from consideration by the small size of its oil globule (0.15–0.17 mm). Agassiz and Whitman (1885) describe similar isolated eggs of this fish from Newport, Rhode Island.

LARVAE: No larvae of this species were taken in the course of this study—the only instance in the survey where fish egg(s) were taken in the absence of the corresponding larvae.

KEYS TO THE EGGS AND LARVAE BY MONTHS

The following keys to the pelagic fish eggs and larvae of the B. I. S. region include only those forms which were taken in the plankton tows over the three-year period of this study (see Table I). Since these collections were usually made offshore in the relatively deep waters of the area, the eggs or larvae of those species whose reproductive activities are confined to the shallow coastal regions (*e. g.*, the winter flounder) are not for the most part represented. Similarly, some of the species which quite certainly spawn in the waters which we worked but whose eggs or larvae did not appear in our collections are not included in these keys—*e. g.*, menhaden, sea robin, tautog eggs, hake eggs, yellowtail and windowpane flounder eggs, etc.

The keys are presented by months throughout a full calendar year. Due to varying hydrographic conditions or to a lack of basic life-history information, it is extremely difficult to state the exact extent of the spawning seasons and hence the precise period during which the pelagic eggs and larvae of different species occur in any one year or from year to year. Therefore, when using the key for a particular month, we recommend checking at least the succeeding and the preceding monthly keys for other possible species. Reference should be made not only to other months where the keys so indicate but also to the text and references cited therein. Of course the keys are entirely artificial and arbitrary. They have many shortcomings and should be used only with the greatest discretion; if they are used at all for areas outside southern New England waters, even greater caution should be exercised. Under no delusion as to their adequacy, we include the keys here as a preliminary step in the identification of the pelagic fish eggs and larvae from this region, but in the hope that their use may spare succeeding workers some of the time it has taken us to complete this study.

JANUARY

Eggs: COD (diameter 1.16–1.82 mm; no oil globule; see p. 194 for other possibilities)

Larvae: I) Up to 5.0 mm ±
    LONGHORN SCULPIN (slender body form, p. 191)
  II) 25.0–35.0 mm ±
    HERRING (long slender body; convoluted intestine; origin of anal fin far posterior to termination of dorsal; see p. 179)

FEBRUARY AND MARCH

Egg: COD (see *January*)

Larvae: I) 2 dorsal and 2–3 ventral sharply-defined pigment bars
    COD (4.0–10.0 mm ±; ventral pigment bars longer than opposing dorsal bars; see p. 194 and Bigelow and Welsh, 1925: 413, 428–430)
  II) No well defined separate dorsal and ventral pigment bars
    LONGHORN SCULPIN (7.0–10.0 mm ±; see p. 191)

APRIL

Eggs: MACKEREL (diameter 0.88–1.38 mm; oil globule not less than 0.28 mm; see pp. 181, 182 for other possibilities; also see Sette, 1943: 166)

Larvae: I) Ventral fins modified into sucker
    LUMPFISH (5.0 mm; see p. 191 for specific characters)
  II) No ventral sucker
    a) 20.0–30.0 mm ± long
      WRYMOUTH (adult characters recognizable, p. 192)
    b) 10.0–20.0 mm ± long
      COD (larval pigment pattern—see *February* and *March* I, or adult fin formation)
    c) 10.0 mm ± long
      1) Slender body form
        LONGHORN SCULPIN (average length longer than brassy sculpin; see IIc2)

2) Stubby body form

Brassy Sculpin (avarage length 5.0–10.0 mm; see p. 190)

d) 5.0 mm ± long

1) Elongate ventral fins and blunt caudal

Hake (seepp. 195–197 for discussion of *Urophycis chuss* and *U. tenuis*; see also Hildebrand and Cable, 1938: 613–626)

2) Ventrals inconspicuous and caudal pointed

Yellowtail (typical flounder larvae, probably indistinguishable from winter flounder until fin-ray counts are possible; see p. 198)

MAY

Eggs: I) Diameter 0.88 mm or more

Mackerel (see *April*)

II) Diameter less than 0.8 mm

Butterfish (sometimes one, sometimes several oil globules, 0.10–0.25 mm; see p. 184)

Larvae: I) Ventral fins modified into sucker

Lumpfish (5.0–10.0 mm ±; see p. 191)

II) No ventral sucker

a) 10.0–25.0 mm ± long

Cod (see *February* and *March* I, and *April* IIb)

b) 3.0–10.0 mm ± long

1) Elongate ventral fins and blunt caudal

Hake (see *April* IId1)

2) Ventrals relatively inconspicuous

i) Typical flounder larvae; numerous dorsal and anal fin rays differentiating at 10.0 mm ±; relatively deep body

Yellowtail (see p. 198)

ii) Relatively thin body with continuous fin fold; dorsal and anal fin rays differentiating at 8.0 mm

Brassy Sculpin (8.0–10.0 mm ±; see p. 190)

iii) Prominent oil globule at yolk sac stage (3.0–4.0 mm); irregularly spaced dorsal and ventral rows of chromatophores on posterior half of body in 4.0–8.0 mm stage

Mackerel (3.0–6.0 mm ±; see p. 183; see also Sette, 1943: 170–171, and Bigelow and Welsh, 1925: 189 and 208)

iv) Sparse pigmentation, with some concentration over lower intestine; blunt head

Butterfish (2.15–3.5 mm; see p. 186)

JUNE

Eggs: I) Diameter over 1.5 mm
    GOOSEFISH (diameter 1.67–3.11 mm; oil globule 0.4–0.56 mm; see p. 200 and Bigelow and Welsh, 1925: 529–531)
  II) Diameter less than 1.4 mm
    a) No oil globule
      CUNNER (usual diameter 0.75–0.85 mm, but some larger; see p. 189 for cunner *vs*. tautog; see also Kuntz and Radcliffe, 1917: 99–102)
    b) Oil globule(s) present
      1) Diameter range 0.7–0.8 mm
        BUTTERFISH (see *May* II)
      2) Diameter range 0.68–1.38 mm
        i) Oil globule 0.28–0.35 mm
          MACKEREL (diameter range 0.88–1.38 mm, but most eggs 1.0–1.3 mm; see p. 182 for discussion; see also Sette, 1943: 166)
        ii) Oil globule(s) 0.27 mm or less
          WEAKFISH (egg diameter range 0.68–1.18 mm; 1–4 oil globules down to 0.05 mm; see p. 188; see also Welsh and Breder, 1923: 150–153)

Larvae: I) Elongate ventral fins
    HAKE (5.0–27.0 mm; see *April* IId1)
  II) Ventrals relatively inconspicuous
    a) Oil globules present at yoke sac stage; irregularly spaced dorsal and ventral rows of chromatophores on posterior half of body in subsequent larval stage
      MACKEREL (up to 25.0 mm; see *May* IIb2iii)
    b) No oil globule; pigment pattern not as described above
      1) Larvae slender; vent in middle third of body
        CUNNER (2.5–7.0 mm; see p. 190, and Kuntz and Radcliffe, 1917: 99–102)
      2) Sparse pigmentation, with some concentration over lower intestine; blunt head
        BUTTERFISH (2.15–5.0 mm; see *May* IIb2iv)
      3) Larvae relatively deep-bodied
        i) Vent in anterior third of body
          YELLOWTAIL (10.0 mm ±; numerous dorsal and ventral fin rays differentiated; see p. 198; see also Bigelow and Welsh, 1925: 494–500, as well as *July* IIb1ii)
        ii) Vent in middle of body
          WINDOWPANE (5.0 mm ±; see p. 199; see also Bigelow and Welsh, 1925: 519–520, as well as *July* IIb1i)

JULY

- Eggs: I) No oil globule
    - Cunner (see *June* IIa)
- II) Oil globule(s) present
    - a) Egg diameter range restricted to 0.7–0.8 mm
        - Butterfish (see *May* II)
    - b) Egg diameter range 0.68–1.18 mm
        - Weakfish (see *June* IIb2ii)
- Larvae: I) Obvious syngnathid form
    - a) Head at right angles to axis of body
        - Sea Horse (p. 180)
    - b) Head and tubular snout on same axis as body
        - Pipefish (p. 179)
- II) Nonsyngnathid form
    - a) Elongate ventral fins
        - Hake (5.0–30.0 mm; see *April* IId1)
    - b) Ventrals relatively inconspicuous
        - 1) Typical flounder larvae; numerous dorsal and anal fin rays
            - i) Chromatophores scattered over abdominal region in early larvae; metamorphosis to left-handed condition recognizable by 8.0 mm
                - Windowpane (4.0–8.0 mm; see *June* 11b3ii)
            - ii) Chromatophores confined to posterior margin of abdominal cavity in early larvae; metamorphosis to right-handed condition recognizable by 14.0 mm
                - Yellowtail (10.0 mm ±; see *June* IIb3i)
        - 2) Nonflounder larvae
            - i) Single ventral line of uniformly spaced chromatophores posterior to vent
                - Scup (4.5 mm ±; see p. 187; see also Kuntz and Radcliffe, 1917: 102–105)
            - ii) Uniformly heavy pigmentation over anterior two-thirds of body; vent in middle of body
                - Tautog (3.5 mm ±; see p. 190; see also Kuntz and Radcliffe, 1917: 92–99)
            - iii) Two chief areas of pigment concentration on lateral surface of body—one just posterior to vent, the other halfway from the first area to the tail
                - Whiting (4.0–7.5 mm; see p. 192; see also Kuntz and Radcliffe, 1917: 109–112)
            - iv) Irregular and rather sparse body pigmentation with some concentration above (future) anal fin
                - Weakfish (3.0–5.5 mm ±; see p. 188; see also Welsh and Breder, 1923: 151–157)
            - v) Sparse pigmentation, with some concentration over lower intestine
                - z) Blunt head
                    - Butterfish (2.15–5.0 mm; see *May* IIb2iv)

- zz) Elongate head
  - Cunner (2.5–11.0 mm; see p. 189; see also Kuntz and Radcliffe, 1917: 99–102, and *June* IIb1)

AUGUST

- Eggs: I) No oil globule
  - Cunner (see *June* IIa)
- II) Oil globule (s) present
  - a) Egg diameter range restricted to 0.7–0.8 mm
    - Butterfish (see *May* II)
  - b) Egg diameter range 0.68–1.18 mm
    - Weakfish (see *June* IIb2ii)
- Larvae: I) Elongate ventral fins
  - Hake (3–30.0 mm; see *April* IId1)
- II) Ventrals relatively inconspicuous
  - a) Typical flounder larvae
    - Yellowtail (2.5 mm and up; see *July* IIb1ii)
  - b) Nonflounder larvae
    - 1) Sparse pigmentation, with some concentration over lower intestine
      - i) Blunt head
        - Butterfish (5.0 mm ±; see *May* IIb2iv)
      - ii) Elongate head
        - Cunner (2.5–11.0 mm; see *July* IIb2vzz)
    - 2) Two chief areas of pigment concentration on lateral surface of body—one just posterior to vent, the other halfway from the first area to the tail
      - Whiting (5.0–10.0 mm ±; see *July* IIb2iii)
    - 3) Irregular and rather sparse body pigmentation, with some concentration above (future) anal fin
      - Weakfish (5.0 mm ±; see *July* IIb2iv)

SEPTEMBER

- Eggs: I) Egg diameter range restricted to 0.7–0.8 mm
  - Butterfish (see *May* II)
- II) Egg diameter range 0.68–1.18 mm
  - Weakfish (see *June* IIb2ii)
- Larvae: I) Slender elongate larvae; convoluted intestine; origin of anal fin far posterior to termination of dorsal
  - Herring (10 mm ±; see p. 179)
- II) Relatively short-bodied larvae
  - a) Elongate ventral fin
    - Hake (3.0–30.0 mm; see *April* IId1)
  - b) Ventrals relatively inconspicuous
    - 1) Sparse pigmentation; blunt head
      - Butterfish (3.0–20.0 mm; see *May* IIb2iv)
    - 2) Two chief areas of pigment concentration on lateral surface of body—one just posterior to vent, the other halfway from the first area to the tail

            Whiting (5.0–10.0 mm ±; see *July* IIb2iii)
        - 3) Irregular and rather sparse body pigmentation, with some concentration above (future) anal fin
            Weakfish (5.0 mm ±; see *July* IIb2iv)

OCTOBER

Eggs: Weakfish (see *June* IIb2ii)

Larvae:
- I) Slender elongate larvae; convoluted intestine; origin of anal far posterior to termination of dorsal
    Herring (10.0–15.0 mm ±; see p. 179)
- II) Relatively short-bodied larvae
    - a) Elongate ventral fins
        Hake (3.0–35.0 mm; see *April* IId1)
    - b) Ventrals relatively inconspicuous
        - 1) Sparse pigmentation; blunt head
            Butterfish (3.0–20.0 mm; see *May* IIb2iv)
        - 2) Two chief areas of pigment concentration on lateral surface of body—one just posterior to vent, the other halfway from the first area to the tail
            Whiting (5.0–10.0 mm ±; see *July* IIb2iii)
        - 3) Irregular and rather sparse body pigmentation, with some concentration above (future) anal fin
            Weakfish (5.0 mm ±; see *July* IIb2iv)

NOVEMBER

Eggs: Cod (see *January*)

Larvae:
- I) Slender elongate larvae; convoluted intestine; origin of anal far posterior to termination of dorsal
    Herring (10–20 mm ±; see p. 179)
- II) Relatively short-bodied larvae
    - a) Elongate ventral fin
        Hake (4.0–12.0 mm ±; see *April* IId1)
    - b) Ventrals relatively inconspicuous
        - 1) Two chief areas of pigment concentration on lateral surface of body, one just posterior to vent, the other halfway from the first area to the tail
            Whiting (5.0–10.0 mm ±; see *July* IIb2iii)
        - 2) Flounder larvae; large head
            Fluke (6.0–8.0 mm ±; see Hildebrand and Cable, 1930: 469–474; see also p. 198)

DECEMBER

Eggs: Cod (see *January*)

Larvae:
- I) Slender elongate larvae; convoluted intestine; origin of anal far posterior to termination of dorsal
    Herring (12–30 mm; see p. 179)
- II) Flounder larvae; large head
    Fluke (10 mm. ±; see *November* IIb2)

DISCUSSION

In this survey we were originally concerned with two objectives. The first was to determine what species of pelagic fish eggs and larvae were present in B. I. S. both on a seasonal and an annual basis. Our second objective involved, "One of the most interesting and economically important fields of study . . . , the involuntary migrations of the early stages of fishes," as stated by Bigelow (1928), who was primarily concerned in this connection with the effects of such migrations on the older fish populations in different areas.

As the study progressed, a third objective developed—namely, to note if there were any marked variations in egg production from year to year in any particular species as measured by our sampling. If this were so, it might be possible to identify dominant year-classes at their inception, and hence, with a knowledge of annual growth rates, it might also be possible to predict the relative strengths of successive age-groups when they first enter the commercial catch. Such prediction, which has been attempted by Sette (1943) for mackerel, should be of inestimable value to fishermen; in years when the prediction for a particular species is low it could afford an opportunity to plan for diversionary effort to other forms, and when it is high it could provide fishermen with advance notice of advantages not regularly available.

The first objective, the determination of the pelagic fish eggs and larvae in B. I. S., has been accomplished, and the results are described in the preceding pages. Of the 33 species of adult fish described by Merriman and Warfel (1948) in their analysis of the commercial trawl catch over the same three-year period in this area, eight are eliminated from consideration in the present study by virtue of their breeding habits—the five elasmobranchs, the alewife (because it spawns in fresh water), the filefish (because it apparently does not spawn at the northern end of its range), and the winter flounder (because it spawns inshore in estuaries and its eggs are demersal). This leaves 25 demersal or semidemersal species whose planktonic eggs or larvae might be expected in our plankton hauls. Actually only 14 appeared, either as eggs or larvae or both. Of the 11 missing species, the sea raven and ocean pout lay demersal eggs, and their larvae presumably live so close to the bottom that their capture (even by the bottom stramin net) would not be likely; the puffer, which for the most part lives and spawns in shallow water only a few fathoms deep, is also in this category. Of the remaining eight species that were missing, the sea bass (comparatively rare in the trawl catches of Merriman and Warfel, 1948) probably does not spawn in this immediate area to any great degree; the kingfish (exceedingly rare in these trawl catches) probably does not achieve successful spawning in the region; the spotted hake (clearly a more typically southern fish) almost certainly does not spawn so far north in its range; and the haddock and witch flounder (one specimen of each taken in the three-year trawl hauls) were so rare that their eggs or larvae would hardly be expected unless they were carried in from the outside by the prevailing current. On the other hand, the four-spotted flounder and the two sea robins unquestionably spawn in coastal southern New England waters, and we have no explanation for the absence of their eggs and larvae from our hauls.

Apart from the fish recorded in the trawl hauls by Merriman and Warfel (1948), our plankton hauls took the eggs or larvae or both of seven other species. Eggs and larvae of both mackerel and weakfish were taken in large numbers. These fish are essentially pelagic forms and their capture by a trawl net in these waters is comparatively rare. We do not know whether they actually spawned in B. I. S. or whether the eggs and larvae were carried in from outside waters; however, it seems probable that these species spawn both outside and inside the area studied. The larvae of the pipefish and seahorse (one of each in three years) are clearly strays from shallow water spawning. The eggs of the brassy sculpin, lumpfish, and wrymouth are demersal and we would expect the larvae to be realtively rare even in the bottom stramin-net hauls; it is of some interest that the two wrymouth larvae were taken in a surface haul, while the seven brassy sculpin larvae and the 16 lumpfish larvae were taken in bottom hauls, the latter being caught in 1944, 1945 and 1946, only in the month of May.

Only once was an egg taken in our tows without the corresponding larvae; this was a single egg of the goosefish, a rare occurrence which needs no elaboration here (p. 199). However, the larvae of 14 species were taken in our tows (surface or bottom or both) without the corresponding eggs. Of these, seven are eliminated by virtue of the fact that the eggs are either demersal (herring, the two sculpins, lumpfish and wrymouth) or are carried in a marsupial pouch (pipefish and sea horse). The remaining seven merit special discussion. Of the scup, Bigelow and Welsh say that it spawns off southern New England from May to August, chiefly in June. Our study (one scup larva in three years) indicates that this species spawns only in the most limited fashion in the immediate region of B. I. S., where the peak of abundance of adults is from midsummer to September and October, probably after reproduction has been completed somewhat further to the south. Tautog also spawn chiefly in June according to Bigelow and Welsh, and they are fairly abundant along southern New England shores. However, we took only three larvae in three years, all in July 1944. This species is rare in the trawl catches from B. I. S., probably because its habitat is strictly coastwise in waters where draggers cannot operate; spawning presumably takes place in rocky areas, where these fish normally live, and in waters much closer inshore than those sampled in most of our survey. Adult silver hake are abundant in the area, but, judging from the absence of eggs in our collections, they apparently do not spawn to any great extent in B. I. S. (p. 192). Bigelow and Welsh do not think it ". . . likely that silver hake spawn inshore far west of Cape Cod." However, the presence of quite small larvae in the bottom stramin-net hauls indicates that spawning may take place not far to the southeast. With the hakes, *Urophycis* spp. (pp. 195–197), much the same situation probably exists. Both the white (*tenuis*) and squirrel (*chuss*) hakes are common elements in the trawl catch; no eggs of these species appear to have been taken in our plankton hauls, but the numerous larvae (73, some in early stages) in the surface tows indicate that spawning must occur nearby. The summer flounder or fluke is fairly abundant in the spring, summer and fall and is said to be an autumn and winter spawner (p. 197). Although its center of reproductive activity is probably further to the south, and although we took no eggs, the size of the four larvae in the bottom haul of November 19, 1944 indicates that some spawning does occur in these latitudes. The dab or yellowtail is taken irregularly in B. I. S. except in the spring and early summer, at which time it is supposed to be spawning. The center of abundance of this species is to the east and southeast, but the fact that larvae, some of them small, were taken in both surface and bottom hauls (on one occasion in abundance) from May through August again indicates that some spawning takes place in neighboring waters. Finally, the windowpane flounder, which is abundant in the region, yielded no eggs and only four larvae in a bottom stramin-net haul on July 23, 1944. Discussion of this question occurs on p. 199; therefore we need only add here that the deeper waters of B. I. S. are apparently unsuitable for spawning by this species, and that, even though reproduction occurs nearby (see

Perlmutter, 1939), the larvae are not common in the immediate area covered by our survey.

Turning to the second objective of this survey—the study of "... the involuntary migrations of the early stages of fishes" (Bigelow, 1928), it would appear (Table II) that only five species of fish with pelagic eggs spawn in off-shore B. I. S. waters with regularity and in abundance. These are mackerel, cod, butterfish, weakfish and cunner, of which the last three are the most prolific in this region (see June and July 1944 in Table II). From Riley (1952) it seems almost certain that, generally speaking, the pelagic eggs which are laid to the north and northwest of Block Island are carried westward until they meet the outflowing surface water from L. I. S., whence they are carried to the south and southeast between the tip of Long Island and Block Island toward the open Atlantic. From year to year there is considerable difference in the rainfall, run-off, and wind direction and velocity during June and July in this region (see below); consequently, there is also considerable difference in the extent of the area covered by the surface water of lowered salinity. Though we have no direct evidence, we surmise that the extent of this outflow from L. I. S. may influence the survival of the eggs and larvae produced in B. I. S.—perhaps in a way similar to the influence exerted by variations in the hydrographic structure of the passage between the Baltic and North Sea on the survival of pelagic fish eggs and larvae. Further discussion of the possible correlation between low rainfall and the production of dominant year-classes appears in later pages. From the capture of larvae but not pelagic eggs (see above), it also seems that a number of species have centers of spawning abundance in waters adjacent to but not in B. I. S. Into this category fall the silver, squirrel, and white hakes as well as the yellowtail flounder, which appear to spawn to the east and southeast in open Atlantic water, and also the tautog and windowpane flounder, which are shallow spawners in this general area but whose larvae are carried only occasionally into the B. I. S. waters sampled by us.

We come now to our third objective, the variations in egg production in the different species from year to year as measured by our sampling. Table II shows that exceptionally large numbers of eggs of butterfish, weakfish, and cunner were taken in June and July 1944. In the same period in 1945 and 1946, though our tows were less intensive, we took relatively small numbers of eggs of these species, excepting the cunner in July 1945. In fact, the overwhelming preponderance of pelagic eggs of these species in 1944, as compared with the next two years, is such that we are led to the hypothesis that hydrographic conditions in this region were suitable for successful spawning of three species which apparently reproduce in B. I. S. at about the same time. If these conditions actually produced dominant year-classes of these three species in 1944, the commercial catch should reflect this fact in subsequent years when the fish first reached market size—in three years for the butterfish and in two years for the weakfish and cunner (Bigelow and Welsh). Taking the data for Connecticut and Rhode Island from the U. S. Fishery Statistics, the catch of butterfish in 1947 was much greater than the catches in the preceding years. In the five years from 1942–1946 the annual catch in this region ranged from 240,000–668,000 lbs., with an average per year of less than 430,000 lbs. In 1947 the catch was over 2,500,000 lbs., an increase of nearly six times the average catch for the past five years and of nearly five times the catch in the previous year, 1946. These figures reflect a real increase in the stock of butterfish and are not the result of a sudden postwar increase in fishing effort; in 1947 the increase in effort over the average from 1942–1946 was only about 40%, and the increase in 1947 over 1946 (so far as we can judge from the data) was less than 20%. Further evidence that the 1944 brood of butterfish was a dominant year-class of exceptional proportions comes from the fact that the catch in 1948 was nearly 2,250,000 lbs. with a fishing effort that was approximately the same as that in 1947. In short, 1944 was such a successful year for the survival of butterfish that the progeny of that spawning gave rise to a vastly increased catch in both 1947 and 1948.[2]

Turning to the weakfish, the landings in 1946 in Rhode Island and Connecticut, when the 1944 year-class first manifested itself in the commercial catch, were 550,900 lbs.; this was an increase of more than 60% over 1945 and much more than that over any other single year back to 1930, which is as far as we have traced the records. The fishing intensity in these waters appears to have been much the same in 1945 and 1946. In 1947 the catch fell to something less than 400,000 lbs., still high by standards over the last 15 years; however,

---

[2] This is added evidence that our identification of butterfish eggs as opposed to those of hake (*Urophycis* spp.) is correct (pp. 183–185). However, in fairness to the argument, we note also a large increase in the catch of hake in Connecticut and Rhode Island in 1947 (2,457,000 lbs.) as opposed to previous years (1942—41,200 lbs., 1943—692,200 lbs., 1944—247,200 lbs., 1945—1,015,400 lbs., and 1946—565,000 lbs.).

since the fishing intensity increased in 1947, it seems that the strong year-class of 1944 weakfish, while it contributed to the large catch in 1946, was not of sufficient strength to carry over another year, at least in such dominant fashion as did the butterfish from 1947 to 1948.

The third of these species which had a successful year-class in 1944 is the cunner. According to our estimate, the growth rate of this species is such that it should have appeared in the commercial catch records two years later, in 1946. In 1945 the landings of cunners in Connecticut and Rhode Island totaled 7,400 lbs., whereas in 1946 the total amounted to 37,400 lbs. Thus the catch in 1946 was five times that of the preceding year with much the same fishing intensity. It is evident that a dominant year-class of *Tautogolabrus adspersus* was also produced in 1944 and that it was responsible for the high catch in 1946.

The above evidence indicates clearly that three different species of fish with pelagic eggs and larvae, spawning at approximately the same time in the same region, produced successful year-classes in one year.

Hence we are led to a search for the conditions which produced dominance in three species simultaneously. During the course of our study, surface and bottom temperatures and salinities were taken in conjunction with the plankton hauls as a matter of routine (see Deevey, 1952: fig. 2, p. 69 of this issue. According to the data there was no significant difference in surface or bottom temperature in the June–July period over the three years. Also, bottom salinity appears to have ranged between relatively narrow limits (31.5–32.0 °/₀₀) in the same period from 1944–1946. However, at the surface, where the eggs of butterfish, weakfish and cunner were taken in such profusion, the salinity was approximately 2.0 °/₀₀ higher throughout June and July 1944 than it was in those months in either 1945 or 1946. This is a very considerable salinity difference, and it is most unfortunate that data for the surface salinity in B. I. S. over a longer period of years is not available for correlation with the catch records of these three species. We therefore turn to other sources of information.

Table VII provides the catch records of these three species together with the available meteorological data from 1929–1948. It is obvious that in the spring and early summer of 1944 both the precipitation and the run-off were low—considerably under the average for the 18-year period. This would appear to correspond with the abnormally high salinity and with the high survival of butterfish, weakfish and cunner eggs in 1944. It becomes of interest, then, to examine the available

TABLE VII. FISH LANDINGS AND AVAILABLE METEOROLOGICAL DATA, 1929-1948

	LANDINGS IN THOUSANDS OF LBS., CONN & R.I.(1)			PRECIPITATION (IN.) MAY, JUNE, JULY(4)	RUN-OFF (IN.) CONN. RIVER, JUNE, JULY(5)	AV. WIND M.P.H. & DIRECTION(4)		MAX. WIND M.P.H. & DIRECTION, DATE(4)		AV. AIR TEMP & DEVIATION (°F)(4)		
DATE	*BUTTER-FISH*	*WEAK-FISH*	*CUNNER*			*JUNE*	*JULY*	*JUNE*	*JULY*	*MAY*	*JUNE*	*JULY*
1929	—	—	—	7.59	1.73	SW –	SW –	W 32 –	NW 29 –	54.3 +1.5	63.8 +2.0	68.7 +0.3
1930	937	184	88(2)	9.13	2.67	SW –	SW –	W 36 1st	SW 26 19th	56.8 +4.0	65.0 +3.2	70 4 +2.0
1931	772	80	103	12.97	3.52	SW –	S –	NE 36 10th	SW 36 22nd	54.4 +1.6	63.5 +1.7	70.0 +1.6
1932	664	75	76(2)	7.97	1.78	SW –	W –	NW 46 23rd	SW 30 27th	53.4 +0.6	61.8 0.0	68.8 +0.4
1933	502	83	41(2)	6.69	1.10	S –	SW –	SW 32 12th	N 49 5th	55.6 +2.8	63.4 +1 6	66.8 -1.6
1934	—	—	—	8.25	1.59	SW –	SW –	SE 38 19th	SW 25 7th	54.9 +2.1	63 6 +1.8	71.0 +2.6
1935	789	67	1(2)	10.40	3.17	SW –	SW –	NE 31 18th	E 29 9th	52 6 -0.2	62.2 +0.4	70 0 +1 6
1936	—	—	—	7.72	1.20	SW –	SW –	NE 38 24th	N 36 9th	54.3 +1.5	63.1 +1.3	68.0 -0.4
1937	610	73	15	9.97	2.87	SW 11.3	SW 11.1	SW 29 1st	SW 27 16th	55.6 +2.8	63 4 +1.6	69.7 +1.3
1938	637	67	45	14.76	2.56	S 13.3	S 12.3	W 36 5th	SW 24 15th	53.1 +0.3	62 4 +0 6	69.6 +1 2
1939	1,001	67	10(3)	6.77	1.66	S 12.5	SW 12.7	S 26 30th	W 42 10th	53.7 +0.9	62 9 +1 1	68.8 +0.4
1940	585	46	9	10.87	2 75	SW 13.7	SW 11 3	NE 30 10th	NE 30 4th	53.1 +0.3	60.8 -1.0	69.4 +1.0
1941	—	—	—	10.35	1.29	SW 15.8	NE 12.6	NE 40 5th	NE 44 29th	55 5 +2 7	62.0 +0.2	67.9 -0.5
1942	244	70	2(3)	10.14	2.12	SW 11.7	SW 12 5	W 25 25th	E 34 11th	55 8 +3.0	63.9 +2.1	69.2 +0.8
1943	664	71	5(3)	10.78	2.54	SW 13.6	SW 12.4	SW 31 28th	NW 34 22nd	53 6 +0.8	65.4 +3.6	69.8 +1.4
1944	322	283	3(3)	7.13	2.06	SW 13.9	SW 12.3	S 37 19th	NW 36 16th	57.4 +4.6	63 6 +1.8	71.2 +2.8
1945	386	339	7	14.09	4.06	SW 13.9	SW 11.4	NE 46 –	S 32 –	53.2 +0.4	64.0 +2.2	69.3 +0.9
1946	529	551	37	10.00	4.38	SW 14.6	SW 11.9	NE 35 –	SW 27 –	53.8 +1.0	61.6 -0.2	67.8 -0.6
1947	2,537	395	19	—	—	—	—	—	—	—	—	—
1948	2,232	243	12	—	—	—	—	—	—	—	—	—
AVERAGES	838	168	30	9.75	2 39							

(1) U. S. Fishery Statistics (1930–1948).

(2) Catch recorded for Rhode Island only.

(3) Catch recorded for Connecticut only.

(4) Precipitation for entire New England area. U. S. Monthly Weather Reviews (1928–1946).

(5) Run-off of Connecticut River at Thompsonville, Conn. U. S. Geological Survey. Surface Water Supply of the U. S.: The North Atlantic Coast.

records to see if below-average rainfall and run-off in any other year or years, in combination or separately, give a similar correspondence with increased landings of the species concerned, allowing the proper time interval for each to grow to a size at which it entered the commercial catch. In 1941 and 1942, although the rainfall was slightly above average, the run-off was below average in both years; in 1944 the catch of weakfish was four times (or more) that in either of the two preceding years, which may be a reflection of the low run-off in 1942 (and 1941?), although neither the butterfish nor the cunner catch appear to have shown a corresponding increase in abundance. In 1939 both precipitation and run-off were below average, even more so than in 1944. However, the catch records (unfortunately incomplete) give no indication that this combination produced dominant year-classes in any of these three species. Carruthers, Lawford and Veley (1951) have recently shown for various North Sea fish that there may be remarkable correlations of brood-strength fluctuations with wind direction and force. Table VII shows that the heaviest blow from the west (42 m. p. h.) in either June or July from 1929 through 1946 took place on July 10, 1939. This wind probably moved the less saline surface water of L. I. S. into B. I. S., and thus it may have counteracted the effects of below-average rainfall and run-off at about the time when egg production was high. Thus there is a possible explanation why the combination of low rainfall and run-off in 1939 apparently did not produce dominant year-classes of butterfish, weakfish, or cunner. Of course the matter is complicated by a lack of knowledge as to when the peak of spawning occurred in each of these three species in 1939; that is, we do not know whether the blow of July 10 coincided with the period of maximum egg production in these waters in that year and hence whether it might have been an effective agent of destruction. In 1936 both the precipitation and the run-off were well below average (Table VII), and from an examination of subsequent catch records there is clear evidence of high survival in two of three species considered here. The butterfish landings jumped from 636,600 lbs. in 1938 to over a million pounds in 1939, and the cunner catch was nearly three times as great in 1938 as it was in 1937. On the other hand, the landings of weakfish from 1937–1939 in Connecticut and Rhode Island waters were almost exactly the same in each year, a fact which brings us to another variable in this study. Two of the three species (butterfish and weakfish) are not year-round residents of

B. I. S. waters, and the extent of their migrations from the south each year is not known. Accordingly, high survival might occur in southern New England waters in any one year, but an increased catch in this area two or three years later would not necessarily follow. In 1932, 1933, and 1934—three successive years—the precipitation and run-off were below normal, conditions which might have been expected to produce high salinity in B. I. S. and possibly good survival of the pelagic fish eggs. Unfortunately the catch records for the critical years (1934–1937) are incomplete, but even so there is no indication that dominant year-classes in any of these three species were produced in these three "dry" years. In 1929 also, precipitation and run-off were below average, but there is no strong evidence from the catch records that dominant year-classes were produced. Turning to 1928, it is unfortunate that the cunner data over the full 19-year span are so incomplete (see Table VII and footnotes). However, the catches in these waters in 1930, 1931, and 1932 were apparently much greater than those in any year through 1948, and if the landings reflect actual abundance it would appear that a dominant year-class of cunner must have been produced in 1928. The meteorological records show a slightly above-average rainfall (10.84) in the May–July period in that year, but run-off data are not available since they were first recorded for August 1928. Hence we are denied evidence as to whether or not 1928 was a year of high salinity in the surface waters of B. I. S. at the time when cunners were spawning. There is also another unsatisfactory element in dealing with data of this sort. While a general estimate of the effort expended in any one year may be obtained from the number of men and boats and the amount of gear, the data do not take into account the *demand.* This factor provides a significant variable (*cf.* Taylor, 1951); thus the above-average landings of butterfish, weakfish, and cunner in 1930 may be no more than a reflection of the onset of the economic depression which characterized the first half of that decade.

From all of the above evidence, unsatisfactory as the data are, it appears quite possible that relatively high survival of butterfish, weakfish, and cunner eggs in B. I. S. is associated with high surface salinity resulting in part at least from low rainfall, low run-off, or a combination of both. The available information for 1944 is especially convincing. The rest of the data in Table VII show that every notable increase in the landings of any of the three species in one year over another, is, with one exception, associated either with a combination of low rainfall and run-off, or at least with below-average run-off. Even the exception, the landings of butterfish in 1943, is dubious; normally butterfish reach commercial size in their third year after the eggs are laid, but it appears from Bigelow and Welsh that many may not be of catchable size until their fourth year, and it is clear that 1939 was low in both rainfall and run-off. However, this postulate would necessitate the assumption that the heavy westerly blow on July 10th, 1939, had an adverse effect on weakfish and cunner spawning but not on butterfish spawning.

If it appears that notable increases in catch correspond for the most part with low rainfall, run-off, or both, the converse is not apparent from the data. In other words, there are years when the addition of fresh water from sky or land was low and when dominant year-classes were not necessarily produced in one or more of the species concerned. However, if we look to high salinity (ca. 32.0 °/₀₀) as an important factor in the survival of the eggs of these species, we must look beyond mere precipitation and run-off records; for example, exceptionally high winds from the right direction at the right time could move less saline water from L. I. S. into B. I. S. with deleterious effect when these fish spawn.

On the basis of the available evidence we believe there is a good chance that prediction of dominant year-classes of these three species could be accomplished with a high degree of success. If this supposition is correct, it would seem from the 1944–1946 plankton hauls that this could be done by making quantitative tows during the spawning period and by making comparative counts from year to year. With more knowledge of the exact spawning period of each species, it might be possible to make such prediction solely by taking surface salinities; or it might even be done by examination of the precipitation, run-off, wind force and wind direction data without ever going to sea.

REFERENCES

Agassiz, Alexander and C. O. Whitman

1885. Studies from the Newport Marine Laboratory. XVI. The development of osseous fishes. I. The pelagic stages of young fishes. Mem. Harv. Mus. comp. Zool., *14* (1) Pt. 1: 1–56.

Barnes, H.

1949. A statistical study of the variation in vertical plankton hauls, with special reference to the loss of the catch with divided hauls. J. Mar. biol. Ass. U. K., N. S. *28:* 429–446.

Bigelow, H. B.
1928. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924), *40* (2): 1–509.
Bigelow, H. B. and William Welsh
1925. Fishes of the Gulf of Maine. Bull. U. S. Bur. Fish (1924), *40* (1): 1–567.
Breder, C. M., Jr.
1929. Field book of marine fishes of the Atlantic Coast from Labrador to Texas. G. P. Putnam's Sons. New York. 332 pp.
Carruthers, J. N., A. L. Lawford and V. F. C. Veley
1951. Fishery Hydrography: Brood-strength fluctuations in various North Sea fish, with suggested methods of prediction. Kieler Meeresforsch., *8* (1): 5–15.
Dannevig, Alf
1919. Canadian fish eggs and larvae. Canad. Fish. Exped. (1914–15). 74 pp.
Deevey, G. B.
1952. A survey of the zooplankton of Block Island Sound, 1943–1946. Bull. Bingham oceanogr. Coll., *13* (3): 65–119.
Hildebrand, S. F.
1943. A review of the American anchovies (family Engraulidae). Bull. Bingham oceanogr. Coll., *8* (2): 1–165.
Hildebrand, S. F. and L. E. Cable
1930. Development and life history of fourteen teleostean fishes at Beaufort, N. C. Bull. U. S. Bur. Fish. (1930), *46:* 383–488.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or sea trouts, family Sciaenidae, of the Atlantic Coast of the United States. Bull. U. S. Bur. Fish. (1933), *48:* 41–117.
1938. Further notes on the development and life history of some teleosts at Beaufort, N. C. Bull. U. S. Bur. Fish. (1937), *48:* 505–642.
Hildebrand, S. F. and W. C. Schroeder
1928. Fishes of Chesapeake Bay. Bull. U. S. Bur. Fish (1927), *43* (1): 1–388.
Jordan, D. S. and B. W. Evermann
1896. A check-list of the fishes and fish-like vertebrates of North and Middle America. Rep. U. S. Comm. Fish. (1895): 207–584.
Kuntz, A. and Lewis Radcliffe
1917. Notes on the embryology and larval development of twelve teleostean fishes. Bull. U. S. Bur. Fish. (1915–1916), *35:* 87–134.
Marshall, Nelson
1946. Observations on the comparative ecology and life history of two sea robins, *Prionotus carolinus* and *Prionotus evolans strigatus.* Copeia, 3: 118–144.
Merriman, Daniel and H. E. Warfel
1948. Studies on the marine resources of southern New England. VII. Analysis of a fish population. In—A symposium on fish populations. Bull. Bingham oceanogr. Coll., *11* (4): 131–163.
Moore, Emmeline
1947. Studies on the marine resources of southern New England. VI. The sand flounder, *Lophopsetta aquosa* (Mitchill); a general study of the

species with special emphasis on age determination by means of scales and otoliths. Bull. Bingham oceanogr. Coll., *11* (3): 1–79.

MORROW, J. E.
1951. Studies on the marine resources of southern New England. VIII. The biology of the longhorn sculpin, *Myoxocephalus octodecimspinosus* Mitchill, with a discussion of the southern New England "trash" fishery. Bull. Bingham oceanogr. Coll., *13* (2): 1–89.

NICHOLS, J. T. AND C. M. BREDER, JR.
1926. The marine fishes of New York and southern New England. Zoologica, *9* (1): 1–192.

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). I. Psettodidae, Bothidae, Pleuronectidae. Brit. Mus. (Nat. Hist.), London. 459 pp.

OLSEN, Y. H. AND DANIEL MERRIMAN
1946. Studies on the marine resources of southern New England. IV. The biology and economic importance of the ocean pout, *Macrozoarces americanus* (Block and Schneider). Bull Bingham oceanogr. Coll., *9* (4): 1–184.

PEARSON, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout *Cynoscion regalis* (Bloch). Fish. Bull., U. S. Fish Wildl. Serv., 36: 79–102.

PERLMUTTER, ALFRED
1939. A biological survey of the salt waters of Long Island, 1938. Section I. An ecological survey of young fish and eggs identified from tow net collections. Suppl. 28th Ann. Rep. N. Y. Cons. Dept., Pt. II: 11–71.

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

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Fish. Bull. U. S. Fish Wildl. Serv., 38: 149–237.

TAYLOR, H. F., ET AL.
1951. Survey of marine fisheries of North Carolina. Univ. of North Carolina Press. Chapel Hill. Pp. 288–471.

U. S. FISH AND WILDLIFE SERVICE
1930–1948. Fishery statistics of the United States. R. H. Fiedler ed., 1930–1941; A. W. Anderson and E. A. Power eds., 1942–1948.

U. S. GEOLOGICAL SURVEY
1929–1948. Surface water supply of the United States: The North Atlantic Coast. Nos. 641, 661, 681, 696, 711, 726, 741, 756, 781, 801, 821, 851, 871, 891, 921, 951, 971, 1001, 1031, 1051, 1081, 1111.

U. S. WEATHER BUREAU
1927–1946. Monthly Weather Review. Vols. 64–74.

Warfel, H. E. and Daniel Merriman
1944. Studies on the marine resources of southern New England. I. An analysis of the fish population of the shore zone. Bull. Bingham oceanogr. Coll., *9* (2): 1–91.

Welsh, W. W. and C. M. Breder, Jr.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U. S. Bur. Fish. (1929), *39:* 141–201.

THE HERRING (*CLUPEA HARENGUS*) OF BLOCK ISLAND SOUND[1]

By Howard L. Sanders

Narragansett Marine Laboratory, University of Rhode Island,
Kingston, R. I.

TABLE OF CONTENTS

ABSTRACT

This study was undertaken to observe the location and seasonal abundance of herring catches in Block Island Sound, to perform racial analyses, and to study the stomach contents both quantitatively and qualitatively. It was found that herring were present in B. I. S. from about January 1 to mid-March and that the shoals were made up of two groups, spent adults and immature adolescents. The mature individuals formed the major portion of the herring population until early February, after which the adolescents were dominant. During January and February the

---

[1] A modification of a thesis prepared at the Bingham Oceanographic Laboratory, Yale University and submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Oceanography from the University of Rhode Island.

This paper originated as a technical report under a contract with the Office of Naval Research.

fish were found in the coldest water, i. e., in a narrow band near and parallel to the shore, but later they dispersed widely as the B. I. S. waters became warmer. The population had a mean vertebral count of 56.48 and a mean scute count of 14.09. The herring fed little during January and the first half of February, but the feeding rate thereafter increased rapidly, with adolescents usually feeding more intensively than adults. The most important single food organism was the copepod *Pseudocalanus minutus*, which constituted more than 70% of the food by number. Herring tend to select larger crustacean components in preference to the smaller ones.

INTRODUCTION

Within the past six years an extensive fishery has developed in the waters of B. I. S. for the sea herring, *Clupea harengus*. As a result, this fish has become numerically and economically one of the most important species caught in these waters during winter months. Most fishermen believe that herring were always abundant in B. I. S., but they suggest that these stocks were not successfully exploited until the balloon net was introduced, a modification of the otter trawl that fishes more efficiently the water immediately above the bottom. Despite its economic importance, no extensive studies of herring in our Atlantic waters have been published, and since detailed information is necessary for the intelligent use of this natural resource, the present investigation was undertaken in the hope of providing some essential information in the limited geographical area concerned. However, it is apparent that similar work on a broader scale is needed for proper interpretation of the results.

ACKNOWLEDGMENT

To the Bingham Oceanographic Laboratory and its staff I am grateful for the necessary equipment made available to me for this study. I also wish to express my sincere thanks to G. A. Riley, E. F. Thompson, Daniel Merriman and Y. H. Olsen for helpful advice and criticism, to Captain Harold McLaughlin for making available the facilities of his dragger MARISE for the collection of specimens and data, to D. M. Sanders for assistance in making this manuscript more readable, to A. H. Leim of the Atlantic Biological Station, St. Andrews, Nova Scotia for making available some of the data of the Atlantic Herring Investigation, and finally, to my wife for her aid in the preparation of the manuscript and plates.

COLLECTION AND ANALYSIS OF DATA

Periodic collections in B. I. S. were made aboard the commercial trawler MARISE beginning December 15, 1950; however, the first herring did not appear in the catch until January 6, 1951, at which time analyses were started on both herring and plankton samples. On eight additional dates from then until March 17, 1951 samples were obtained. The fish were taken from the commercial catches, and the plankton were obtained by means of a Clarke-Bumpus plankton net. Approximately 400 herring were collected.

In the laboratory, the following procedures were followed:

(1) *Examination of the Gonads.* The condition of gonads in adult fish was observed to give a measure of the approximate spawning season. That is, it was noted whether the gonads were large and ripe, or spent.

(2) *Vertebral and Scute Counts.* In order to ascertain populations, vertebral and scute counts were taken. Vertebral counts included all vertebrae from the first nonfused vertebra through the last vertebra or hypural plate. The vertebrae of 101 specimens were counted. A scute count is defined here as the number of nonfused spiny protuberances between the pelvic girdle and the vent. The scutes of 227 specimens were counted.

(3) *Age Determination.* In ascertaining age, the scale annuli were used to establish the age parameters rather than the strength of the various year classes. This limitation had to be imposed because of the poor readability of most of the scales in this population and because of the inadequate number of samples.

(4) *Stomach Analysis.* The organisms found in the stomach contents of herring were identified, counted and measured; the kind of food eaten, the intensity of feeding, and the size of the organisms eaten were thus ascertained. The stomachs of 177 herring, taken from all periods of the investigation, were examined.

(5) *Analysis of the Plankton Sample.* The organisms in all of the plankton samples were identified, counted and measured. A comparison of the zooplankton with organisms in the stomachs of herring taken at the same time and place was used in an attempt to determine whether herring were selecting certain species or certain sizes of zooplankton in preference to others.

(6) *Wet Weight Measurements.* From each of the nine collections, one sample of the stomach contents and another of a plankton tow

were filtered by suction and then weighed, thereby obtaining a quantitative measure of each sample.

OCCURRENCE AND DISTRIBUTION

Herring first appeared in B. I. S. about January 6, 1951, at which time the group was composed of adults that had spawned recently. During the month of January these mature fish formed the entire herring stock, but early in February smaller immature herring, mostly two and three years of age, began to appear in the catch; thereafter these formed a progressively larger proportion of the stock and by the beginning of March they constituted almost the entire population. During the last third of February the older fish began to disappear and by early March they were scarce. The main body of immature herring left B. I. S. by the middle of March, but small numbers were encountered to the end of the month.

It has been demonstrated that there is a slow coastal drift to the southwest along the continental shelf, and since some of this water moves into B. I. S., herring could be brought into the Sound from the northeast if their movements at this time of the year were random rather than definitely migratory. Similar passive movements have been revealed by studies of Icelandic (Johansen, 1927) and Norwegian (Lea, 1919) herring. Marty (1941) demonstrated that the distribution of herring in the Barents Sea depended on the North Cape Current and its branches, and he observed further that spent herring moved eastward with the current after spawning.

In such places as the Bay of Fundy, Long Island Sound and along the New Jersey Coast, commercial catches of herring made during the winter indicate that herring are confined to the colder shallow inshore waters, a winter distribution pattern that is probably characteristic of our Atlantic herring to at least as far north as the Canadian border. During their stay in B. I. S., most of the herring were found in the lower depths of a narrow belt of water one to three miles off the coasts of Connecticut and Rhode Island (see Fig. 1) where the temperature of the water varied from 2–4° C during January and February. Although the temperature probably fluctuates from year to year, the water along the shore is generally colder than that farther offshore. This type of temperature distribution is typical of all coastal water from the Gulf of Maine to Cape Hatteras (Bigelow, 1933) and of most temperate and arctic areas, since the shallow water is more directly

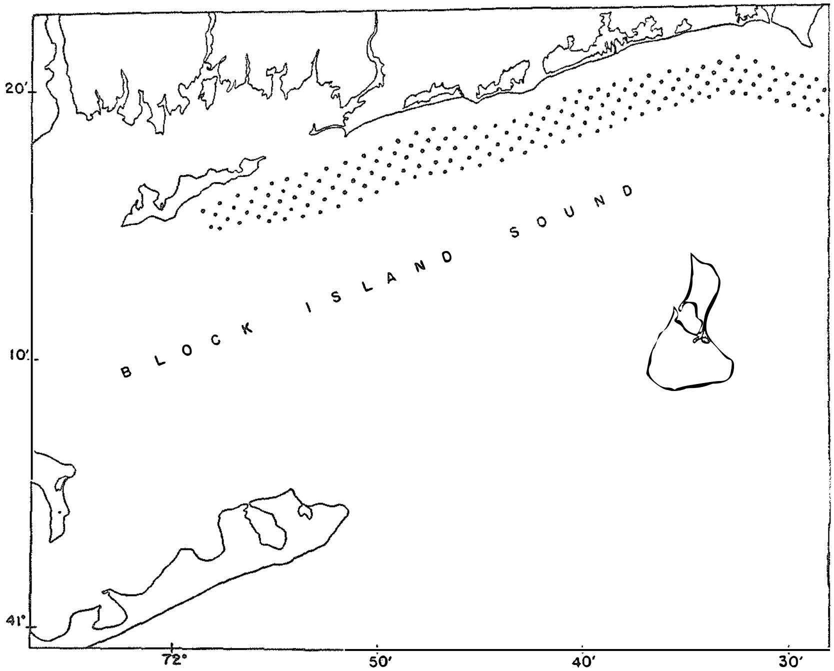


Figure 1. The distribution of herring shoals in B. I. S. during January and February 1951. The region west of the dotted area is restricted militarily and thus was not sampled.

influenced by external temperature than the deeper and better insulated water masses.

Apparently a similar preference for shore waters is described by Manteufel and Boldovsky (1938) in their paper dealing with the wintering of the Barents Sea herring. They found that herring tend to move into waters of lower temperature with the advent of winter and that they then become relatively immobile. Furthermore, they believed that this behavior allowed the fish to exist more economically on its reserves of fat during the winter, since the metabolic demands of these cold-blooded animals would be less in the colder environment. Thus the fish were found along the coasts and in the fjords of Murman, where the characteristic water temperature was about 2° C, only slightly lower than the temperature where herring were found in B. I. S.

One may thus surmise that herring from the region east of B. I. S. follow the coastal residual drift into this Sound during the early winter, where they seek the coldest water and inhabit the lower depths of a

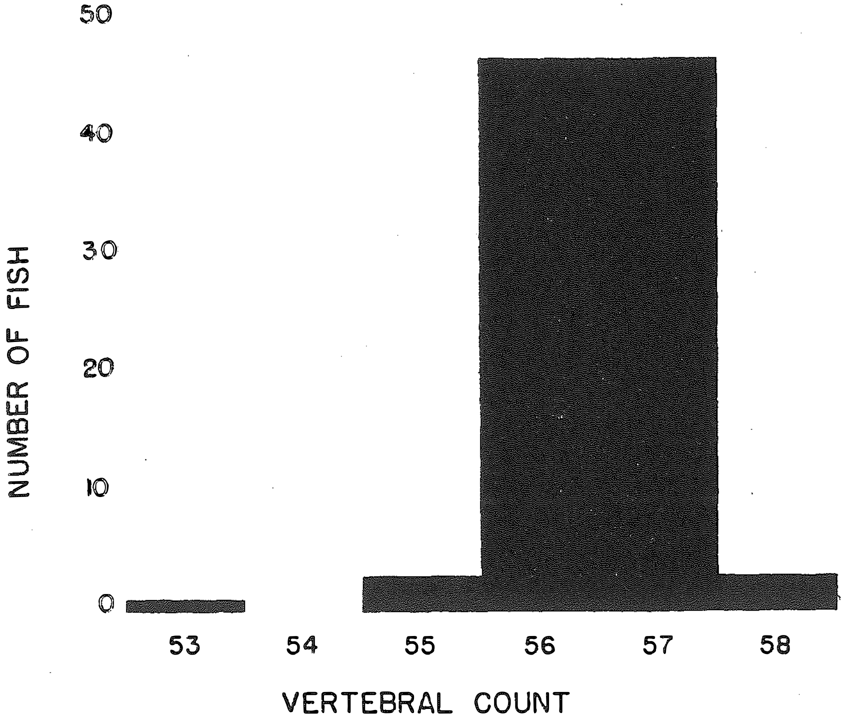


Figure 2. Histogram showing the vertebral count composition of B. I. S. herring. The mean of the population is 56.5653, the standard deviation 0.700.

narrow band of water close inshore. With the dissipation of this cold inshore water in the spring, the herring disperse and become more homogeneously distributed.

RACIAL ANALYSIS

There is little published work on racial investigations of herring populations along the Atlantic Coast of North America. The only work available to the writer at present is a paper by Lea (1919) which deals with age and growth of herring in Canadian waters. Although a small section of his work is concerned with racial characters, unfortunately his results are based on inadequate samples. Nevertheless, they afford the only means by which the writer can compare his own results.

Vertebral Count. The B. I. S. results of vertebral counts are summarized as follows:

Number of specimens	101
Mean count	56.4653
Standard Deviation	0.700
Standard Error of the Mean	0.0693

Thus most of the herring have a vertebral count of 56 or 57 (see Fig. 2), with little spread in the population and with the probable error of the mean very small. However, the mean of the B. I. S. population is so close to the means of some of the populations investigated by Lea (see Table I) that it is obvious that vertebral count in itself cannot be used to distinguish the population.[2] It is quite likely that the B. I. S. population, despite its more southern distribution, spawns at temperatures that are not too different from the populations described by Lea. Bigelow and Welsh (1925) have shown that herring begin to spawn in July in the northern part of the Gulf of Maine and then spawn progressively later southwardly. Thus water temperatures during the spawning of the egg may be similar throughout the entire range, a fact which would account for the relatively little variation in vertebral count along this Atlantic Coast.

Scute Count. The results of scute counts for B. I. S. herring are summarized as follows:

Number of specimens	227
Mean count	14.0925
Standard Deviation	0.8281
Standard Error of the Mean	0.0549

Most of the herring have a scute count of 13, 14, or 15 (see Fig. 3) and the probable error of the mean is very small, thus indicating that the mean of the sample lies very close to the mean of the true population. The mean of the B. I. S. population is significantly higher than all of those described by Lea, excepting the sample taken from the Bay of Fundy (Table I), and consequently this character clearly

---

[2] Preliminary results on population studies carried out in Newfoundland waters, in the Gulf of St. Lawrence, and on the coasts of Nova Scotia by the Atlantic Herring Investigation show a wider spread in the mean vertebral number of Canadian Atlantic Coast populations than do those revealed by Lea (Leim, personal letter).

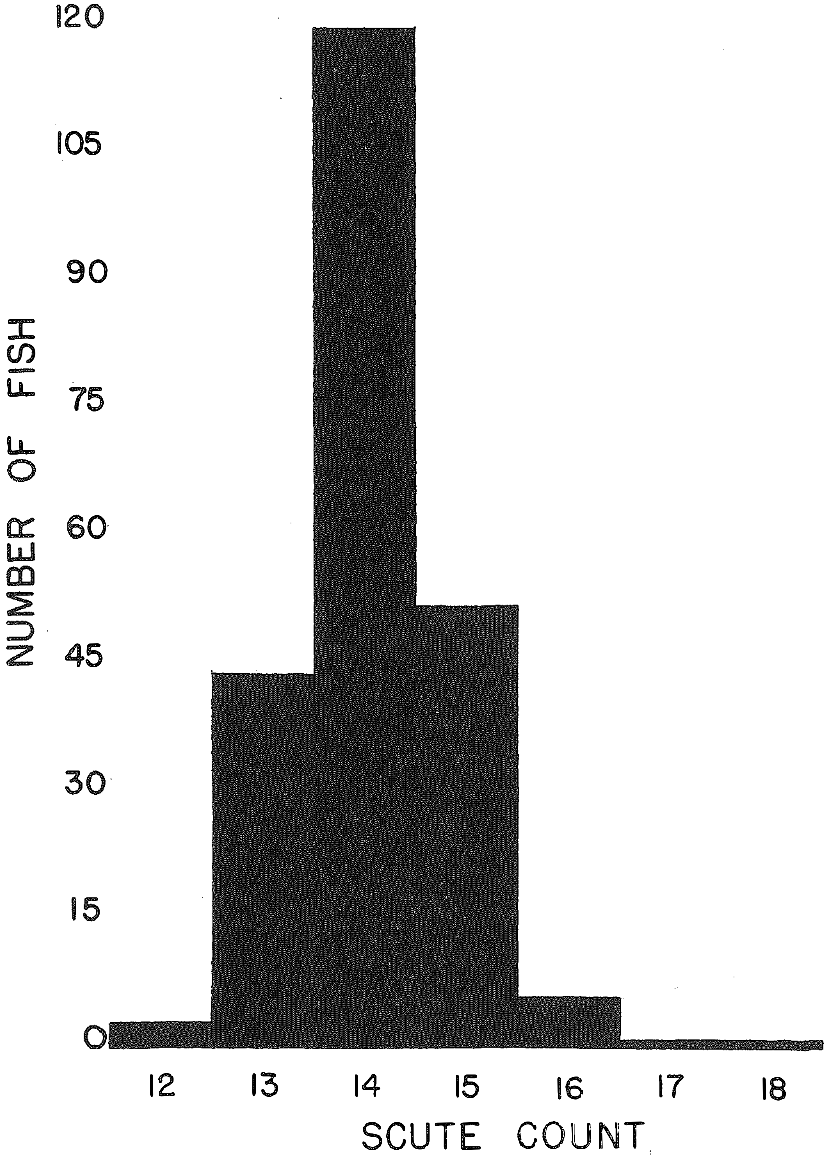


Figure 3. Histogram showing the scute count composition of B. I. S. herring. The mean of the population is 14.0925, the standard deviation 0.8281.

TABLE I. A COMPARISON OF THE B. I. S. HERRING WITH SEVEN OTHER AMERICAN COASTAL POPULATIONS INVESTIGATED BY LEA (1919)

Location	*Date*	*Age*	*Gonads*	*Vert. Count*	*Scute Count*
Newfoundland, west coast	Autumn 1914	Mature	Regenerating	56.8	12.6
Magdalen Islands	May 1914	Mature	Ripe	56.5	12.5
Northumberland Strait	May 21, 1914	Mature	Ripe	56.3	12.5
W. Ardoise, Cape Breton	Aug. 10, 1914	Mature	Ripening	56.5	12.9
Lockeport, Nova Scotia	Nov. 1914	Mature	Ripe?	56.5	12.9
Bay of Fundy	Nov. 1914	Immature	—	56.5	14.1
Gloucester, Mass.	Nov. 1914	Immature	—	56.7	13.2
Block Island Sound	Winter 1951	Mature and immature	Spent	56.46	14.09

separates the B. I. S. population from all except the Bay of Fundy group. However, the adults of the B. I. S. and Bay of Fundy populations need not be confused when the gonad development is noted, for the Bay of Fundy population spawns largely during the summer (Bigelow and Welsh, 1925) while the B. I. S. group appears to spawn well into the fall.

The question arises why the B. I. S. population should agree so closely in one meristic character with the populations investigated by Lea and at the same time vary so markedly in another, except in one instance. This may be interpreted to mean that the scutes and vertebrae are laid down at different stages during embryological development, in which case somewhat different hydrographic conditions may effect each character. If some of the races are spring spawners, as is indicated by Lea's data, then the water on the whole will get warmer as the animal develops. Conversely, if a population spawns in the fall, as is the case in B. I. S., the water will be colder during the later stages of development. But theoretically the temperature could be the same at some particular stage in the development of both spring and fall stocks, and if so, the temperatures would be different for any earlier or later stage. Hence, the development of one meristic character might be subject to the same temperature effect in both stocks, whereas another character, developing earlier or later, would not.

Another possible explanation for this phenomenon can be based on the assumption that different meristic characters manifest different degrees of sensitivity to hydrographic conditions. As a result, one character may be markedly modified while another is hardly altered at all.

At this point it should be obvious that much more work needs to be done not only on meristic characters but on life histories throughout

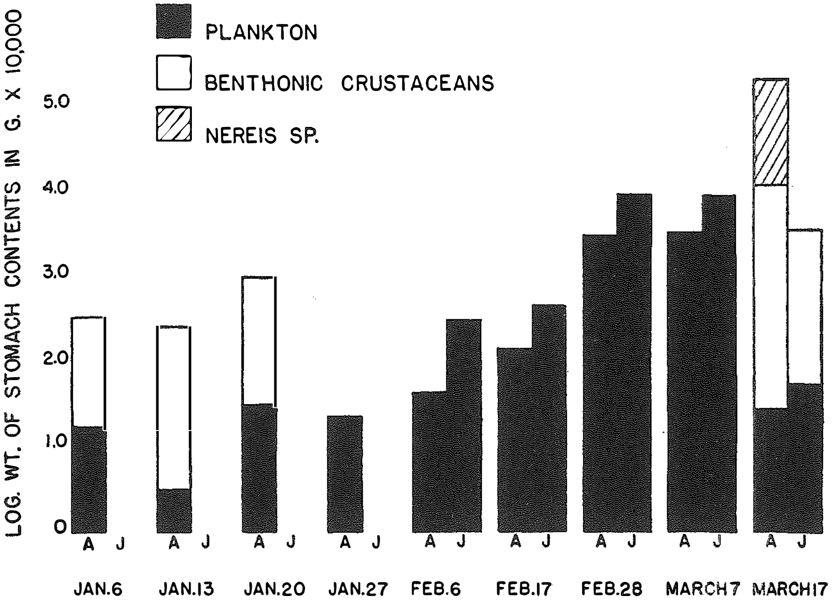


Figure 4. The gross composition of the stomach contents and the feeding intensities of both adult and juvenile herring in B. I. S. during the winter of 1951.

the entire range of the herring along this coast. Only in this way can the different races be delimited and their importance to the fishery evaluated.

FOOD AND FEEDING

The Food. Plankton and benthonic invertebrates make up the food of the herring in B. I. S. In regard to plankton, the most important single organism is the copepod *Pseudocalanus minutus*, its importance being due to its tremendous abundance. It forms more than 80% of the zooplankton population in the lower water layers of B. I. S. during the winter and about 73% of the plankton by count in the stomachs of herring. Other planktonic organisms commonly found in stomach analyses are the copepods *Centropages typicus, Temora longicornis,* and the nauplius and cypris larvae of the barnacle, *Balanus balanoides.* Less commonly encountered are the copepods *Oithona similis, Acartia tonsa,* and the chaetognath *Sagitta elegans.* These organisms are essentially the same plankton that form the main constituents of the herring's food in the littoral waters of Denmark (Jespersen, 1928; 1932).

The benthonic invertebrates, except on a single date, were never eaten in large enough numbers by the herring to permit an evaluation of the different organisms involved. The species found in the stomachs were: the shrimp, *Crago septemspinosus;* the mysid, *Michtheimysis stenolepis;* the cumacid, *Diastylis* sp.; the amphipods, *Dulichia monocantha* and *Monoculodes edwardsi;* and the heteronereid stage of the polychaete worm *Nereis* sp. The one common denominator of all of these animals is that they are active and nonburrowing forms, at least during that stage of their life history when they were captured.

These results are in agreement with the findings of both Jespersen (1936) and Chajanova (1939) who observed that benthonic invertebrates were moderately common in the diet of the herring only in the winter, a phenomenon no doubt related to the fact that herring are found near the bottom during this season of the year.

The Feeding Cycle. European investigators have noted, with a single possible exception (Jespersen, 1928), that herring during the course of a year follow a feeding rhythm that appears independent of its food. The maximum feeding intensity occurs in spring and is followed by a continuous decrease until late autumn, when feeding almost ceases. Later, during the winter, the feeding tempo increases slowly at first and then much more rapidly in early spring.

Observations on the feeding of B. I. S. herring appear to agree closely with the cycle just described. During January the feeding is at a very low intensity, but by mid-February the rate accelerates and remains high until the herring disappear from B. I. S. in March (see Fig. 4). During the winter period of depressed feeding, benthonic invertebrates, such as amphipods, macrurans, cumacids and mysids, make up a relatively large component of the food. Later, as the feeding intensity increases, the food is almost exclusively planktonic. The single exception to this is found in the March 17 sample, which may merely represent an atypical situation induced by a local reproductive swarm of heteronereid worms.

Another aspect of this investigation that conforms with results of European biologists is the fact that adolescents fed at a higher rate of intensity than adults on all comparable dates during the period in question, again excepting March 17, when adults may have been more efficient in capturing relatively large food, i. e., the heteronereid worms.

According to Deevey (1952) there is no significant reduction in the quantity of zooplankton in B. I. S. during the winter. Furthermore,

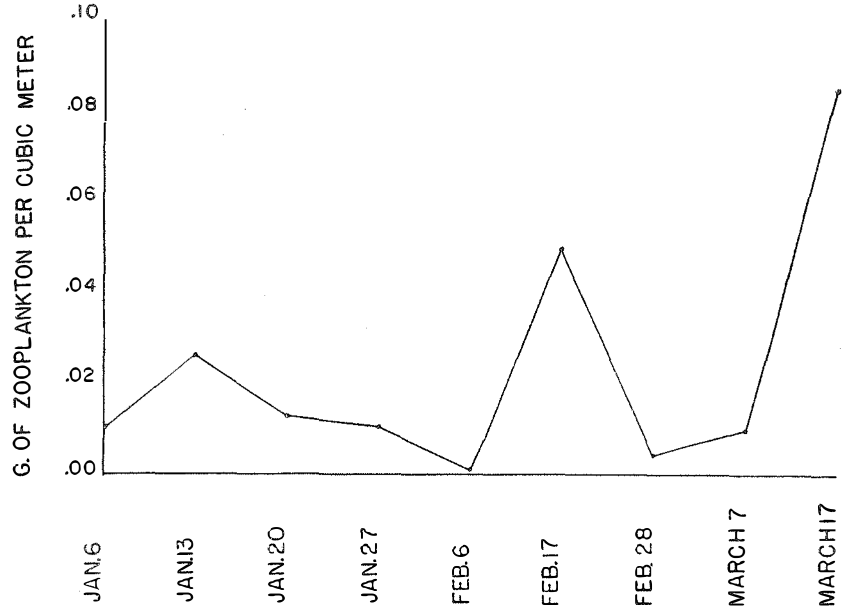


Figure 5. The abundance of zooplankton in the surface waters of B. I. S. on specific dates during the winter of 1951.

from the data available, there is no apparent correlation between the feeding intensity of the herring and the size of the plankton samples taken near the surface during the period of this investigation (see Figs. 4 and 5). On only two occasions were plankton samples successfully obtained from the water mass immediately above the bottom, and in both instances the sample from the bottom was significantly larger than that taken near the surface. Meager as the data may be, there is at least an indication that the herring do not feed actively even though plankton is available throughout the water column.

In all waters north of Cape Cod, where the zooplankton population is greatly reduced during the winter months, plankton feeders probably adapt themselves physiologically in some manner to the varying seasonal abundance of their food. The B. I. S. population, at the southern periphery of the herring's range, is probably derived from more northern ancestors who laid down this intrinsic feeding cycle. Thus, during the period of depressed feeding, the B. I. S. herring seek the coldest available water, where the metabolic demands are the least.

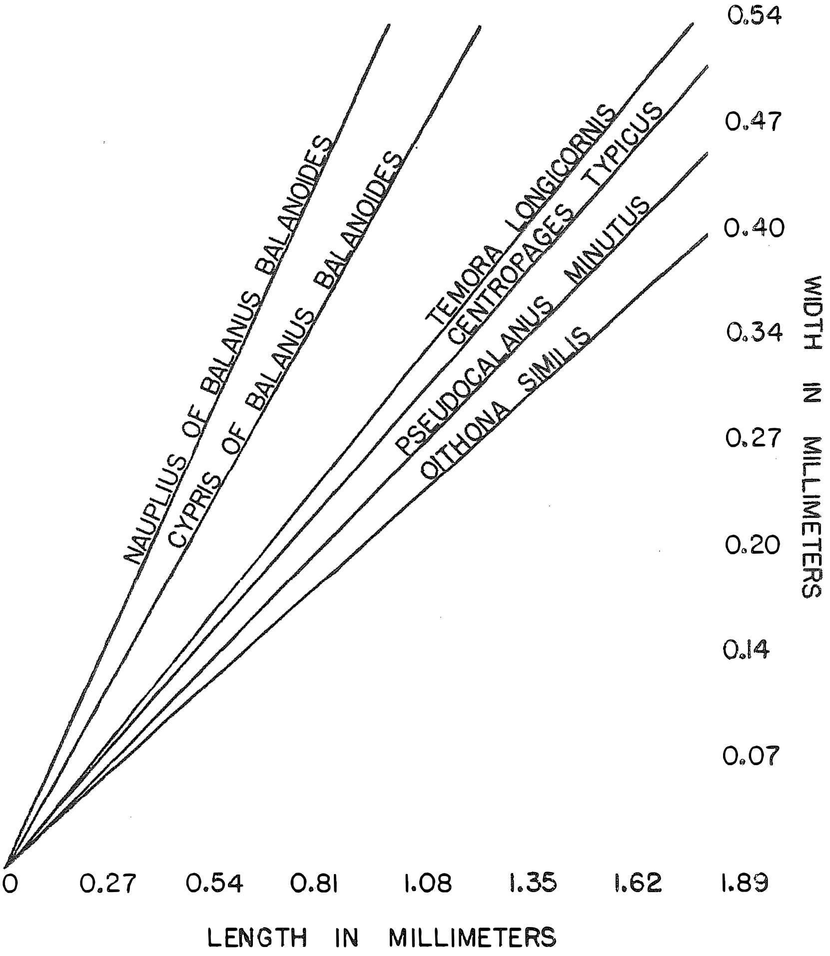


Figure 6. The length-width relationships of some common plankton.

Food Selectivity. Much debate has been focused on the subject of how herring feed; some workers have maintained that herring feed by mechanically straining out organisms while others have contended that they perform a definite act of capture. Most of the evidence to date indicates that herring consciously select their food. For example, various investigators found that coelenterates, bryozoa larvae, pelecypod larvae, appendicularians, *Sagitta*, echinoderm larvae, cladocerans, and the smaller copepods were more common in the plankton

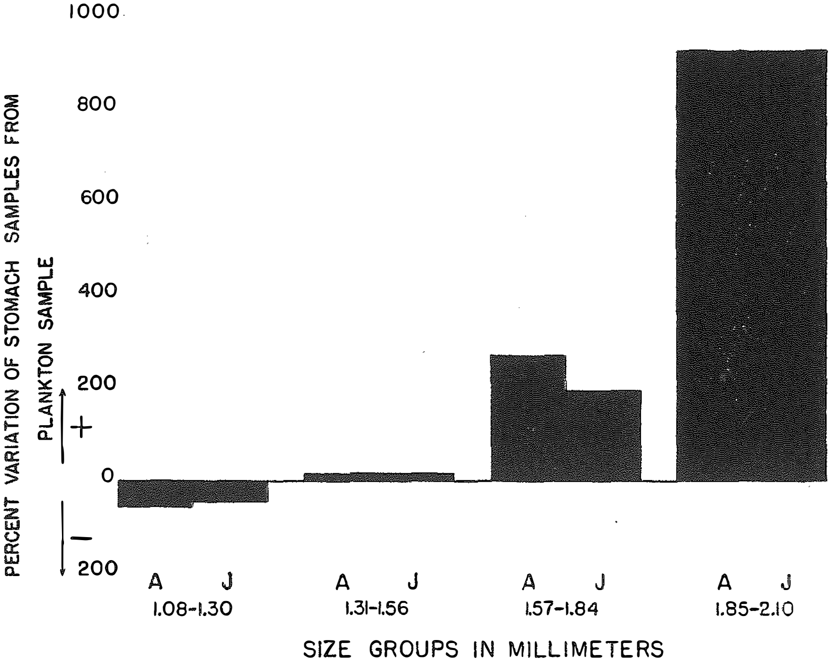


Figure 7. The feeding selectivity of herring in regard to size of food.

than in the stomach contents of herring. On the other hand, some of the larger copepods, such as *Calanus finmarchicus* and *Temora longicornis*, were always of the same or of a higher ratio in the stomach contents than in the plankton.

In an attempt to further clarify the problem, measurements of the gill-rakers and of various components of the plankton were made. The distance between the gill-raker bars of an adult herring (29 cm long) was determined as 0.21 mm, and the distance between the teeth on each bar was found to be the same, 0.21 mm.[3] With these critical calculations established, a series of length-width measurements were made of the dominant zooplankton constituent, *Pseudocalanus minutus*, and it was found that an animal 0.21 mm wide would be 0.81 mm long. Length measurements of other major components of the B. I. S.

---

[3] In an adolescent herring (17.8 cm long) the distance between the gill-raker bars was the same (0.21 mm) and the distance between the teeth only slightly less (0.19 mm).

plankton were also taken, and it will be seen in Fig. 6 that most of the important plankton organisms are proportionately wider than *Pseudocalanus.*

An attempt was then made to compare the length component of the plankton retained by the gill-rakers against the similar component in the surrounding water mass (Fig. 7). The plankton of the water mass was subdivided into four size groups so that the smallest of these four groups was significantly larger than the critical length of *Pseudocalanus* (0.81 mm) that would be retained by the gill-rakers. Thus, if the selection of plankton organisms above the critical size is merely mechanical, then the percentage of the different size groups of plankton should be identical in both stomach and water mass. As shown in Fig. 7, this appears not to be so, since herring apparently select the larger organisms more intensively than the smaller ones from the sizes available. From these results it appears that there is definite selectivity by the herring unless some undetermined physical factor is at work which selects larger particles in preference to smaller ones.

Furthermore, one might assume that the larger of two species of copepods would be selected more intensively. In the plankton tows of February 17, 1951, the mean length of *Pseudocalanus* was 1.21 mm, while that of *Centropages typicus* was found to be 1.53 mm. Therefore, the average *Centropages* should be selected more intensively than the average *Pseudocalanus,* and a comparison of the bottom plankton tow with stomach contents of both adult and adolescent herring supports this supposition (see Table II). However, when the stomach contents are compared with the plankton from the surface, the reverse situation obtains. In view of the fact that *Centropages typicus* is primarily a surface form (Bigelow, 1926; Wilson, 1932; see also Table II) and that it apparently does not engage in diurnal vertical migration (Johnson and Raymont, 1939), the apparent discrepancy between the stomach contents and the surface plankton might be explained by the fact that herring do not feed in the upper water layers during winter. Further evidence to support this contention is found in the fact that during the winter months the fishermen in B. I. S. make heavy catches of herring with gear that fishes only the water immediately over the bottom.

Further evidence to support the hypothesis of selectivity is found in a consideration of other planktonic organisms. The cypris larva of *Balanus balanoides,* although it constitutes only a trace of the bottom samples, makes up an appreciable fraction of the plankton in the stomachs (see Table II); while its mean size of 1.13 mm is slightly shorter than that of *Pseudocalanus,* it is a significantly broader organism (see Fig. 6) and is apparently selected more intensively. On the other hand, *Oithona similis,* which is more abundant in the bottom plankton sample than in the stomach contents and which is both smaller and relatively narrower than *Pseudocalanus,* is less intensively selected (Fig. 6).

TABLE II. THE COMPOSITION OF THE ZOOPLANKTON COMPONENTS OF VARIOUS SAMPLES TAKEN FEBRUARY 17, 1951; IN PERCENT.

	Plankton tows		*Stomach analyses*	
Species	*Surface*	*Bottom*	*Adolescents*	*Adults*
Pseudocalanus minutus	47.01	91.28	78.45	83.33
Centropages typicus	29.74	2.01	9.40	9.92
Balanus balanoides (cypris)	0.55	—	8.07	4.50
Oithona similis	2.20	4.69	0.46	0.45
Temora longicornis	1.65	—	2.24	0.45
Sagitta elegans	1.10	—	0.46	0.90
Sagitta elegans egg	0.55	—	—	—
Gadus morhua egg	—	—	0.46	0.46
Clymenestra rostrata	0.55	—	—	—
Calanus finmarchicus	2.20	—	—	—
Acartia tonsa	1.65	—	—	—
Cyphonautes larvae	4.40	0.68	—	—
Polychaete larvae	1.10	—	—	—
Gastropod larvae	9.35	—	—	—

If herring see their food, one can logically assume that the larger potential food particles are seen more readily than smaller ones, so that a greater percentage of larger organisms should be found in the stomach than in the water mass.

From these observations it appears that the hypothesis of size selectivity is probably applicable to the crustacean component of the plankton, but the validity of this hypothesis in regard to other groups in the plankton is less certain. Soft-bodied organisms decompose quite rapidly in the stomach, and hence they are difficult to evaluate. Various investigators (Jespersen, 1928; Cheng, 1941) indicate that the arrow worm, *Sagitta elegans,* as well as ctenophores and coelenterates are found less commonly in the stomach of herring than in the plankton. On occasions, only the bristles from *Sagitta* or the combs from ctenophores have been found in stomachs where the copepods were excellently preserved.

SUMMARY

1. Herring (*Clupea harengus*) were found in large numbers in B. I. S. from January 6 to March 15, 1951.

2. The mature spent fish entered the B. I. S. waters a month or so before the immature herring and remained until the beginning of March. The adolescents were present in small numbers as late as April.

3. During January and February, herring were restricted to a narrow strip of water close to and parallel with the shore, this being the coldest water region in B. I. S. at that time. As the water warmed in March, the fish dispersed and became more evenly distributed throughout the Sound.

4. A vertebral count of 56.48 has been determined for herring of B. I. S., a number which agrees closely with counts for more northern populations. The scute count of 14.09, on the other hand, appears to distinguish this population from most of those of more northern waters.

5. The herring fed but little during January and the first half of February, but after mid-February the feeding rate increased rapidly.

6. The adolescents fed more intensively than the adults.

7. During the period of feeble feeding, benthonic invertebrates constituted the major food component; later the food became largely planktonic.

8. The most important single planktonic organism that served as food was the copepod, *Pseudocalanus minutus*, making up more than 70% of the food by count.

9. Evidence indicates that the herring consciously select the larger forms of planktonic crustaceans in preference to smaller organisms.

REFERENCES[4]

Bigelow, H. B.

1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924), *40* (2): 1–509.

1933. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. Pap. phys. Oceanogr., *2* (4): 1–135.

Bigelow, H. B. and W. W. Welsh

1925. Fishes of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924), *40* (1): 1–567.

---

[4] A complete bibliography will be found in the original thesis deposited in the Library of the University of Rhode Island.

Chajanova, L. A.

1939. Nutrition of the White Sea herring. Inst. Mar. Fish. Oceanogr. USSR (VNIRO): 279–299 (Eng. summary, 297–299).

Cheng, C.

1941. Ecological relations between the herring and the plankton of the northeast coast of England. Hull Bull. Mar. Ecol., *1* (5): 239–254.

Deevey, G. B.

1952. The zooplankton of Block Island Sound, 1943–1946. Bull. Bingham Oceanogr. Coll., *13* (3): 65–119.

Jespersen, P.

1928. Investigations on the food of the herring in Danish waters. Medd. Komm. Havundersøg., Plankton *2* (2): 39–150.

1932. On the food of the herring in Icelandic waters. Medd. Komm. Havundersøg., Plankton *2* (3): 1–34.

1936. The food of the herring in the waters round Bornholm. Medd. Komm. Havundersøg., Plankton *3* (2): 1–40.

Johansen, A. C.

1927. On the migrations of the herring. J. Cons. int. Explor. Mer., *2* (1): 1–27.

Johnson, W. H. and J. E. G. Raymont

1939. The reactions of the planktonic copepod, *Centropages typicus,* to light and gravity. Biol. Bull. Woods Hole, *77* (2): 200–215.

Lea, Einar

1919. Age and growth of the herring in Canadian waters. Canad. Fish. Exped., 1914–15. Dep. Naval Serv. (1919), Ottawa: 75–164.

Leim, A. H.

1951. Personal letter dated April 18.

Manteufel, B. P. and G. V. Boldovsky

1938. The wintering of the Barents Sea herring and the causes of its winter migrations into the fiords of the Murman Coast. Trans. Knipovich Polar Scient. Inst. Sea-Fish. Oceanogr., *1:* 5–58 (Eng. summary, 57–58).

Marty, J. J.

1941. On the life cycle of the Murman herring (*Clupea harengus harengus*). Trans. Knipovich Polar Scient. Inst. Sea-Fish. Oceanogr., *7:* 38–124 (Eng. summary, 122–124).

Wilson, C. B.

1932. The copepods of the Woods Hole region Massachusetts. Bull. U. S. nat. Mus., *158:* 1–635.