Memoirs of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE
Vol. LIV. No. 4

STUDIES OF THE WATERS OF THE CONTINENTAL SHELF, CAPE COD TO CHESAPEAKE BAY

III

A VOLUMETRIC STUDY OF THE ZOOPLANKTON

BY

Henry B. Bigelow and Mary Sears

CAMBRIDGE, U.S.A.
Printed for the Museum
1939

STUDIES OF THE WATERS OF THE CONTINENTAL SHELF, CAPE COD TO CHESAPEAKE BAY. III.[1] A VOLUMETRIC STUDY OF THE ZOOPLANKTON

By Henry B. Bigelow and Mary Sears

Contribution No. 194
From the Woods Hole Oceanographic Institution

[1] Parts I and II appeared in Papers in Physical Oceanography and Meteorology, Vol. II, No. 4, 1933 and Vol. IV. No. 1, 1935.

CONTENTS

INTRODUCTION

In April, 1929, the U. S. Bureau of Fisheries commenced an investigation of the distribution of the eggs and larvae of the mackerel in the waters of the continental shelf between Cape Cod and Latitude about 36°, a work continued during the vernal half year, in the three subsequent years. And while the collection of plankton was only a secondary goal, samples were systematically obtained on all cruises, and turned over to us for study.

Plankton investigations, we conceive, fall into two chief groups: (a) population and distribution studies of particular species or groups of species, or studies of the relationship of one species to another (e.g., feeding habits of fishes); and (b) attempts to assay the richness of one part of the sea or another, either in organic production, or as a feeding ground for larger animals. Studies of the first of these categories depend on enumerations of the specimens present, whether of different species or of different growth stages of given species. And the data that have been presented in the great majority of recent publications on zooplankton have been of this sort. If, however, we attempt to approach the matter from the other angle, information as to the mass of organic matter that is present in the sea from time to time and from place to place becomes of prime import. And very seldom can this be deduced from a knowledge of the numbers of units of which this mass is composed, because different planktonic animals, whether different species or different stages in the growth of one species, vary so widely in size that counts of total numbers are apt to prove very deceptive, if interpreted as indices to total mass. Part I of this report attempts to give at least a rough picture of the latter for the part of the sea in question, together with the proportions in which the leading species enter into it. Part II includes such information as to the distribution of individual species as our own analyses have yielded.

In studies of this sort, the vegetable and animal fractions of the plankton can be considered either as a unit, or separately: the latter course has seemed to us preferable, because of the basic difference between the nutritional requirements of the two categories. We must realize, however, whether for the zooplankton or for the phytoplankton, that measurements of mass—however precise these may be—are only one step in our path toward a knowledge of the productivity of the sea in organic substance. A second, coincident, and equally vital requirement is a knowledge of the rate of overturn, which can come only from population studies based on enumerations of individuals combined with classification of age-frequencies. A third essential step is the chemical analysis of the groups of organisms concerned, for these differ one from another, in the proportional components of proteins, carbohydrates, fats, and sundry other compounds.

The present report, confined to a survey of the mass distribution of the larger animal plankton, is offered in the hope that it may serve as a preliminary approach to the broader field outlined above.

The detailed data (which cannot be reproduced here for lack of space) are on file at the Woods Hole Oceanographic Institution.

ACKNOWLEDGMENTS

Mr. O. E. Sette, Dr. Roderick Macdonald, and Dr. George L. Clarke collaborated in identifying the plankton caught during 1929, Miss Alice Beale in identifying that caught during 1930 and part of 1931. And Dr. Th. von Brand has assisted us by making the ether extracts and the weighings used in our discussions of the area as a feeding ground for plankton-feeding fish.

GEOGRAPHIC LIMITS AND SUBDIVISIONS OF THE AREA

The account is confined to the continental shelf, out to the 200-meter contour, from the offing of Martha's Vineyard, westward and southward to about Latitude 36°. One cruise only (February 1931) extended south of Cape Hatteras. Neither was the number of hauls seaward from the 200-meter contour large enough, for any general estimate of plankton volumes in the slope water.

For convenience in regional comparisons, we have arbitrarily divided the area into a northern sector north from (and including) the Atlantic City profile, a southern sector, south of the latter, an inshore belt extending 30 miles out from the coast, and an offshore belt, thence seaward to the 200-meter contour (Fig. 1).

HISTORY AND SOURCES OF INFORMATION

So far as we have been able to learn, the first published account of the zooplanktonic communities of the region in question was Rathbun's (1889) report on tow-net catches made in April-May 1887, in connection with the mackerel investigations of that year. During subsequent years, several notices appeared of the occurrences of individual planktonic groups for restricted localities, e.g., of the copepods of the New Jersey coast (Fowler, 1912), of medusae, ctenophores, copepods, and amphipods, etc., of the Woods Hole region (Fish, 1925; Hargitt, 1905; Holmes, 1905; Mayer, 1912; Wheeler, 1901; Wilson, 1932), of copepods

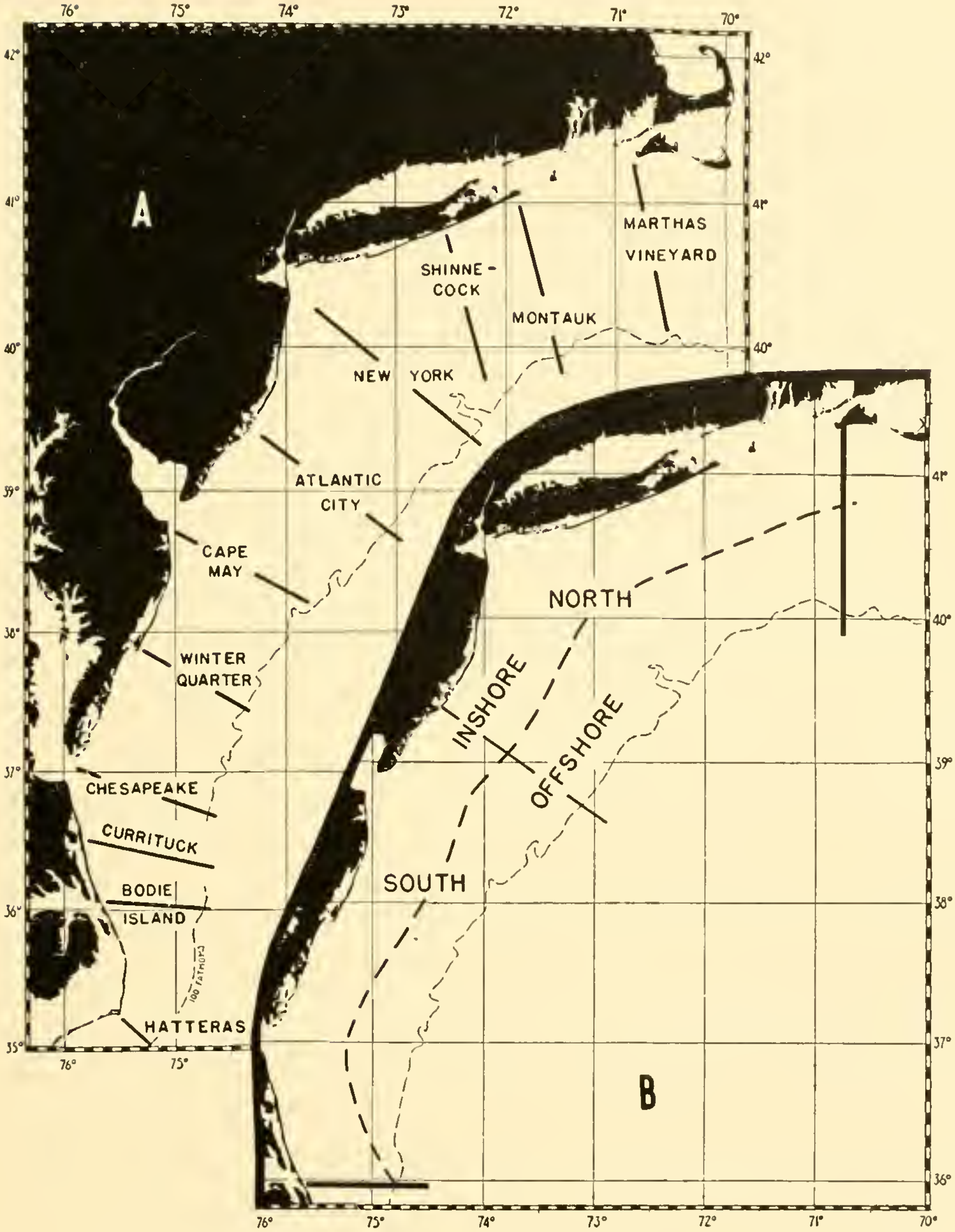


Fig. 1. Charts of the area: A, Locations of profiles; B, Sub-divisions of the area as employed in the present report.

and other groups for Chesapeake Bay (Cowles, 1930; Wilson, 1932a). But it was not until 1913 that any systematic survey of the plankton of the continental shelf was undertaken. In that summer, the U. S. Fisheries Schooner "Grampus" collected samples at a grid of stations between the offings of Cape Cod and of Chesapeake Bay, as well as in the Gulf of Maine (Bigelow, 1915). And she surveyed these same waters again in 1916, both in August and in November (Bigelow, 1922). No data had, however, been obtained for any other year until 1929, when "Albatross II" carried out cruises in April, May, June, and July. And these were repeated in the following months and years:

1930—February, April (2 cruises), May, June (2 cruises), July;

1931—February, May, June, July;

1932—February, May (4 cruises), June (3 cruises).

"Atlantis" of the Woods Hole Oceanographic Institution, also made a cruise in October 1931. And periodic collecting was carried out from the Institution, both with a pump-filter and with tow nets, at a station a few miles off Martha's Vineyard, from late June 1935 to September 1936 (Clarke and Zinn, 1937).

We have drawn freely from all of the foregoing. But the collections made by the U. S. Bureau of Fisheries during the years 1929–1932, as outlined above have been the chief basis for the present report, which forms a sequel to earlier accounts of the temperature and of the salinity of the same region (Bigelow, 1933; Bigelow and Sears, 1935).

METHODS

Collection

The observing stations (with few exceptions) were located along the profiles indicated on Figure 1, so spaced that on each profile the inshore belt, the mid-belt, and the outer edge of the shelf were sampled at points seldom more than 15–20 miles apart, and often much closer (for position of stations, etc., see Bigelow, 1933, p. 104). The plan was for observations to be made at approximately the same localities, on all the cruises, and this was adhered to as far as practicable,[1] six hundred and four plankton stations on the continental shelf being occupied in all, 377 of them in the northern sector, 227 in the southern, 330 in the inshore belt, and 274 offshore.

Most of the hauls made by "Atlantis" in October 1931 were vertical, those by "Albatross II", in 1929, horizontal, at the surface, and (except when in very

[1] Bad weather sometimes interfered, and some of the cruises were abbreviated.

shallow water, or when the sea was very rough) at one or more subsurface levels at each station. In subsequent years, on "Albatross II", oblique hauls were employed to obviate the chief shortcoming of horizontal towing, namely, that it may be a matter of chance whether the net hits or misses the strata where the planktonic population is richest or poorest.[1]

Ideally, hauls of this type should be made by lowering the net close to the bottom and by towing in a diagonal direction up to the surface. This, however, is seldom practical, the best substitute being to tow in a series of short horizontal steps at frequent intervals from bottom to surface.

The standard procedure in the present case (seldom, however, attained *in toto*), was to tow for two minutes at each five meter level, the hauls often being abbreviated to one meter of towing at every ten meter level, at the deep stations, in order to shorten the time required. The column strained in this way diverged, on the average, by about 15° from the horizontal. At a towing speed averaging 1.2 knots or 37 meters per minute (as observed repeatedly), the oblique column fished through was thus about 370–518 meters long, at stations where the vertical depth was 20–30 meters, or about 777 meters where the depth was 200 meters. The chief drawback to hauls of this sort, from near bottom to surface, is that they give no information as to the degree of stratification of the communities at different levels. To meet this difficulty, two or more nets were attached on the wire at a time, 20–35 meters apart, on the cruises subsequent to February 1931. Unfortunately, a considerable proportion of the hauls left, unsampled, a stratum next the bottom, equalling as much as 50% of the whole vertical distance in extreme cases.

The nets were either 1-meter, or ½-meter in diameter, of silk, the forepart with 29–38 meshes per linear inch, the rear part with 48–54 meshes per inch. Nets of these meshes and diameters may be expected adequately to sample planktonic animals of the various groups from the size of the copepod, Centropages, up to fish fry. Many or most of the smaller adult copepods (Oithona), smaller larval copepods of all species, and other minute animals pass through. And failure to sample these is mentioned repeatedly in the following pages.

Measurements and Calculations

Dry weight would be the most reliable index, easily obtainable, to the mass of the plankton, if the desiccation and weighing could be done soon after the col-

[1] For a recent discussion of the advantages of oblique towing, see Walford, 1938.

lections were made. But, for so large a number of samples, this would have required much more assistance than was available. And so much of the oil from copepods—and other substances as well, both from these and from other groups—dissolves out into the preservative that long preservation of the samples robs dry weighing of much of its initial advantage over volumetric measurement, which is a much simpler procedure.

We may also point out that "volume" is usually translatable into "wet (preserved) weight" within a reasonable limit of error, for while the specific gravities of different groups of planktonic animals differ considerably—both in life and after preservation (e.g., as between shelled pteropods and ctenophores), this is comparatively constant within each of the major groups.

Selected samples, from the collections of 1929, showed the following weight-volume relationship, when weighed in water:

Calanus, 20 c.c. by displacement; "wet weight," 18.35 gms;

Sagitta elegans, 20 c.c. by displacement; "wet weight," 21.34 gms;

Limacina, 20 c.c. by displacement, "wet weight," 20.18 gms.

The method of volumetric measurement that has most often been used in the past consists simply of allowing the catch to settle for a given length of time, in a graduated cylinder of convenient size, and of then measuring its bulk. It has, however, been universally appreciated that the resultant measurements have only a comparative value, because they include the interspaces between the animals, as well as the latter themselves. Savage (1931, p. 5) has, in fact, shown that such measurements may average more than twice as large as those obtained, for the same samples by the so-called displacement method.[1] And comparative tests, that we have made for the entire series of "Albatross II" catches for the year 1929, have similarly shown a wide disparity, with volumes averaging 2–4 times as large by "settlement" as by "displacement," for all types of plankton combined, the difference being greatest for plankton dominated by sagittae (extreme case, 105 c.c. by displacement; 935 c.c. by settlement), least for plankton consisting chiefly of Calanus (210 c.c. by displacement; 260 c.c. by settlement). All measurements in the present report have, therefore, been made by displacement as follows:

The sample of plankton is first drained, through a bolting silk strainer with meshes as fine as that of the nets in which the catch was taken. The semi-dried mass is then added to a known volume of water, when the resultant increase in

[1] See Johnstone, 1908, p. 130 for a general discussion of these methods.

volume is equal to that of the sample, plus the few drops of liquid that may still adhere to the latter after draining.

In the preliminary catches of 1929, the respective percentages of the several constituent species or groups were determined either after these had been sorted out, or in some cases, roughly estimated. In the subsequent catches, the volumes of the species represented were arrived at as follows:

The total catch was first sorted into such of its constituent parts as were most readily separable, e.g., into the chaetognaths, euphausiids, larger medusae, adult amphipods, pteropods, and "residue," this last consisting chiefly of copepods, with other forms of similarly small size. Each of these groupings was then measured by the same displacement method as used in obtaining the total volume. A random and well mixed sample of at least 100 specimens[1] was then taken from each grouping, and the number of specimens counted, for each species represented. In order next to calculate the proportional volumes of the several species included in each grouping, and so to arrive at the total volume of each species in the total catch, it was necessary to weight each according to the average size of its members. In the cases of *Calanus finmarchicus*, *Centropages typicus*, and *Thysanoessa inermis*, the weightings were based on actual measurements of the volume per 100 specimens of large series of adults, covering the average size range. Volumetric comparison with these, by eye, then gave a rough ratio for weighting the younger stages of these same species, as well as for the other species.

The following actual example may serve more graphically to illustrate the procedure:

Station, Montauk V, June 12, 1930, total volume of catch, 60 c.c., or 480 c.c. per 20 minutes towing with a 1-meter net; volume of "residue," 59 c.c., or 472 c.c., per standard tow; number of individuals of each species represented among 119 counted specimens in sample of "residue", 61 *Calanus finmarchicus*, 1 *Centropages typicus*, 52 *Metridia lucens*, 5 *Pseudocalanus minutus*. Weights derived as above, Calanus, 25; Centropages, 4; Metridia, 25; Pseudocalanus, 2. Calculated percentages (volumetric), in "residue", Calanus, 53.7%; Centropages, 0.1%; Metridia, 45.7%; Pseudocalanus, 0.3%. The volume of "residue" being 472 c.c. for the standard haul, the calculated volumes for the several species work out at 253 c.c. of Calanus; $<$ 1 c.c. of Centropages; 216 c.c. of Metridia, and 1 c.c. of Pseudocalanus.

Comparison of catches made in horizontal hauls at the surface and deeper

[1] Fewer, if there were not that many.

in 1929, and in oblique hauls through shoaler and deeper sections of the water column in 1931 and 1932, afford some information as to the degree of stratification of the plankton in different months. Since open nets were used, it is obvious that the volumes taken in the deeper tows represent not only the abundance prevailing at the towing level, but also whatever was caught while the nets were being lowered and hauled in again. And this contamination might well be great enough entirely to obscure the picture in individual cases—if, for example, it chanced that the net was hauled up through a dense swarm of one organism or another. But at most of the stations, inside the 200-meter contour, the vertical sectors averaged less than 1/7 as long as the horizontal sectors in the cases of the horizontal hauls, and only about 1/15 as long as the horizontal sectors in the cases of obliques. It may, therefore, be assumed that this contamination is not an important factor for our purposes in these shoal waters, when considerable numbers of catches are averaged. Consequently, we have not attempted to correct for it.[1]

In order to render the catches made in horizontal tows comparable (from the standpoint of depth) with those made in obliques, we have further assumed that the catches of the latter may be accepted as representative of the mid-depths of the water columns sampled. And the depths stated in the following discussion are so derived.

We have credited a value of 1 to catches < 1 c.c., in the calculations of average volumes and ratios, while in the case of the latter, we have also treated values of 0 as equivalent to 1 c.c., for the sake of simplicity. Likewise, in the tables giving percentages and abundance, a dash signifies that the particular subdivision was not visited on a particular cruise; a 0 that the species was not detected in that particular subdivision, though taken in another; a blank that it was not detected in any subdivision on a particular cruise.

Expression of Results

The fact that the catches were taken in nets of different sizes, as well as in hauls of different lengths, some oblique, some vertical, and some horizontal, makes it necessary to reduce all the measurements to one common basis in order to render the results comparable, one with another.

The elements on which such a reduction must be based for any particular haul are:— (a) the diameter of the net used, (b) the duration of the haul in time, (c) the average speed of the vessel (or else the linear extent of the haul), and (d)

[1] For a case of such correction, see Bigelow and Sears, 1937, p. 69.

the efficiency of the particular net used. In the cases of horizontal and oblique hauls, the first two elements are precisely known, hence the first reduction is to "catch per unit time per unit net-opening"; the standards here adopted being 20 minutes of hauling with a net 1 meter in diameter. Up to this point, the reduction is precise mathematically. But it does not yet provide a standard of comparison, unless "time" can be translated directly into "length of water column fished". Close attention was, therefore, paid to the speed of the ship, on all the cruises of "Albatross II" and of "Atlantis", and records by R.P.M. of the propeller, and by ship's log, show that this was close to 1.2 knots for the series as a whole. But whoever has had experience with the differences in the velocities and directions of currents at different levels in coastwise waters where the circulation is governed by the tide, will appreciate that the rate at which a ship is moving, relative to the surface water may differ considerably from the rate of a net relative to the water at some deeper level. Rather than attempt the calculation of the linear extent of each individual tow, we have, therefore, thought it preferable to assume an average speed of 1.2 knots in all the calculations, and the catches of the horizontal and oblique hauls were reduced to the common standard accordingly.

On this basis, the linear extent of the standard tow of 20 minutes would average 741 meters. And there would be as good justification for expressing the volumes caught "per unit volume of water" as "per unit time," for the one of these expressions includes the same probable errors as the other. But we must impress upon the reader that neither of these expressions is susceptible of direct translation into "volume of plankton present," whether per unit time or per unit volume of water, because of uncertainty as to the efficiency of the nets (discussed on p. 198). Hence, to avoid any possible misconception as to the reliability of the observations, we have endeavored to draw a sharp distinction, in this respect throughout the descriptive sections of the present report. It has also been suggested to us that "catch per unit volume of water" might suggest a higher degree of precision than "catch per unit tow", whereas actually the two are interchangeable. We have, therefore, adopted the latter.

All the results, then, are expressed as catch, in c.c. per 20 minutes towing with a 1-meter net at an assumed speed of 1.2 knots (2222 meters per hour), unless otherwise stated.

VALIDITY OF CALCULATED RESULTS

No modern student of plankton, we fancy, would claim that quantitative calculations, based on tow nettings, can be any more than approximations to the truth.

To begin with, we must face what may be termed the "catching error" inherent in the tow net method. We have no intention of reviving the controversies as to the reliability of the latter that gave planktonologists so much concern during the last quarter of the nineteenth century. It seems pertinent, however, to remind the reader that a tow net, of the usual conical form, and of mesh appropriate for the capture of planktonic organisms, filters somewhat less than the amount of water that would pass through a simple hoop of equal diameter, the loss (i.e., the amount regurgitated) depending on the shape of the net, on the proportionate areas occupied by the threads and by the spaces between the latter, and on the pressure, i.e., on the velocity with which the net is drawn through the water. The slower the towing, the more complete filtration, as every planktonologist knows from observation. In the case of fine meshed silk (e.g., #20), the loss may be so serious at ordinary towing speeds as to necessitate special types of net, to increase the filtering surface relative to the mouth opening. And even with silk as coarse meshed as #0 (38 meshes per linear inch), such as used in the fore parts of our nets, only about 30% as much water would pass through a given area, drawn transversely at 2 knots, as through an open cylinder of the same area, according to the relationship between pressure and filtration in Hensen's (1895) experiments[1].

This loss is so minimized by the increase in straining area relative to mouth opening, resulting from the conical form, that it probably averaged less than 10%, at the usual towing speed for our nets, though experiments at various hands have proved that the catches made in parallel hauls with similar nets may vary as much as 10–30% or even more (see Winsor and Walford, 1936, p. 190, for a recent discussion). Neither is clogging likely to be serious, for nets such as those used, except on rare occasions when diatoms or Phaeocystis may swarm, or when the gelatinous bodies of ctenophores, appendicularians, etc., may block the meshes. Much more serious is the uncertainty as to what relation the fraction of the plankton that is adequately sampled bears to the remainder that the net fails to capture, it being common knowledge that no one type of net will equally well sample the various size categories of planktonic animals. The nets used in the present studies (meshes, 38–54 per linear inch) being comparatively coarse, the failure of small copepods such as Oithona, or the young of others, to figure more largely in the following volumetric lists, does not necessarily mean that

[1] Pressure at the given velocity calculated from the formula, $p=\sqrt{\frac{v^2}{2g}}$.

they may not actually have been present in considerably greater abundance (numerically, at least) than the catches would suggest.

In extended surveys, errors also creep in through the fact that it is necessary to classify the hauls by the time—i.e., by the duration of the tow—, for in most cases, no precise measure of the speed of the net through the water, i.e., the distance, is available, as already remarked (p. 196).

While errors of the sorts just mentioned may reach extreme proportions in individual cases, they can usually be minimized by combining a sufficiently extensive series of data. More vital is the question whether the grid formed by the stations, in any particular plankton survey, has been close enough to warrant generalization for the included area as a whole. In this respect, the consistency of results seems to us sufficient warrant, as already argued by Walford (1938) for a similar survey carried out on George's Bank.

If these shortcomings of various kinds should chance to be cumulative for a given haul, the calculated volume for the latter may very likely be as much as 100% in error—perhaps more. But, when so many observations are in hand, the plus or minus error no doubt averages much less than this—perhaps not more than 20–30%, which is far smaller than the variations observed among the values that form the basis of study. And since the latter also show very clear consistency, both regional and secular, not only for the volumes of plankton as a whole, but also for the more abundant of the constituent species, we think no further argument is needed in justification of our conclusion that the picture they have yielded may be accepted as representative (within reasonable limits) of the larger zooplankton from place to place within the area, from season to season, and from year to year, for the period 1930–1932.

The basis for comparison between this group of years and the year 1929 is not so solid, because of the use in that year of horizontal hauls. The best we can do, in this case, is to assume that the average catch, of the two or more of these that were made at different levels at each station, at least approximates the correct average for the water column as a whole, bottom to surface. It is probable that this is close to the truth through the period February-April, i.e., before any marked stratification has developed. But from June on, as the plankton like the temperature tends to become increasingly stratified, it becomes increasingly doubtful how thick the stratum is, for which the yield of a net working horizontally, at any particular level, can be accepted as representative.

PART I. THE VOLUME OF THE ZOOPLANKTON AS A UNIT

The Water Column as a Whole

The volumes in c.c. per standard haul for each month of the series are shown on Figures 2–6, 8–9, and average and maximum volumes for the several subdivisions in the following table:

Month	Year	Inshore		Offshore		North		South		Total area Surveyed	
		Av.	Max.	Av.	Max.	Av.	Max.	Av.	Max.	Av.	Max.
February	1930	249	1000	49	128	111	497	175	1000	144	1000
	1931	218	432	109	140	57	108	200	432	153	432
	1932	550	2400	83	306	57	91	472	2400	368	2400
April	1929	203	520	349	1701	312	520	224	1701	263	1701
	1930	302	1124	322	1026	396	1124	244	700	199	1124
May	1929	243	1448	326	805	334	805	198	1448	273	1448
	1930	467	1294	1026	3288	689	1847	746	3288	714	3288
	1931	385	821	622	1880	507	1880	436	821	487	1880
	1932	274	771	329	1026	285	1026	320	746	299	1026
June	1929	174	541	294	447	249	541	168	514	219	541
	1930	430	1712	311	789	420	1712	242	900	381	1712
	1931	535	978	777	1756	654	1756	578	1373	626	1756
	1932	232	478	302	790	228	467	333	790	261	790
July	1929	296	550	211	474	285	550	203	512	257	550[1]
	1930	600	1681	341	800	448	1681	—	—	448	1681
	1931	702	1410	912	2341	782	2341	—	—	782	2341
October	1931	—	—	234	560	236	331	231	560	234	560

[1] One haul of 67109 c.c. omitted.

The most striking feature of volumetric distribution throughout has been the irregularity from station to station, often with volumes differing up to a hundred fold, between localities only a few miles apart. As a concrete illustration, we may instance the fact that the maximum volume was 3 times as large as the minimum, even on the cruise (May 24–28, 1932) when the difference between the two was smallest. And on the occasion, when widest (July 10–18, 1930), the range was 373 to one.

Comparatively regular gradients nevertheless appear, both secular and regional, when averages are compared, for subdivisions large enough to include several stations each, as follows:

Seasonal Cycle

February. February may be chosen as the starting point in our survey, it being highly probable (though not yet actually proven) that the zooplanktonic community in the waters in question, as in boreal seas in general, is at its lowest ebb, at the end of winter, or in early spring.

The three surveys for this month (1930, 1931, 1932) agree in showing the

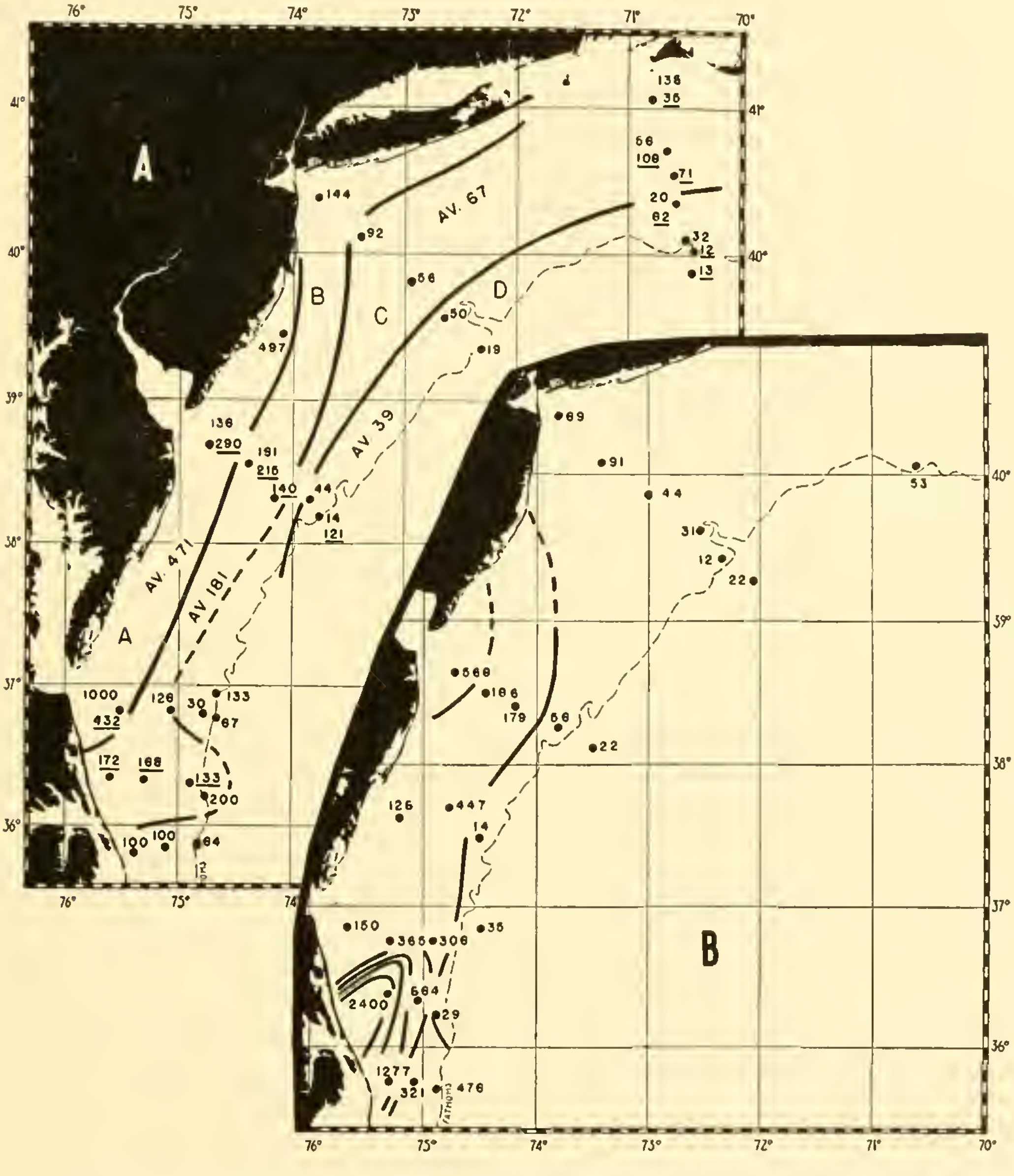


Fig. 2. Volumes of plankton, per standard haul: A, February 5-13, 1930 and February 13-March 5, 1931 (underlined); B, February 10-March 1, 1932, contour lines 100, 500, 1000, 1500, 2000 c.c.

volumes as largest over the inner half of the shelf, and to the south, decreasing offshore and to the north (Fig. 2), though with great irregularity from station to station, as is, in fact, the case throughout the year.

The magnitude of this inshore-offshore gradient in winters of normal temperature may be illustrated by the fact that, of the 37 tows made in 1930 and 1931, the average of the ten closest to shore was 294 c.c., four yielding more than 250 c.c., with fourteen hauls over the mid-belt of the shelf averaging 104 c.c., whereas thirteen along the continental edge averaged only 72 c.c., with four alone of the latter yielding as much as 100 c.c. The plankton thus averaged roughly twice as voluminous inshore as along the mid-belt of the shelf, four times as voluminous as along the outer edge of the latter. And in most cases the inshore-offshore relationship was of this same order along individual profiles, though with occasional exceptions as in 1930 off Cape May, where the volume was 136 c.c. at the inshore station, but 191 c.c. at the station next seaward, and again in 1931, off Martha's Vineyard where the catch closest to land was only 35 c.c., but 108 c.c. farther out.

The contrast prevailing at this season between small volumes in the northeastern sector (bounded by the New York profile) and large in the southern is even more striking, February volumes having averaged only about 1/3 as great for the former as for the latter in 1930 and in 1931 combined, and 1/10 as great in 1932. Furthermore, no catch as great as 200 c.c. was made in the eastern sector in any February, whereas fourteen such February catches were recorded to the south and west. But this abundance seems not to extend south of Cape Hatteras "which may be regarded as the southern boundary in winter to the cold boreal water" (Bigelow, 1933, p. 11), tows made in 1931 in the vicinity of the Cape having yielded only 15, 80, 92, and 205 c.c. respectively.

April. The sequence of events in the development of the plankton, with the advance of spring, is obscured in our data by the long period that elapsed between the first and second surveys of each year, no collections having been made in March. In 1930, which we must perforce accept as representative, being the only year when collections were made both in February and in April, average volumes had increased about eight or nine fold from the one month to the other over the offshore belt, northward and eastward from the Barnegat profile, where the catch averaged 325 c.c. in early April, contrasting with 39 c.c. in February. In the southern sector, however, the volume of plankton still averaged about the same order of magnitude in April (244 c.c.) as it had in February (175 c.c.).

This combination of relatively stationary conditions in the south, with marked augmentation in the north resulted—in the year in question—in a reversal of the north-south relationship that existed in February, so that by early April, the volume of plankton averaged nearly three times as great (419 c.c.)

eastward from the New York profile, as south of the latter (157 c.c.), instead of only about 1/3 as great, as it had at the end of the winter, this being a case where the north-south gradient would have been hidden, had the comparison been made between sectors separated by the boundary (Atlantic City profile) that has usually proved significant.

Unfortunately, it was not possible to include the immediate offing of Chesapeake Bay in this calculation, lacking an oblique haul there in that April. A very rich surface catch (1200 c.c.) was made there, it is true, in that month, but we have no information as to whether the average volume had or had not increased at this particular locality meantime. And volumes for April similarly averaged larger in the northern sector than in the southern in 1929, as well.

Vernal augmentation spread southward in 1930, between the first and third weeks of April as far as the offing of Chesapeake Bay, causing a five-fold increase since February, along the mid-belt of the shelf, as illustrated by the expanding outlines of the area where the catches were greater than 500 c.c. (Fig. 3A, B). And there is evidence of some slight alteration of the same order to the south of the Bay as well, where the late April average was 181 c.c. (6 stations, oblique hauls), contrasting with 98 c.c. (3 stations, 1 oblique, 2 horizontal hauls), early in the month. Consequently, the plankton averaged much the richest along the mid-belt of the shelf by mid-April of that year (16 stations, average, 496 c.c.),[1] whereas the coastal waters—which had been richest in February—were now relatively barren (8 stations, average, 192 c.c.), as was also the case along the continental edge (8 stations, average, 133 c.c.).

The facts, (a) that the richest aggregations recorded for February and April (Fig. 2, 3) have not been at the most easterly stations, and (b) that the plankton of the Gulf of Maine is on the whole sparse in late winter and early spring (Bigelow, 1926; Fish and Johnson, 1937), combined with the vernal histories of the dominant species, individually, is sufficient evidence that in years when volumes increase significantly in early spring, this results chiefly from local reproduction, not from immigration from waters farther to the east. Neither have we any evidence of mass immigration from offshore, or from the south, at this season.

May. In one of the years (1930) when April can be compared with May, the area that had been well populated (> 500 c.c.) during the earlier month, had expanded seaward to the continental edge, by the latter, all along from the offing of Chesapeake Bay to that of Montauk (though apparently no farther eastward),

[1] In early April, only two stations yielded more than 500 c.c. (Fig. 3A), both of them east of New York. In late April this was the case at nine stations scattered as far south as Chesapeake Bay.

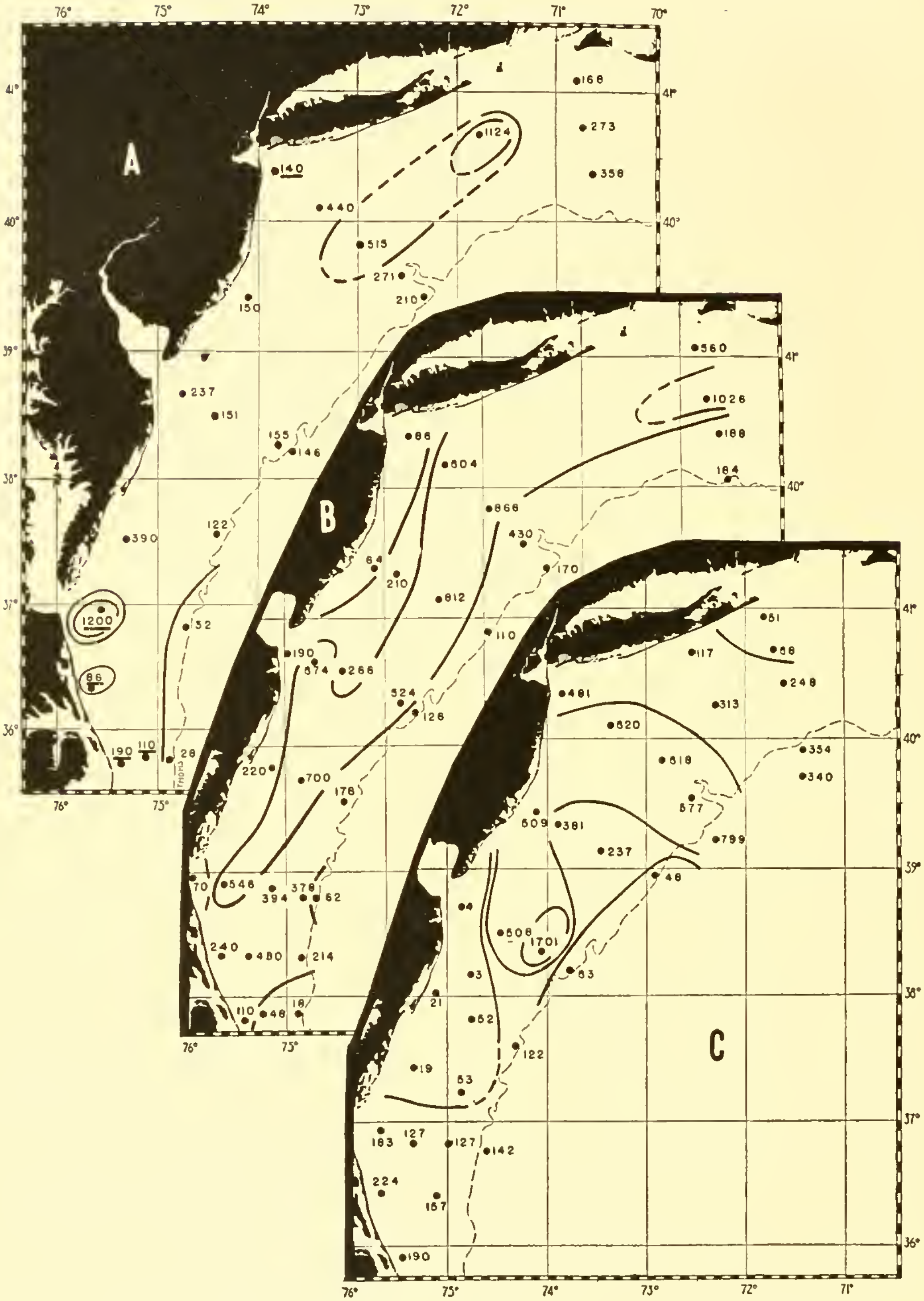


Fig. 3. Volumes of plankton, per standard haul, contour lines for 100, 500, 1000 c.c: A, April 3-11, 1930, with surface hauls underlined: B, April 22–May 1, 1930; C, April 14–24, 1929.

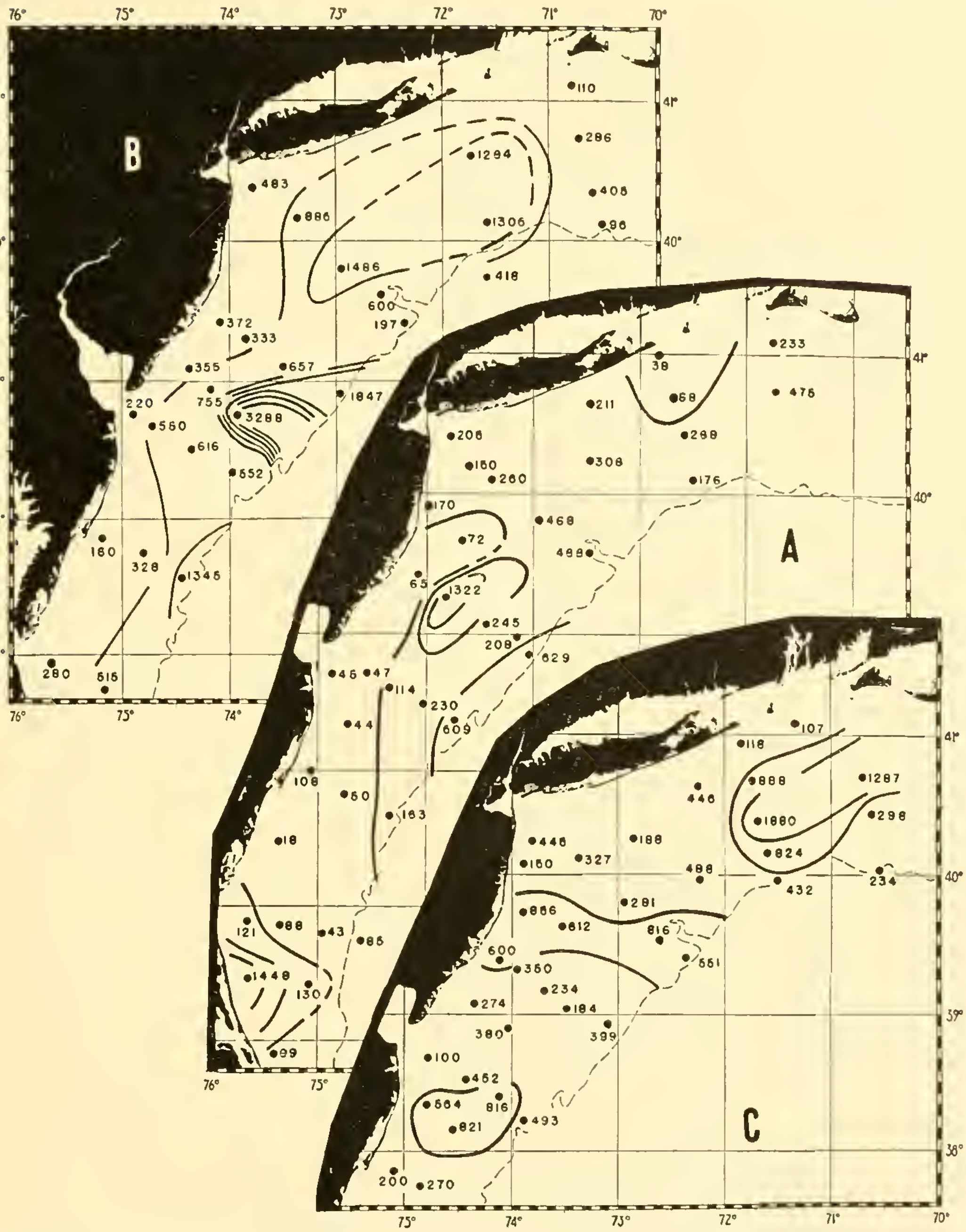


Fig. 4. Volumes of plankton, per standard haul, contour lines 100, 500, 1000, 1500, 2000, 2500, 3000: A, May 10–18, 1929; B, May 12-23, 1930; C, May 16–22, 1931.

coupled with the development of considerable pools richer than 1000 c.c. (Fig. 4B). A considerable increase in the volumes of plankton had also taken place inshore between the offings of Delaware Bay and of New York, where three stations now averaged 358 c.c., contrasting with only 113 c.c. at the end of April. As a result of these changes, the volume of plankton averaged approximately twice as great in that May as it had in April, both in the northern sector and in the southern, with an alteration of the same order, inshore as well as offshore. But it is doubtful whether any significant or general alteration had taken place in this respect from the one month to the next, in 1929. In fact, the volume of plankton may not have averaged significantly higher in April or in May of that year than at the end of the preceding winter.[1] And it is certain that no significant augmentation took place between February and May in 1932, contrasting with the great increase that certainly took place during that interval both in 1930 and 1931 (Fig. 4), unless possibly for a brief period in March or April, months for which no information is available for that particular year.

Averages for the different subdivisions suggest, however, that differences from year to year in these respects are not wide enough to obscure the general rule that in May the offshore belt supports an appreciably larger volume of plankton than the inshore belt (in fact, this was the case to a greater or less extent in each year). But no prevailing difference for this month is suggested, between the northern sector and the southern.

June. In one year of the series (1931) the average volume continued to increase somewhat in each subdivision, from May to June (Table, p. 200). In each of the other three years, a decrease was, however, recorded. Thus, in 1929, when the rich (>500 c.c.) areas continued about as scattered in June as in May (Fig. 4A, 6A), average volumes fell between mid-May and early June from about 334 c.c. to about 249 c.c. in the northern sector, from 198 c.c. to 168 c.c. in the southern with corresponding decreases in the maxima from 1448 c.c. in May to 541 c.c. in June. And it appears that the vernal maximum,—whether for extent of the rich (>500 c.c.) area, or for average and maximum volumes,—was also reached by May, in 1930, for in that year the average volume for the area as a whole[2] decreased from about 714 c.c. in that month to about 381 c.c. for June, the rich (> 500 c.c.) areas meantime contracting by the end of the latter month to a few scattered centers, one close to Delaware Bay (due to a local swarm of *Sagitta*

[1] We have no February data for 1929.

[2] The June cruises of 1930 extended southward only as far as the mouth of Delaware Bay.

elegans), one near the edge of the shelf off New York, and others near shore off Montauk Point and Martha's Vineyard (Cf. Fig. 4B with Fig. 5B). And seven successive surveys (Fig. 7), at close intervals in 1932, again showed the trend as

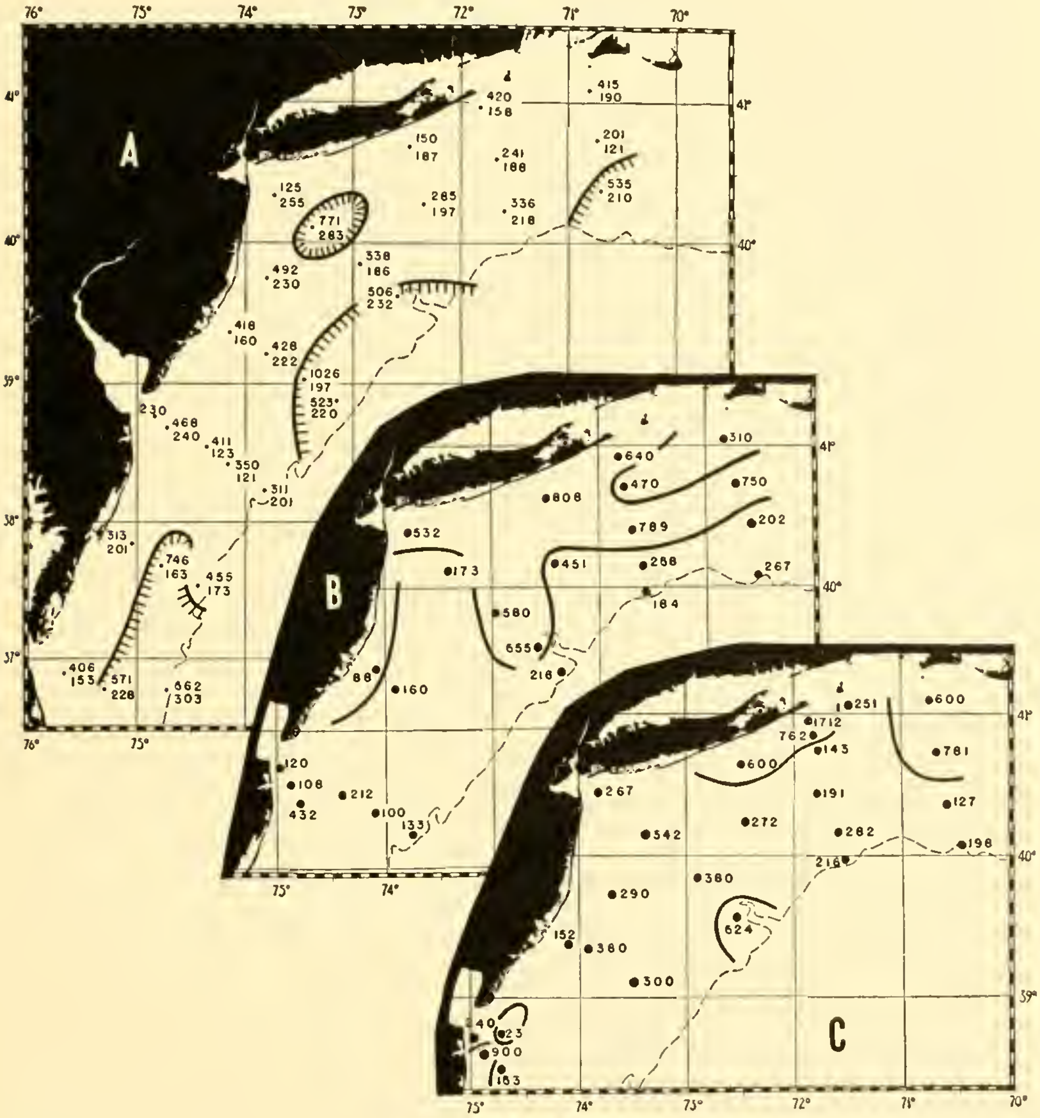


Fig. 5. Volumes of plankton, per standard haul: A, maximum and minimum at each station for the four May cruises of 1932, hatched areas where catches were greater than 500 c.c.; B, June 7–18, 1930; C, June 24–July 1, 1930. Contour lines 100 and 500 c.c. in B and C.

generally downward from early May (299 c.c.) to late June (261 c.c.), except in the southernmost sector, an alteration which seems sufficiently consistent to be accepted as significant, though not large.

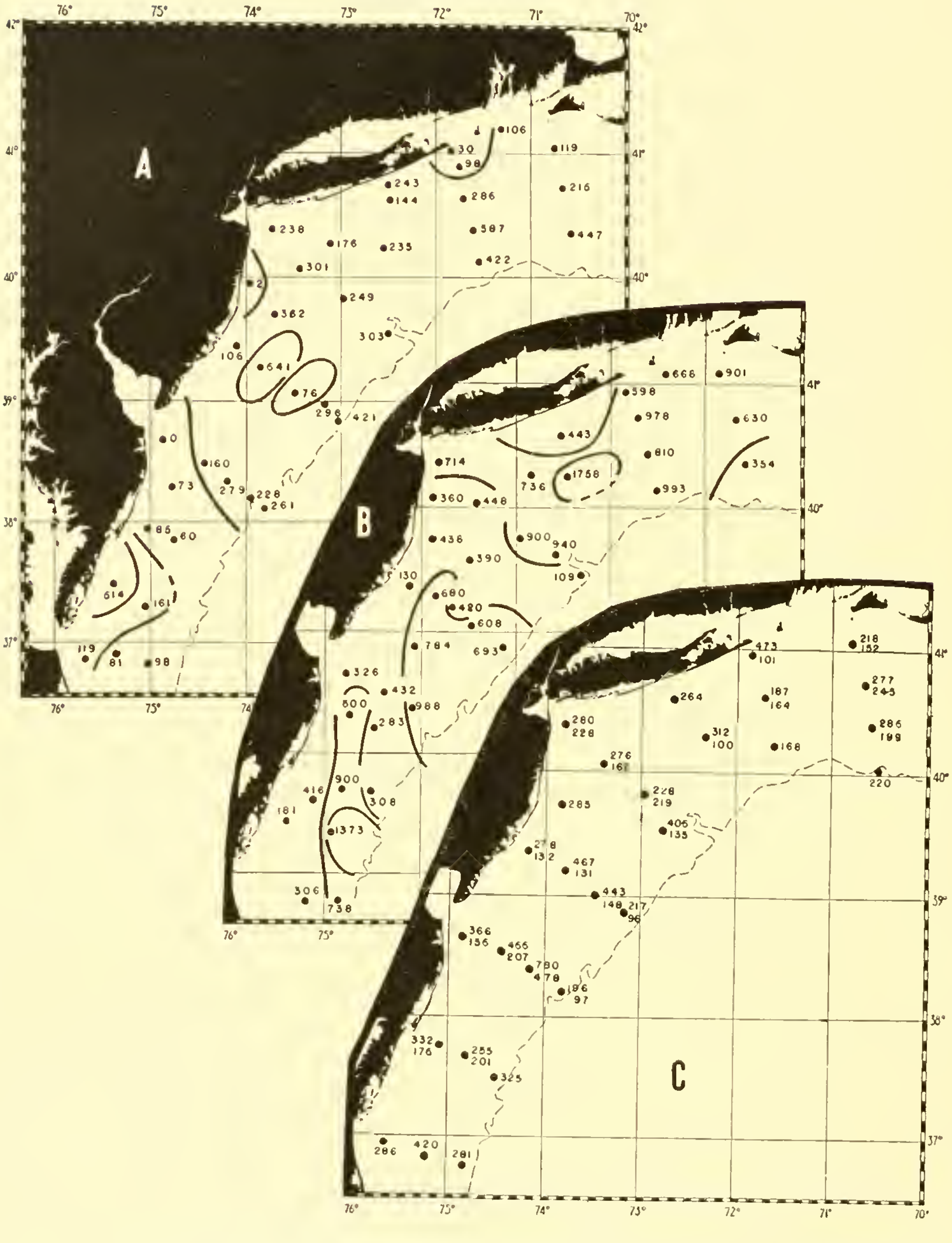


Fig. 6. Volumes of plankton, per standard haul, contour lines 100, 500, 1000 c.c: A, May 28–June 5, 1929; B, June 12–19, 1931; C, maximum and minimum at each station for the three June cruises of 1932.

Thus, it appears that while the alteration—for the area as a whole—is not likely to be great in either direction, from May through June, the trend is more likely to be downward than upward, at this season in any given year.

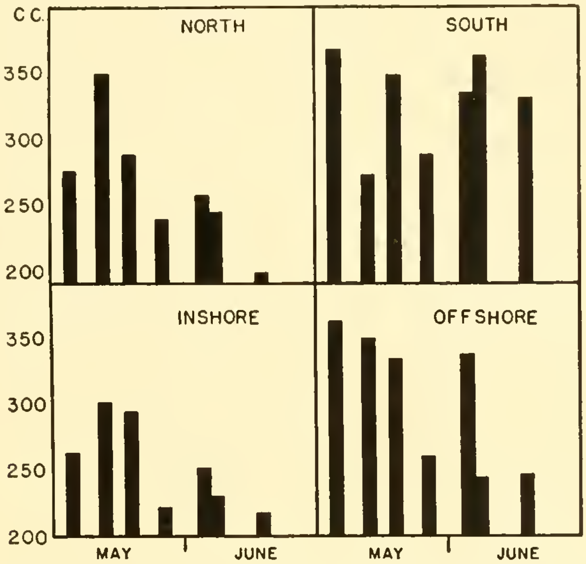


Fig. 7. Average volumes of plankton, in the different subdivisions, in May and June, 1932.

July. In the only year (1929), when a general survey was carried out in July, as well as in June, the average volume of plankton had ostensibly increased somewhat from the one month (June, average, 219 c.c.) to the next (July, average, 257 c.c.),[1] southward from the New York profile, but had decreased somewhat near the eastern boundary of the area (average, Montauk-Martha's Vineyard profiles, 275 c.c., in June; 250 c.c. in July). And while these changes were so small that they may best be interpreted as evidence of a roughly stationary state, so far as the average abundance is concerned, a corresponding shift in the center of population from east of the New York profile to south of the latter, may be regularly characteristic of this season, since a similar shift, westward, also took place between mid- and late June and mid-July of 1930 and 1931, as illustrated by the following average volumes for the Martha's Vineyard and Montauk profiles, contrasted with the New York and Barnegat profiles:

Year	Season	Barnegat-New York	Martha's Vineyard-Montauk
1930	Late June	327	478
	Mid-July	605	403
1931	Mid-June	535	730
	Mid-July	852	711

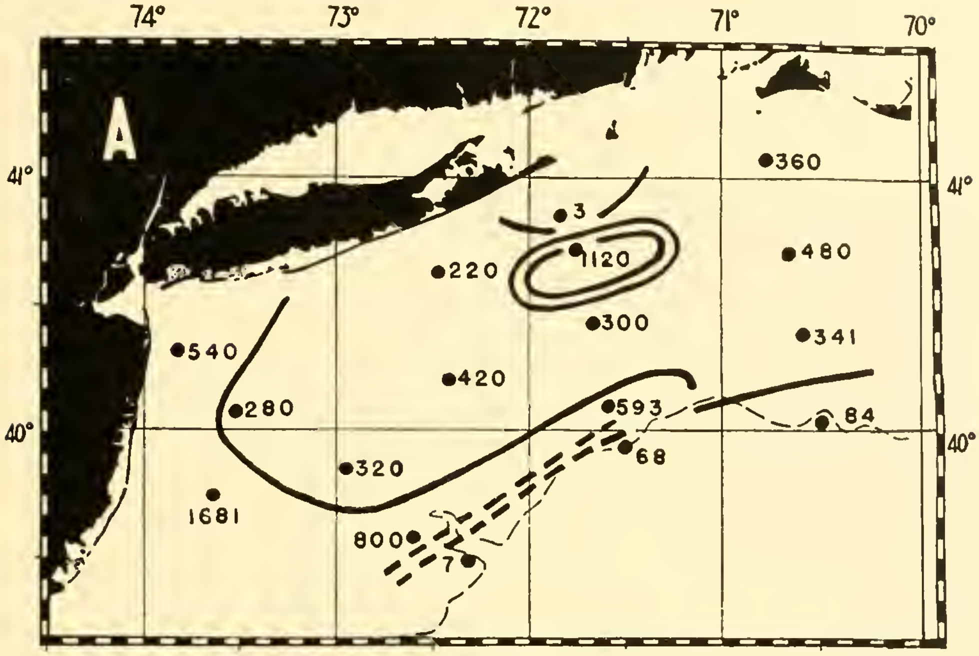
[1] One large haul (67109 c.c.) omitted from calculations of the July value.

An interesting feature of the volumetric picture for July is the striking irregularity of distribution, with centers of great abundance sporadically scattered on the shelf. In such cases, it is not unusual to make a poor catch close to an extraordinarily rich one. One haul, for example, off Montauk, on July 10, 1930, produced only 3 c.c., but another not ten miles away yielded 1120 c.c., chiefly, *Calanus finmarchicus*. And other instances of this same sort might be cited, On the other hand, three productive (> 500 c.c.) hauls from contiguous localities (Fig. 8A) in the offing of New York may perhaps have formed part of a center of abundance to the south of the area surveyed in that July.

Autumn. No quantitative information is available for the months of August and September. In 1931 (Fig. 9B), however, the volume of plankton in the offshore belt had decreased from an average of 714 c.c. in July to 236 c.c. in October in the northeastern sector, and from an average of 743 c.c. in June to 231 c.c. in October in the southern. In fact, only one of the stations yielded as much as 500 c.c. in that month. The contrast between the richer and the poorer catches on the offshore part of the shelf (the inshore belt was not sampled), was, however, no less striking in October (richest haul about 20 times the poorest) than it had been in the preceding summer (richest about 14 times the poorest). Hence, great irregularity of quantitative distribution appears to be as characteristic of a population that is (or recently has been) declining, as of one that is increasing, or near its maximum.

The only year (1916) in which towing was done in late autumn, was one when the summer plankton seems to have been more than usually abundant, following tardy vernal warming and consequent low summer temperatures. It appears from the original notes on the horizontal catches made by the late William Welch (no vertical or oblique tows were made) that the inshore waters still supported considerable amounts of plankton of one sort or another in that November, for "rich" catches were recorded locally on the inner half of the shelf south of Martha's Vineyard, close to Delaware Bay, and close in to Chesapeake Bay, contrasting, however, with only "fair" to "scanty" catches near the outer edge of the shelf all along from the offing of Martha's Vineyard to that of Chesapeake Bay. So far as these data go, in combination with those for 1931, they point toward a comparatively stable state for the last half of autumn.

There are no quantitative data for December or January, but it is likely that these months, and perhaps early February, see a progressive impoverishment in most years, especially in the northern half of the area, leading to the barrenness prevailing at the end of the winter. But considerable production may



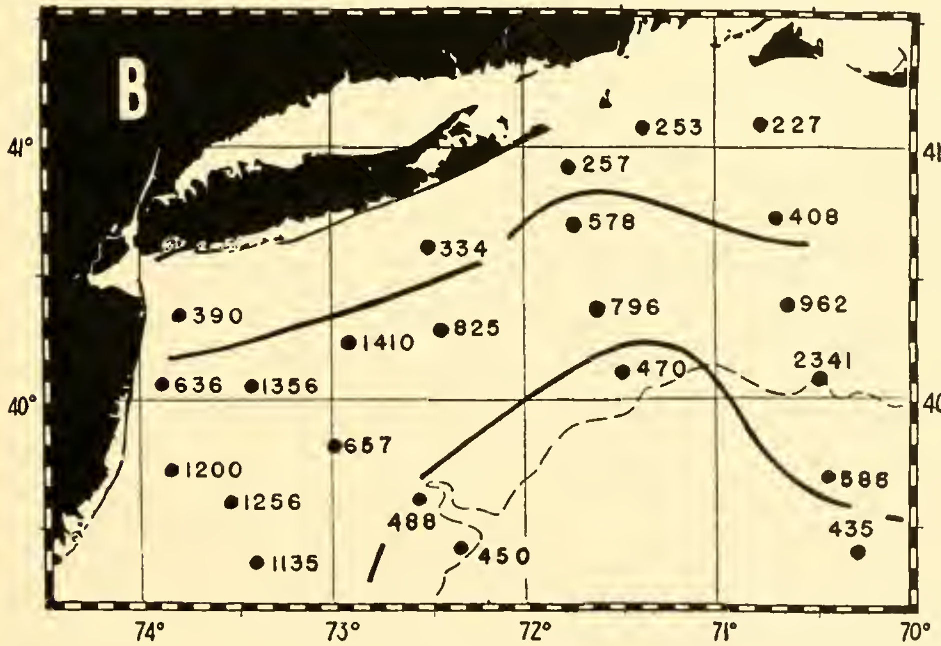


Fig. 8. Volumes of plankton, per standard haul, contour lines 100, 500, 1000 c.c.:–A, July 10–18, 1930; B, July 10–16, 1931.

take place in the southernmost sector in a normal February, judging from the fact that the center of abundance lies inshore and to the south in that month, as described above (p. 201), and the probability of this is especially strong in warm winters, to judge from the volumes that were recorded in February 1932 (p. 200).

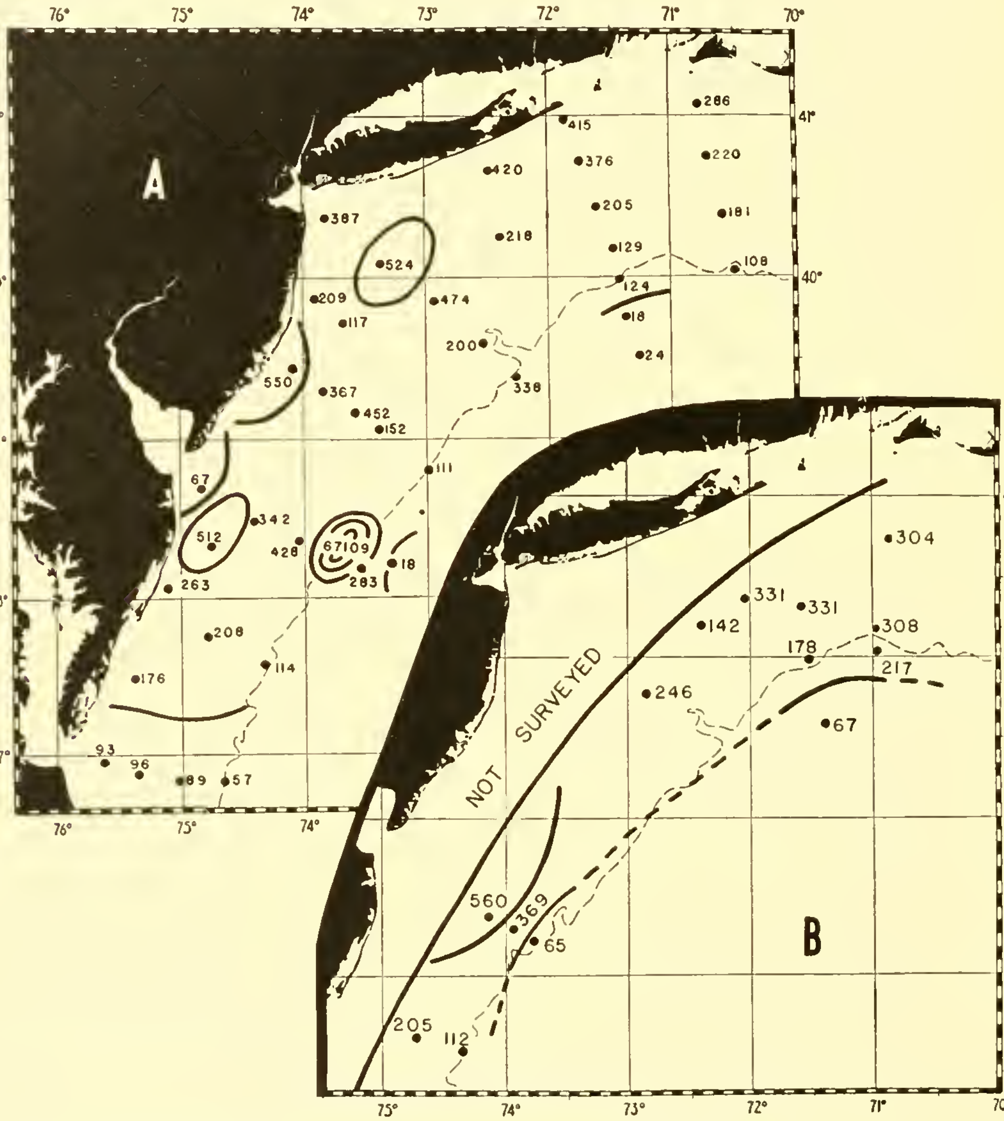


Fig. 9. Volumes of plankton, per standard haul, contours 100, 500, 1000, 50000 c.c.: A, July 11–August 1, 1929; B, October 19–28, 1931, as calculated from vertical tows.

Annual Differences

In February, the plankton was decidedly more abundant in the southern sector after the warm winter of 1932 (average, 472 c.c., maximum, 2400 c.c.,

Fig. 2B), than in either 1930 or 1931 (average, 175–200 c.c., maximum, 1000 c.c.) which were much alike in this respect. Whether this means that more animals survived the preceding months in 1932, than usual, on account of the abnormally high temperatures of that winter, or whether vernal augmentation had already started at the time of that February survey is an open question. However, we may take 1932 as an example of the extreme in the variation to be expected in the one direction, i.e., in a February of extraordinary abundance. We might perhaps expect the other extreme—a great paucity—after an unusually severe winter. Unfortunately, data are lacking here, for while 1929 was the coldest February for which we have a complete temperature survey (Bigelow, 1933), no contemporaneous plankton tows were made.

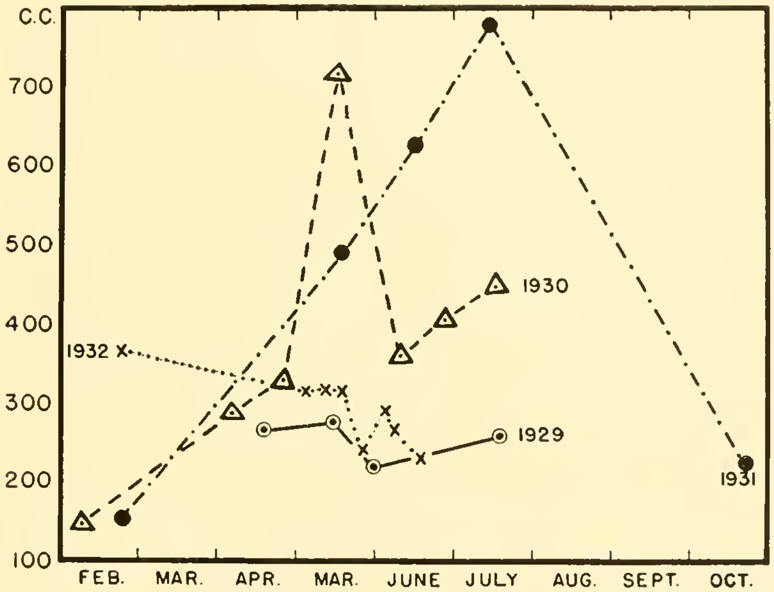


Fig. 10. Average volumes of plankton, for the area as a whole, in different months, for the several years.

The most interesting aspects of the annual comparison for spring and summer (Fig. 10) are that vernal augmentation was most pronounced, and summer volumes consequently greatest, in a year (1931) when the amount of plankton had averaged relatively small at the end of the winter, whereas there was no general augmentation of the plankton during the spring in the year (1932) when volumes had averaged largest in February: on the contrary, a slight impoverishment. But the facts that vernal augmentation was certainly of no great magnitude in 1929 either, following a cold winter (summer volumes consequently low), and that the positive anomaly of temperature existing in February 1932 had been entirely obliterated by that May, forbids our invoking temperature to explain year to year differences of this sort, unless the causes lie in conditions prevailing some time earlier in the season.

According to present information, the plankton as a whole may be expected to average about twice as voluminous, in our area, in a rich year as in a poor, at the end of the winter, a difference increasing to about 3 to 1 by midsummer.

Quantitative data, for the summers of 1913 and 1916, are not sufficient for inclusion in the preceding comparison, though the qualitative pictures for these two years are of much interest as representative of a warm and of a cold summer respectively.

Vertical Distribution

Studies of the vertical distribution of a mixed population are complicated by the fact that the existing state may depend on the precise proportions in which different species may enter into the general stock at any particular time and place. A case in point is the antithetical influence that would be exerted by a preponderance of Centropages, which usually has its center of abundance near the surface (p. 324) as contrasted with a preponderance of Calanus, which, through much of the year, is most abundant some distance below the surface (p. 310). We have also to distinguish between two categories of stratification that may be largely independent, first, that which results from diurnal vertical migrations, and second, what we name the "residual" stratification upon which the diurnal is superimposed. For the sake of clarity, it seems desirable to consider these two types separately.

Diurnal Stratification

The volumetric ratio of deep catch to shoal has varied widely from place to place on every cruise, by day as well as by night, depending largely on the precise qualitative composition of the community. In February, for example, of 1932—the only year, when hauls were made at two levels in that month,—the ratio of deep catch (22–24 meters) to shoal (7 meters) was about 0.3 to 1 at 3 A.M. on the 12th, midway out on the shelf off Cape May, where Euthemisto and Paracalanus jointly constituted 43% of the catch, but about 1 to 1 at midnight on the 26th, at about the same relative position off Bodie Island, where *Metridia lucens* was the leading species (38%). But the ratio, deep volume to shoal, averaged nearly the same between 8 A.M. and 4 P.M. (0.9 to 1, 5 cases) as between 8 P.M. and 4 A.M. (0.7 to 1, 8 cases), for that cruise as a whole. Evidently diurnal migration does not assume mass proportions at this time of year, either because the particular species concerned do not show this type of phototropic response on a broad scale, under the conditions of illumination then existing, or because the effects are then nullified by turbulent movements of the water.

But this ratio averaged significantly larger, however, during the hours of high illumination than during those of low, on each of the pertinent cruises for April, May, and June, as follows:

Average ratio of subsurface volume to surface volume, day and night, 1929

April; 8 A.M.–4 P.M., 12–30 M., 28.8 to 1, 5 cases; 31–70 M., 1.4 to 1, 6 cases.
8 P.M.–4 A.M., 12–30 M., 1.2 to 1, 9 cases; 31–70 M., 0.6 to 1, 5 cases.
May; 8 A.M.–4 P.M., 12–30 M., 9.2 to 1, 4 cases; 39–64 M., 3.2 to 1, 3 cases.
8 P.M.–4 A.M., 12–30 M., 1.2 to 1, 4 cases; 39–64 M., 1.0 to 1, 2 cases.
June; 8 A.M.–4 P.M., 12–30 M., 5.5 to 1, 11 cases; 34–71 M., 2.4 to 1, 7 cases.
8 P.M.–4 A.M., 12–30 M., 1.9 to 1, 15 cases; 34–71 M., 3.9 to 1, 5 cases.

Average ratio of deep (> 20 meters) volumes to shoal (5–10 meters), day and night, 1931 and 1932

1931, May; 8 A.M.–4 P.M., 19–32 M., 10.9 to 1, 7 cases; 39–64 M., 3.2 to 1, 3 cases.
8 P.M.–4 A.M., 19–32 M., 2.1 to 1, 5 cases; 39–64 M., 1 to 1, 2 cases.
June; 8 A.M.–4 P.M., 22 M., 6.8 to 1, 12 cases; 39 M., 7.4 to 1, 6 cases.
8 P.M.–4 A.M., 22 M., 2.0 to 1, 11 cases; 39 M., 1.6 to 1, 2 cases.
1932, May; 8 A.M.–4 P.M., 17–36 M., 1.4 to 1, 17 cases.
8 P.M.–4 A.M., 17–36 M., 0.9 to 1, 30 cases.
June; 8 A.M.–4 P.M., 20–28 M., 20.5 to 1, 14 cases.
8 P.M.–4 A.M., 20–28 M., 1.1 to 1, 22 cases.

Combination of the foregoing shows the ratio of volumes at, say, 18–36 meters, relative to that at 10–0 meters, to have averaged about 10.4 to 1 by day (37 cases) contrasted with 1.0 to 1 by night,[1] for April and May as a whole. Thus it is evidently characteristic of our area and of the particular assemblage of planktonic animals there existing, that diurnal migrations do attain sufficient magnitude during spring and early summer, to cause considerable enrichment of the mid-depths by day, at the expense of the surface stratum, the stratification that is temporarily built up in that way, being largely obliterated by night.

But the day-night contrast was usually much narrower at depths greater than 35 meters than in the mid-strata. In fact, no sign of diurnal alteration in this respect was recorded at 35 meters at the one station, where successive hauls

[1] Meaning by "day," 8 A.M.–4 P.M., and by "night," 8 P.M.–4 A.M.

were made several hours apart, though it was well marked at 20 meters and at 10 meters. Hence, we hazard the guess that diurnal migrations do not significantly affect the mass distribution of the plankton much below 40 meters depth.

Diurnal stratification, though still widespread, is much less pronounced in June, to judge from an average ratio, deep catch to shoal, of about 3.8 to 1 by day and of 2.2 to 1 by night (47 cases) for that month in 1929, 1931, and 1932 combined, while on one of the cruises (June 1929) a contrast of the opposite order was recorded for the 39–64 meter level. And the difference in this respect, between the hours of strong illumination and weak, averaged still smaller in July, as follows:

Ratio of deep to surface volumes,[1] July 1929

8 A.M.–4 P.M., 10–30 M., 8.3 to 1, 7 cases; 30–60 M., 4.0 to 1, 6 cases; > 60 M., 3.3 to 1, 3 cases.
8 P.M.–4 A.M., 10–30 M., 7.8 to 1, 5 cases; 30–60 M., 3.2 to 1, 3 cases; > 60 M., 2.0 to 1, 4 cases.

Ratio of deep volumes to those at 7–10 meters, July 1931

8 A.M.–4 P.M., 20–30 M., 5.8 to 1, 4 cases.
8 P.M.–4 A.M., 20–30 M., 4.8 to 1, 5 cases.

But these July ratios, being consistently larger by day than by night, show that diurnal migration is a factor to be taken into account, even at this time of year, though its effects appear then to be strongly opposed by the vertical distribution of temperature (p. 219), at least for the particular assemblage of species with which we are concerned.

We have no information as to diurnal migrations, for autumn, or early winter.

The physical factors most obviously to be considered, in connection with vernal intensification of diurnal migration as a mass phenomenon, followed by weakening, in midsummer, are (1) increasing vertical stability of the water column, (2) the intensity of illumination, and (3) vernal warming of the surface. During the winter, and first two months of spring, when temperature and salinity are close to uniform from surface to bottom, over our area as a whole, the water has no significant vertical stability. And the vertical turbulence is evidently active enough to counteract any general tendency that may exist for the planktonic community to carry out diurnal migrations through February, when illumination is still relatively weak. In short, the plankton, like the other characteristics of the water, is kept thoroughly stirred, down to a depth of about 30

[1] The tabulation is confined to the groups in which there were at least three cases.

meters. In this connection, we should perhaps remind the reader that vertical stability influences the vertical distribution of the planktonic community chiefly by its control of vertical circulation, for the vertical gradient of specific gravity is not great enough, even when the water is most stable, seriously to affect the rate of vertical swimming for active organisms, or the rate of sinking, for passive.

It seems probable that the development of diurnal migrations on a mass scale by April, in spite of the fact that vertical stability still continues negligible, and vertical stirring consequently active, results from the increasing stimulus to phototropic response provided by the increasing intensity of illumination. Then, as the season advances, the vernal warming from above, combined with some decrease in the salinity of the surface waters (Bigelow, 1933; Bigelow and Sears, 1935) progressively renders the water column so much more stable that a corresponding frictional force (wind or current) would produce only about 1/3 as active stirring in the upper 40 meters of our area, as a whole, in June, and 1/8 as active in July as it would in mid-May[1]. The mechanical barrier to effective vertical swimming, thus breaks down in the stratum within which it was previously strongest. The positive phototropic stimulus to diurnal migration also continues to strengthen, during the late spring and early summer, as the intensity of illumination and the length of day increase, with increasing declination of the sun. These factors in combination, offer a reasonable explanation for the fact that diurnal migrations have proved to have much more effect on the vertica distribution of the planktonic community in April, May, and June, than in February. And the evidence discussed on page 219, indicates that its decline, as a mass phenomenon from June to July is due to the barrier to upward swimming imposed by the high temperature to which the surface warms in midsummer.

Vertical stratification other than diurnal

In February, the oblique tows made in 1932, at the groups of stations where two or more levels were sampled, yielded volumes averaging about as large at 20–27 meters (average, 267 c.c.) as at 3–8 meters (average, 251 c.c.), but only 13% as large at 39–49 meters (35 c.c.). And the vertical gradient is still stronger if the one richest catch for each depth-category, be omitted from the calculation. Nor was there any apparent evidence of any mass effects, by diurnal migration, in that month (p. 214). It thus appears that while some of the February stations showed one stratum considerably the more productive, and other stations the

[1] Calculations by C. O'D. Iselin.

other, the plankton, on the whole, was distributed nearly uniformly, down to about 25–30 meters, but that it averaged less than one fourth as abundant in deeper water, a state probably reflecting the dominance of the community by Centropages and by Limacina at this season, and the prevailing scarcity of Calanus (p. 305).

But the center of population evidently tends to sink some 20–30 meters below the surface by early spring, there to continue until early summer, for the catches averaged 3 to 15 times as large from hauls centering at 12–30 meters as from those centering shoaler than 10 meters, in six of the seven cruises of record, April–June,—the one exception being May 1932, when the volume of plankton averaged about the same at the one level as at the other. And the fact that the ratio of average volume at 20–30 meters to volume at 10 meters or shoaler averaged 10.5 to 1 in July 1929, and 25.7 to 1 in that month of 1931, contrasting with about 3.8 to 1 for May and about 3.1 to 1 for June (all cruises combined) is evidence that concentration of plankton in the mid-depths tends to become still more pronounced as summer advances. It, also, appears that this enrichment, relative to the superficial stratum, likewise tends to extend to the deepest water on the shelf from June to July—though in lesser degree—for the ratio of volume at depths greater than 60 meters to those at the surface rose from 1.3 to 1 in May, and 1.9 to 1 in June, to 3.6 to 1 in July, in the one year (1929) when pertinent data were obtained.

It seems certain that the type of stratification, described above, is not the result of diurnal migration—general though that phenomenon be from April on—, because the observational series for April, May, and June includes a smaller number (70) of day time hauls, that would tend to magnify the effects of such migrations, than of night hauls (104) that would tend to obscure them, while the picture for July includes about as many hauls of the one category as of the other (11 day, 10 night). Neither can the initiation of vertical stratification of plankton be credited to temperature, for while this factor seems of great importance later in the season (p. 219), enrichment of the mid-level relative to the surface is established early in the spring, i.e., long before the upper strata have warmed to a value that could be considered unfavorable for the species concerned. An alteration in the qualitative composition of the plankton, does, however, offer a reasonable explanation, for while the community was dominated in the one February of record by Limacina and Centropages (combined, 67%), species that are usually most abundant near the surface, they have, on the average, been greatly surpassed, from April through July, by *Calanus finmarchicus* and *Sagitta elegans,* both of which average most abundant at mid-depths, as illustrated by the following tabulation, for the cruises on which hauls were made at two or more levels:

AVERAGE PERCENTAGE IN TOTAL CATCH

	Feb.	April	May	June	July
Centropages and Limacina	67%	13%	19%	11%	17%
Calanus finmarchicus and *Sagitta elegans*	2	68	43	55	64

Comparison between catches and temperatures at the mid-towing levels, argues strongly, however, that the progressive warming of the surface is the factor chiefly responsible for the rather abrupt intensification of the vertical plankton gradient, with corresponding impoverishment of the surface locally, that takes place from June to July, as was, indeed, forecast long ago, by the relationship between the stratum of chief abundance of Calanus and the temperature (Bigelow, 1922).

The fact that the majority of the dominant species are boreal, not arctic, would make it unlikely that any thermal control of vertical distribution would become operative until the surface had warmed above, say, 14°, nor do the data yield any suggestion of it in April or May, except perhaps at two stations close to the southern boundary of the area, where (in 1929) volumes were twice and eleven times as great at 15–30 meters, as at the surface, in temperatures of 17.8°–18.6°. The catches continued, in fact, to average nearly as large from one temperature as from another, through June, in one of the years (1932) when subsurface readings were obtained in that month — perhaps because of the scarcity of Calanus — although the surface had already warmed above 16° over considerable areas. A negative correlation had, however, developed by June between average catch and temperature, in the other pertinent year (1931), though with wide irregularity from station to station, as appears from the following tabulation.

	<12°	12.1°—16°	>16°
June 1931	903 c. c. 38 cases	322 c. c. 11 cases	313 c. c. 4 cases
June 1932	302 c. c. 46 cases	225 c. c. 28 cases	251 c. c. 14 cases

And the limitation of plankton by high temperature (again independent of depth) proved more obvious by July in each of the two years (1929, 1931) when tows were made at two levels in that month as follows:

	< 12°	12.1°–16°	16°–18°	18°–20°	> 20°
July 1929	383 c. c. 23 cases	485 c. c. 8 cases	—	149 c. c. 16 cases	77 c. c. 24 cases
July 1931	1025 c. c. 21 cases	664 c. c. 3 cases	280 c. c. 4 cases	127 c. c. 7 cases	197 c. c. 3 cases

Similar evidence lies in the fact that 7 out of 8 catches of 1000 c.c. for July 1931 were in hauls where the temperature at the mid-towing level was lower than 11° and none where it was warmer than 14°. It seems definitely established, therefore, that temperature and not depth *per se*, nor illumination (which is about the same in July as in June) is the factor responsible for the fact that the colder levels average several times as productive of zooplankton in midsummer as the warmer.

The thermal contrast between July, on the one hand, and May–June, on the other, consists not only in higher surface temperature, but also in the development of a more pronounced thermocline, raising the question whether the latter be significant in the present connection, or whether we have simply to do with the relative suitability of different temperatures for the particular species concerned.

Unfortunately, a definite answer cannot be expected from available data, because it seldom happened that the one haul was made just above the thermocline, and the other just below it, the picture being especially obscure for 1929, when the vertical intervals between hauls were, as a rule, broad enough to include both the thermocline and a considerable column of water within which the vertical gradient of temperature was small. The following comparison between the vertical gradient for temperature per unit depth and the ratio of shoal catch to deep, at stations (1929 and 1931 combined) where the depth intervals between the midpoints of successive hauls were not greater than 30 meters, might, it is true, suggest a very strong positive correlation between the two, if taken by itself.

Temperature difference per 10 meter depth	Average ratio of shoaler catch to next deeper	Extreme ratios	Cases
0–2°	1 to 3.4	1 to 0.5; 1 to 22.6	9
2.1–4°	1 to 2.6	1 to 0.5; 1 to 9.0	10
4.1–6°	1 to 18.6	1 to 0.4; 1 to 142.1	12
6.1–8°	1 to 41.4	1 to 4.8; 1 to 140.1	4

But it happened that the deeper haul was either made in water colder than 17°, or the shoaler in water warmer than 12°, wherever the thermal gradient per 10 meters was greater than 4°. In other words, either the one catch was made within the thermal range which appears most favorable for boreal plankton, or the other was made at a temperature that is much less so. In short, it is doubtful whether the steepness of the thermal gradient, *per se*, is of any importance in the distributional picture now under discussion.

The fact that the boreal plankton remains on the whole so definitely concentrated in the cooler part of the water column at the season when the surface is warmest, in spite of the widespread tendency toward diurnal migration, introduces interesting speculations as to the physiological mechanisms and responses involved—phototropism, geotropism (both of these perhaps being reversible by temperature), and also the possibility that such animals as Calanus, etc., may simply become immobilized at a temperature unfavorably high, and thus passively sink down again, to a more favorable environment.

We have no information as to vertical distribution for the community as a whole, for the autumn or early winter.

Comparison With Other Areas

The great majority of zooplankton studies that have appeared during the last quarter century have been based on the enumeration of individuals, and when measurements have been made of the volumes of plankton present, these have in most cases been only incidental to the main thesis of the particular investigation in hand. For example, the only systematic records of volumes of zooplankton as distinct from phytoplankton that are included in the extensive lists of collections made by the Fisheries Services of the various North European countries in different years between 1902–1912, published by the International Council for the Exploration of the Sea in their several series of bulletins, are those contributed by the Swedish Fisheries Service for the Skagerak and for the Baltic (Conseil Permanent International pour l'Exploration de la Mer, 1904–1907). And it is obvious that there can be no basis for comparison between volumetric studies and numerical, unless one or the other includes some indication as to the relationship between the number of individuals and their volumes.

It is perhaps somewhat astonishing that such should be the case, because a majority of the campaigns of towing have received their impetus from fisheries investigations, from which standpoint, it would seem perhaps not less important to know the mass of animal plankton present than to know the number of individual animals making up that mass—at least if the point at issue be the foodstuffs available for fishes.

The result has been that while a vast body of information has been accumulated about life histories of the species of planktonic animals that are the most numerous in northern seas and the most important there as food for herring or other fishes, about the variations in their populations in space and time, and about their community associations, we still have only the haziest ideas as to the mass of animal substance that is characteristic of any part of the sea, at any depth, at any time of year—and even less idea as to how much may be produced annually. In this respect, the study of the zooplankton has lagged far behind that of the phytoplankton.

We also face the further difficulty that only a rough comparison is possible in most cases, even between different studies primarily volumetric, because of differences in the methods of collection and in the precision with which necessary information as to towing speeds, etc., has been presented. For example, the coarse nets used on the "Thor" and "Dana" expeditions (Jespersen, 1917, 1923, 1935), adequately sample only the larger planktonic animals such as are more abundant on the high seas, but fail for everything smaller than the largest copepods, i.e., for many of the species that are often predominant inshore, as illustrated by the fact that catches with a 2-meter stramin net, at eight of our own stations in June 1932, averaged only about 1/6 as voluminous as those made at the same stations with the silk net, when reduced to a common standard. On the other hand, fine meshed nets (#20 silk, 173 meshes per linear inch), such as have often been employed in quantitative studies, fail for the larger animals, but yield a combined catch of smaller zooplankton and of phytoplankton. Hence, catches made in them very seldom give a measure of the total animal fraction of the planktonic community, as distinct from the vegetable fraction.

Consequently, the allowances that must be made for divergences in procedure limit to the roughest such comparisons as we are able to make between our area and others where the volume of animal plankton has been recorded.

The following tables, summarizing the more extensive of the volumetric measurements of the zooplanktonic community as a whole, that have been made off the east coast of North America and off the northwestern coasts of Europe, are here expressed arbitrarily as cubic centimeters per cubic meter of water, rather than per unit tow, in the hope of giving the reader a more graphic picture (for a discussion of the methods of expression, see p. 197).

Volume of Plankton along the east coast of North America and West Greenland

Locality	Season	Authority	Settlement (S), or Displacement (D)	Calculated average, c. c. per cubic meter	Estimated c. c. per cu. meter by displacement
Cape Cod to Chesapeake Bay	Feb., 1930-1932		D	0.4	0.4
	Apr., 1929-1930			0.5	0.5
	May, 1929-1932			0.8	0.8
	June, 1929-1932			0.7	0.7
	July, 1929-1931			0.8	0.8
	Oct., 1931			0.4	0.4
Martha's Vineyard	Sept.-Oct., 1935	Clarke and Zinn (1937)	S	0.08	0.04
	Nov.-Dec., 1935			1.4	0.7
	Jan.-Mar., 1936			1.9	0.9
	Apr.-June, 1936			0.24	0.12
	July-Aug., 1936			0.19	0.09
Gulf of Maine	July-Aug., 1913, 1916	Bigelow (1926)	S	0.7	0.35
	March, 1920			0.4	0.2
	April, 1932	Fish and Johnson [1] (1937)	D	0.7	0.7
	May, 1932			0.34	0.34
	June, 1932			0.21	0.21
	Aug.-Sept., 1932			0.16	0.16
	September, 1933	Redfield (unpublished data)	D	0.21	0.21
	October, 1933			0.13	0.13
	December, 1933			0.17	0.17
	January, 1934			0.12	0.12
	March, 1934			0.05	0.05
	April-May, 1934			0.16	0.16
	May-June, 1934			0.26	0.26
	June-July, 1934			0.32	0.32
	September, 1934			0.5	0.5
Bay of Fundy	April, 1932	Fish and Johnson (1937)	D	0.04	0.04
	May, 1932			0.19	0.19
	June, 1932			0.2	0.2
	Aug.-Sept., 1932			0.09	0.09
Nova Scotia, Newfoundland Shelf	May, 1915	Huntsman (1919)	S	0.9	0.45
	June, 1915			0.5	0.25
	July, 1915			0.6	0.3
Gulf of St. Lawrence	May-June, 1915	Huntsman (1919)	S	0.5	0.25
	August, 1915			0.5	0.25
West Greenland	August, 1924	Størmer [2] (1929)		0.35	0.17

[1] Dr. Fish informs us that the towing speed was very nearly 1.5 miles per hour.

[2] Stas. 32–63, 250–0 meters.

These series are all comparable with our own data, in that phytoplankton does not enter into the resultant volumes in more than minimal proportions. And the number of observations on which the average is based is large enough in each case for results to appear significant. But, in some cases, the measurement was by "settlement," which yields results averaging more than twice as large as does the "displacement" method. If allowance be made for this difference in method, the tabulation suggests that there is but little latitudinal difference, in the richness of plankton from the offing of Chesapeake Bay northward to the Gulf of Maine, in late winter or in early spring, when the zooplankton (near its yearly minimum for the continental shelf as a whole) averages only about 0.2–0.3 c.c. per cubic meter. But from May through July, the catches have averaged at least twice as large west and south from Cape Cod (about 0.6–0.7 c.c. per cubic meter) as for the Gulf of Maine (including the Bay of Fundy), for eastern Canadian waters, or for West Greenland, with the sector between Cape Cod and Delaware Bay averaging somewhat the richest of all, at the season of maximum abundance; the Bay of Fundy, and the Gulf of St. Lawrence somewhat the poorest.

The largest volume per cubic meter, as yet actually recorded from American waters is 116.1 c.c., at the edge of the continental shelf off Delaware Bay on July 18, 1929. But this—being the product of a local swarm of salpae—cannot be regarded as representative of more than the actual column of water fished. No doubt, a net drawn through one of the windrows of Aurellia, for example,—that are so commonly encountered in northern seas in summer—would yield a catch as large or larger. Aside from this (which may well have been equalled on many unrecorded occasions elsewhere), the maximum is 6.9 c.c. per cubic meter, in the offing of New Jersey, May 20, 1930. The Gulf of St. Lawrence ranks second in this respect, with 9.4 c.c. measured by the "settlement" method, equivalent to perhaps 4–5 c.c. by displacement (Huntsman, 1919), the Gulf of Maine third (4.3 c.c. per cubic meter by "settlement," or perhaps about 2 c.c. by displacement, Bigelow, 1926, Table, p. 94), while the maxima so far recorded for West Greenland and for the Scotian shelf are only 2.6 c.c. and 2.1 c.c., respectively by "settlement," corresponding to about 1 c.c. by displacement.

It has long been a matter of common knowledge that rich concentrations of plankton occur in summer in the upper water layers around Iceland. Assuming a towing speed of 1.5 knots, Damas' (1905, p. 15) record of a catch of more than 1000 c.c. of young Calanus alone in a five minute haul at the surface with a one meter net—frequently quoted as an instance of extraordinary abundance of

Volume of Plankton in North European Waters

Locality	Season	Authority	Settlement (S), Draining (Dr.), or Displacement (D).	Calculated average, c. c. per cubic meter	Estimated c. c. per cu. meter by displacement
Iceland	July, 1924	Størmer (1929)	S	0.4	0.2
Iceland, Faroes, Ireland		Jespersen (1923)	Dr.[1]	0.84	0.84
Southern Norwegian Sea	July-August, 1924	Størmer (1929)	S	0.6	0.3
North Sea	June, 1926 Aug., 1926 Nov., 1926	Savage (1931)	S	1.15 1.0 1.2	0.57 0.5 0.6
		Jesperson (1923)	Dr.[1]	0.013	0.013
English Channel	April, 1925 May, 1925 June, 1925 July, 1925 Aug., 1925	Russell (1927) [2]	S	0.03 0.20 0.04 0.11 0.10	0.01 0.10 0.02 0.05 0.05
Skagerak	Feb., 1903 Aug., 1903 Nov., 1903 May, 1904 Aug., 1904 Nov., 1904 Aug., 1906	Conseil permanent international pour l'exploration de la mer (1904–1907)	S	0.08 0.09 0.28 0.18 0.09 0.32 0.04	0.04 0.05 0.14 0.09 0.05 0.16 0.02
Baltic	Aug., 1903 Aug., 1904 Aug., 1906	Conseil permanent international pour l'exploration de la mer (1904–1907)	S	0.04 0.45 0.07	0.02 0.22 0.04
	May-June, 1931	Mielk and Künne (1935, p. 69)	S	0.95	0.5

plankton—corresponds to about 6 c.c. per cubic meter, if the volumetric measurement was made by displacement, which ranks with the richer catches in the Gulf

[1] We have found by experiment that measurement by "draining" agrees closely with that by "displacement."

[2] We are informed by Dr. Russell that his towing speed was between 1.5 and 2 knots.

of St. Lawrence, and south of New York. It is more impressive, in the present connection that the average of 0.84 c.c., for 82 "Thor" catches between Iceland, the Faroes, and Ireland (Jespersen, 1923, p. 4, Fig. 1; Schmidt, 1912, p. 8) may well have represented a community richer than any that has thus far been reported for any considerable area in the western Atlantic, most of the smaller copepods, etc., having very likely been lost through the coarse-meshed nets that were used. And while Størmer (1929) reported much smaller volumes from Icelandic waters (average, 0.4 c.c. per cubic meter, by settlement, or perhaps 0.2 c.c. by displacement) his measurements were made at two stations only, and after removing some of the more bulky forms (medusae, etc.).

The average recorded by Størmer (1929) at 23 "Michael Sars" stations, in the southern part of the Norwegian Sea of about 0.6 c.c. per cubic meter, with a maximum for any one haul of about 3.4 c.c. per cubic meter, is about half that for our own area (p. 223), if allowance be made for the difference between measurements by "settlement" and by "displacement."

In the North Sea, many measurements of plankton volume, per cubic meter, were long ago made by Apstein (1906) and Kraefft (1910), yielding very large values. But their catches were made in such fine nets (173 meshes per linear inch) that the recorded volumes include the phytoplanktonic fraction, nor do the published data afford any way of estimating the volume of the zooplanktonic fraction, as distinct from the latter, and this applies equally to the volumes given for the Baltic and North Sea, by Mielck (1911), Lücke (1912), and Büse (1915). On the other hand, the very low average (corresponding to 0.013 c.c. per cubic meter) reported for the North Sea by Jespersen (1923, Fig. 1), may be chargeable—at least in part—to the very coarse mesh of his stramin nets. Volumes for the North Sea calculated from the lists more recently published by Savage, (1931, Tables 13–17), in connection with his studies of the food of the herring, agree closely with the summer average for our own area, when reduced to the "displacement" basis according to Savage's comparison of methods, though the maximum reported by him of 7 c.c. per cubic meter by "settlement" was somewhat lower.[1]

Zooplankton would appear to be considerably less abundant in the English Channel than in the North Sea, according to Russell's (1925, 1927) records. And Dr. Russell writes us that "the mixed oceanic and coastal water near the continental shelf is probably richer, and the English Channel and southern North Sea are rather poorer in plankton content" (quoted from a letter of January 28,

[1] For description of the type of net employed, see Cons. Int., Publ. Circ., No. 84.

1938), though this regional contrast may be not as wide as the calculated volumes indicate, because the nets used in the Channel would retain "only the more bulky of the planktonic organisms" (Russell, 1927). And the long series of vertical tows made by the Swedish Fisheries Service show a decided poverty in the Skagerak, as contrasted with the North Sea, with the English Channel, or with the coastal waters of northeastern America as a whole. But the volumes—chiefly copepods—reported for the western part of the Baltic by Mielck and Künne (1935, p. 69) correspond quite closely to the averages east of Great Britain, when reduced to a common standard (see Table, p. 225). And this also applied in two surveys out of three, to the region farther east and north in the Baltic examined by the Swedish cruises in August of 1903, 1904, and 1906.

The foregoing comparisons point to the waters between Iceland, the Faroes, and Scotland as probably somewhat more productive of zooplankton, at the season of chief abundance than is any other considerable sector of the boreal belt (including tributary seas), of the North Atlantic. In fact, it would not be astonishing if these waters should finally prove to support 4–6 times as large a volume of plankton, as does the most closely competing region, to judge from the allowance to be made for the size of mesh used in the nets. Next in rank, come the American sector between Cape Cod and Chesapeake Bay on the one side of the Atlantic, and the North Sea on the other, the former with an average of about 0.7–0.8 c.c. per cubic meter, at the peak season, as measured by displacement, the latter with 1.4–1.9 c.c., as measured by settlement, which corresponds to perhaps 0.5–0.6 c.c. by displacement. And it is further interesting that 1932 was a poor year for plankton in each of these areas, on opposite sides of the Atlantic (Savage, 1937). The Gulf of Maine and Scotian shelf in the west and the southern North Sea and Baltic in the east, similarly fall together at the season when the plankton is richest, but with somewhat smaller volumes, corresponding to about 0.2–0.4 c.c., or perhaps somewhat less, by displacement. But no attempt has been made to estimate the total yearly production (volumetric) of zooplankton for any part of the sea—so far as we are aware. And the relative ranking on this basis may differ widely from the foregoing, with Icelandic waters, where active production is probably confined to a short season, perhaps falling below our own waters and below the North Sea region.

The striking feature of the comparison is not the demonstrated diversity, i.e., that one boreal locality may average several times as rich as another, whether for the column of water as a whole on the continental shelf, or for the upper strata farther out to sea, but rather, that the average volumes for different regions, at the season of maximum abundance (Tables, pp. 223, 225), should differ so little, one from another, relative to the volume of water containing them. If allowance be made for the method of measurement and for the size of mesh, the extreme range is only from about 1 to about 8 volumes of animal plankton, of the size of medium-sized copepods and larger, per 10 million volumes of water, though individual catches may run as high as 1100 volumes or more (p. 224).

There would be little profit in extending the comparison farther afield, because the published records of volumetric abundance for other seas are based chiefly on catches made in nets either of mesh so fine that they retain the vegetable as well as the animal fraction, e.g., Hensen's (1890) study of volumetric distribution between Bermuda and the Cape Verdes, and Boschma's (1936), for the East Indies, or so coarse that they may have lost a considerable fraction of the stock of animals in some localities, but perhaps very little at others. We need merely remind the reader of Jespersen's (1923, 1924) well known demonstration, based on catches with very coarse (stramin) nets, of poverty in the Mediterranean and in the Sargasso Sea region, contrasted with richness in the northeastern Atlantic, and of his more recent comparison (1935, Fig. 27) between the upper water layers in various parts of the Atlantic and Pacific at mid- and low latitudes.

RELATIVE ABUNDANCE OF DIFFERENT SPECIES

Dominant species. Previous information (p. 192) had shown that the waters on the continental shelf more than a few miles out from the land, and from Cape Cod as far west as the offing of New York are dominated in late summer and autumn by much the same boreal communities—lead by *Calanus finmarchicus*—as characterize the Gulf of Maine to the eastward. And similar conditions had been found to extend southward at least to the latitude of Chesapeake Bay in a cool summer (illustrated by 1916), though in a warm one (e.g., 1913), the waters in this southern sector may be monopolized locally by swarms of neritic species of ctenophores, on the one hand, or of salpae (of oceanic origin), on the other, with a considerable variety of other warm oceanic visitors recorded here and there, though never in any significant volume.

The records for the period, 1929–1932, now add the information that the same boreal "Calanus" community similarly dominates our area as a whole, southward at least to Latitude 36° N., from the end of the winter, through spring and early summer, in the relative proportions tabulated below, and that immigrants from the warm oceanic community that constantly inhabit the waters along the continental edge, are no more important, volumetrically, on the shelf during the vernal half year than they are in summer or autumn.

Average Percentages in the Total Zooplankton of Species that have Formed 1% or more, by Volume, in any One of the Subdivisions

Date	Sector	C. finmarchicus	C. typicus	M. lucens	P. parvus	P. minutus	L. retroversa	S. elegans	S. serratodentata	E. compressa	Euphausiids	Ctenophores	A. digitale	Leptoline medusae	Crab larvae	O. labradoriensis	Salps	Doliolum	C. limacina	Oceanic copepods
Feb., 1930	Inshore	3	49	<1		6	<1	7	21	<1	1						<1			
	Offshore	10	2	12		7	8	4	20	2	20						2			
	North	9	11	4		6	4	17	31	<1	2						<1			
	South	1	59	1		7	<1	<1	14	<1	4						<1			
	Total area	5	41	4		7	2	6	20	1	3						<1			
1931	Inshore	13	<1	<1		2	<1	55	25	1										
	Offshore	28	11	21		8	<1	15	2	3										
	North	9	2	3		20	<1	51	1	1										
	South	16	5	10		2	<1	37	18	2										
	Total area	19	5	9		5	<1	38	15	2										
1932	Inshore	1	31	6	6	4	41	<1	3	1							<1			<1
	Offshore	1	6	15	19	<1	9	<1	18	9							2			3
	North	15	14	12	21	1	1	<1	3	12							<1			7
	South	1	29	7	6	1	41	<1	5	1							<1			2
	Total area	1	29	7	8	3	38	<1	5	2							<1			<1
April, 1929	Inshore	56	11	0		<1	9	5	12	<1	<1									
	Offshore	73	6	5		2	<1	<1	4	<1	2									
	North	73	6	4		2	4	3	<1	<1	2									
	South	58	12	1		<1	5	0	17	<1	<1									
	Total area	66	9	3		1	4	2	8	<1	1									
1930	Inshore	40	11	5		11	12	7	3	3	<1									
	Offshore	40	3	27		5	13	4	3	2	1									
	North	44	2	18		6	12	11	2	2	1									
	South	36	15	12		9	9	3	5	4	<1									
	Total area	41	7	16		8	6	8	3	2	<1									
May, 1929	Inshore	21	6	<1		<1	18	9	1	<1	8	25		1	2	1	0	0		
	Offshore	47	5	2		<1	6	10	3	<1	2	0		<1	<1	<1	1	1		
	North	41	4	1		<1	15	14	<1	<1	5	0		<1	<1	<1	1	0		
	South	18	8	1		<1	9	1	7	<1	1	46		2	3	<1	<1	2		
	Total area	33	5	1		<1	12	9	2	<1	4	13		<1	1	<1	<1	1		
1930	Inshore	35	5	2		<1	24	13	<1	5	<1		2		1					
	Offshore	25	1	6		<1	56	3	1	3	<1		<1		<1					
	North	38	1	8		<1	36	6	<1	3	<1		<1		<1					
	South	18	3	1		<1	55	8	<1	3	<1		1		<1					
	Total area	29	2	5		<1	45	7	1	4	<1		<1		<1					
1931	Inshore	30	<1	<1		7	12	34	<1	<1				8	<1	1				
	Offshore	69	<1	9		5	4	3	<1	<1				1	<1	1				
	North	61	<1	6		7	3	11	<1	<1				3	<1	1				
	South	24	<1	3		4	21	36	<1	<1				8	<1	1				
	Total area	52	<1	5		6	8	17	<1	<1				4	<1	1				
1932	Inshore	8	6	3		12	29	10	1	<1	<1		7	2	4	8	0		<1	<1
	Offshore	28	1	14		5	17	2	2	<1	7		1	<1	1	4	3		1	2
	North	21	3	10		6	25	4	1	<1	5		4	2	1	8	2		<1	<1
	South	10	15	6		11	21	2	2	<1	3		4	<1	5	3	1		1	2
	Total area	16	8	8		8	23	6	2	<1	4		4	1	3	6	1		1	1
June, 1929	Inshore	25	9	6		1	9	23	1	3	1			1	5	1	0		3	
	Offshore	46	4	9		<1	3	11	2	<1	6			0	1	1	9		1	
	North	43	2	4		1	6	22	<1	<1	6			1	3	1	5		1	
	South	17	16	6		<1	4	1	1	5	1			1	2	1	4		6	
	Total area	37	6	5		<1	5	18	1	1	5			1	2	1	3		1	
1930	Inshore	41	1	<1		<1	20	19	<1	9	<1		1	<1	1	<1	0		<1	
	Offshore	61	<1	7		<1	6	4	<1	3	2		<1	<1	<1	<1	<1		<1	
	North	57	<1	3		1	18	8	<1	5	1		1	<1	1	<1	<1		<1	
	South	17	<1	<1		<1	1	48	<1	17	<1		<1	<1	<1	<1	0		<1	
	Total area	52	<1	2		<1	15	13	<1	7	1		1	<1	1	<1	<1		<1	
1931	Inshore	59	2	1		6	1	25	<1	<1	<1		<1	1	2	<1	0		<1	
	Offshore	74	1	3		2	<1	11	2	<1	<1		<1	<1	<1	<1	1		<1	
	North	76	1	2		5	<1	9	1	<1	<1		<1	<1	2	<1	<1		<1	
	South	41	2	1		3	3	39	2	<1	<1		<1	<1	1	<1	0		1	
	Total area	65	1	2		4	1	17	1	<1	<1		<1	<1	1	<1	<1		<1	
1932	Inshore	8	14	2		4	6	14	<1	<1	2		28	2	2	<1	0		2	
	Offshore	26	7	12		3	12	4	2	1	6		6	<1	<1	<1	9		8	
	North	18	6	6		4	7	17	1	1	4		19	2	<1	<1	2		1	
	South	14	17	4		3	12	8	4	2	4		15	<1	<1	<1	8		9	
	Total area	16	11	6		3	9	12	2	1	4		17	1	2	<1	4		5	
July, 1929	Inshore	27	20	<1	1	<1	2	35	<1	1	1	<1		2	<1		0	1		<1
	Offshore	32	14	4	<1	<1	<1	21	3	1	6	4		<1	<1		7	3		3
	North	35	19	2	1	<1	1	28	1	1	3	<1		2	<1		3	0		<1
	South	9	13	<1	1	<1	2	36	2	2	<1	5		<1	1		1	5		4
	Total area	29	18	1	1	<1	1	30	1	1	2	2		1	1		2	1		2
1930	Inshore	47	35	<1		<1	3	7	<1	6	<1	<1		<1	<1		0			<1
	Offshore	69	3	7		<1	4	5	<1	<1	<1	<1		0	<1		<1			<1
	North	57	20	3		<1	3	6	<1	6	<1	<1		<1	<1		<1			<1
1931	Inshore	57	20	<1		3	3	6	<1	<1	<1	<1		3	<1		0			<1
	Offshore	64	1	<1		1	0	2	<1	<1	<1	<1		<1	<1		24			<1
	North	61	12	<1		1	1	4	<1	<1	<1	<1		1	<1		11			<1
Oct., 1931	Offshore	7	34	7	17	2	<1	5	5	<1	<1						<1			5
	North	8	47	11	26	1	<1	3	2	<1	<1						0			1
	South	7	14	2	12	4	<1	7	9	<1	<1						1			12

Monthly Succession

February. The only species that have averaged more than 1% (by volume) of the total catches, in any one of the years, for the region as a whole, in February are the following:—*Calanus finmarchicus, Centropages typicus, Euthemisto compressa, Limacina retroversa, Metridia lucens, Paracalanus parvus, Pseudocalanus minutus, Sagitta elegans,* and *Sagitta serratodentata.* Combined, these have constituted from 86% to 94%, by volume, of the winter catches. In no instance, in fact, was as much as 50 c.c. of any other species taken at any of the February stations.

The tabulation (p. 229) of relative percentages shows that in a given year, either *Centropages typicus, Sagitta elegans,* or *Limacina retroversa* may be the leading species at this season. As a rule, this applies, also, for individual localities where rich (> 300 c.c.) catches were made, the only notable exception, being for one station, where *Sagitta serratodentata* ranked high. *Calanus finmarchicus* (dominant later in the season) occupies a minor, or at most an intermediate position inshore at the end of winter, ranking fifth there, on the average, while offshore, it ranks second (next to Metridia). In February, Calanus has also averaged more important to the north of the Cape May profile (ranking third, for the three years combined), than southward (ranking fifth); so, too, Euthemisto. On the other hand, *Centropages typicus* was relatively much more important in the south than in the north, in the two years when it occurred in significant proportion in either subdivision. In the cases of the other dominant species, the north-south relationships have been so irregular that no general rule can be derived from so short a series of observations.

The February list of dominant species includes no benthonic derivatives of any sort, no neritic larvae, no visitors from offshore; evidence that contributions from the coast line, and from the bottom beneath, on the one hand, or from the continental slope, on the other, are negligible.[1] Neither does it include any immigrants, whether from colder coastal waters to the north, or from warmer to the south.

But the following additional species have occasionally constituted 1%, or more, at individual stations in February, north of Latitude 36° N.:

Aglantha digitale, 4 stations, 1–10 c.c., 1–7%; *Candacia armata,* 1 station, 27 c.c., 5%; *Centropages hamatus,* 1 station, 10 c.c., 1%; Crago sp., 2 stations, 4–22 c.c., 3–15%; cumaceans, 2 stations, 2–6 c.c., 1–4%; Eucalanus sp., 1 station, 2 c.c., 1%;

[1] Perhaps on account of failure regularly to sample close to bottom, see page 193.

Euphausia sp., 2 stations, 9 and 28 c.c., 9 and 32%; *Nematoscelis megalops*, 4 stations, 5–40 c.c., 25–81%; *Neomysis americana*, 1 station, 4 c.c., 2%; Oithona sp., 3 stations, 1–30 c.c., 1–2%; *Pleuromamma gracilis*, 5 stations, 4–15 c.c., 10–41%; *Rhincalanus nasutus*, 1 station, 9 c.c., 2%; salps, 2 stations, 11–17 c.c., 32–57%; *Thysanoessa inermis*, 1 station, 16 c.c., 3%.

The winter stations occupied in 1931, in the immediate vicinity of Cape Hatteras, show that the eight species which dominate to the northward of Latitude 36° N., are outclassed farther south, by species of oceanic origin, for while the former category constituted only 11–12% of the average catch there, Noctiluca formed 8%, *Sagitta enflata*, 11%, and oceanic copepods, 42%, with the remaining 34% consisting of a varied assemblage of oceanic decapods, amphipods, siphonophores, and medusae, among which some 51 species were identified.

April. The same species have not only dominated in April (Fig. 11B), as in February, but, in combination, they have formed about the same average proportion of the total catches (89–93%), for the area as a whole. And their combined importance is not appreciably affected by the entrance by April into the "dominant" category of a new member—euphausiids—for these were still in low percentage (1%) and counterbalanced by a decline on the part of Paracalanus. In fact, the seven leading species monopolized the large (> 500 c.c.) catches, even more strongly (80% in each of the 19 cases) in April than in February.

The most instructive feature of the lists for April, compared with February, of the one year (1930) when surveys were made in both, is that *Calanus finmarchicus* had increased so greatly, in relative importance, from the one month to the other as to make it by far the most prominant species in the northern sector, while in the southern sector, it was dominant at the time of the first April cruise of that year, and about equalled its closest rivals (Centropages and Pseudocalanus) at the time of the second. The area where Calanus averaged 20% or more of the total volume of plankton (confined to localities in the northeast in February) had also expanded by early April to cover the waters generally (though with local exceptions) down to the offing of Chesapeake Bay. And the fact that Calanus was present in even larger percentage in April of 1929 (when no information was obtained in February), than of 1930, is evidence that the seasonal sequence recorded in the latter year may be accepted as normal. This increase in Calanus was, in fact, chiefly responsible for the great augmentation of the plankton as a whole that took place in the early spring of 1930 (p. 203). And this statement applies not only to the region as a whole, but to individual localities as well, for wherever the total catch was much larger in that April, than it had been in the

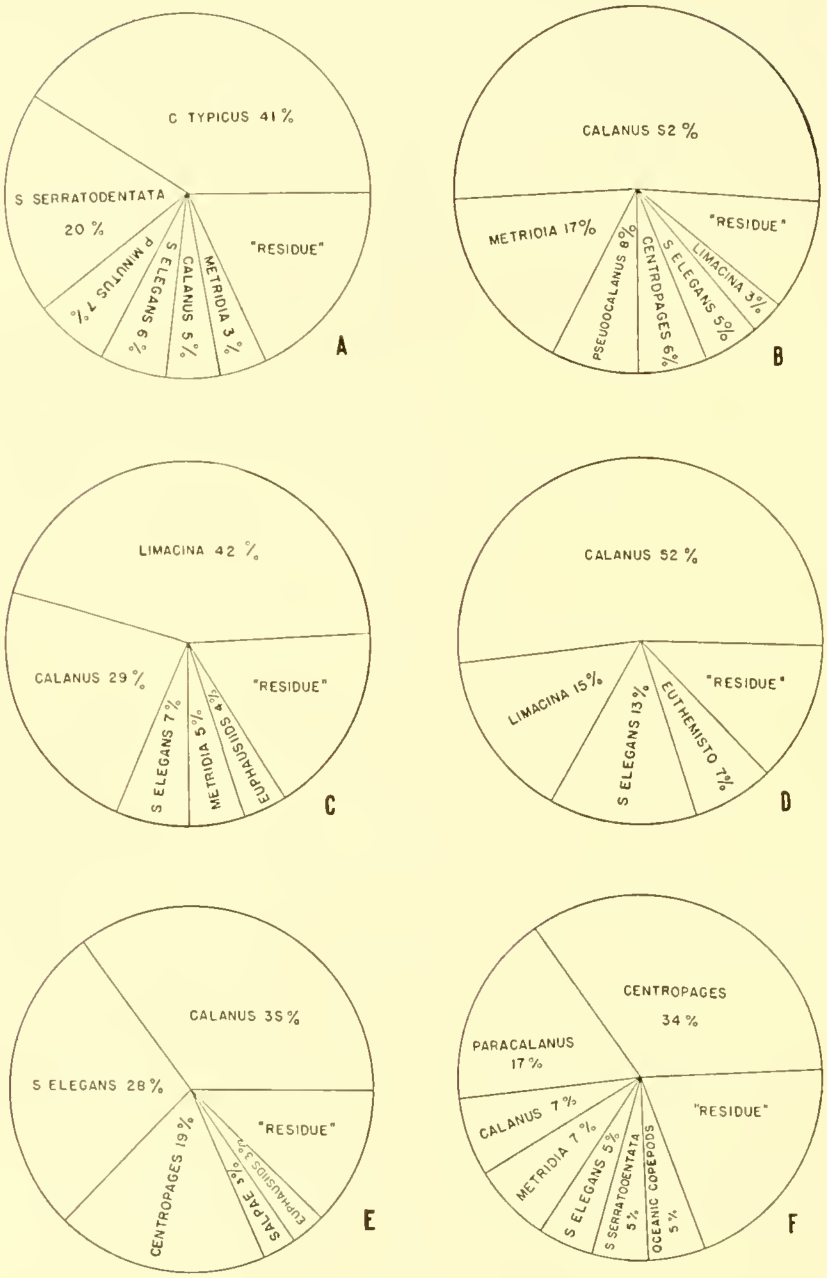


Fig. 11. Percentages (by volume) of dominant species in average catch for the area as a whole: A, February 5–13, 1930; B, April 3–11, 1930; C, May 12–23, 1930; D, June 7–18, 1930; E, July 11–August 1, 1929, and F, October 19–28, 1931.

preceding February, the percentage of Calanus was also much larger, whereas its percentage was higher in some cases, and lower in others at stations where little alteration had taken place in total volume.

It also deserves emphasis that Calanus—so far as can be judged from the rather unsatisfactory series—is the only member of the dominant group that usually experiences a great and general augmentation in relative abundance, within the confines of our area, in early spring. At the same time, it appears to be rather more common in April than in February—perhaps forecasting greater diversity in the general averages in May—for species other than the dominants, to form as much as 1% of the community, at individual stations, the recorded instances being:

> *Aglantha digitale*, 4 stations, 2–10 c.c., 1–8%; amphipods, 4 stations, 3–22 c.c., 1–9%; annelid worms, 1 station, 47 c.c., 24%; *Anomalocera pattersoni*, 1 station, 1 c.c., 12%; *Candacia armata*, 1 station, 4 c.c., 3%; *Centropages hamatus*, 5 stations, 3–35 c.c., 1–15%; Corycaeus sp., 1 station, 2 c.c., 1%; decapod larvae, 6 stations, 2–82 c.c., 1–43%; euphausiid larvae, 17 stations, 3–60 c.c., 1–54%; *Eucalanus attenuatus*, 6 stations, 3–18 c.c., 1–29%; Euchaeta sp., 1 station, 2 c.c., 1%; *Euchirella rostrata*, 2 stations, 3–6 c.c., 2–3%; leptomedusae, 2 stations, 12–25 c.c., 21–21%; *Lucifer typus*, 1 station, 8 c.c., 7%; *Nematoscelis megalops*, 1 station, 23 c.c., 1%; *Oikopleura labradoriensis*, 1 station, 9 c.c., 3%; *Pleuromamma gracilis*, 2 stations, 2–9 c.c., 1–5%; *Rhincalanus nasutus*, 4 stations, 5–40 c.c., 4–30%; oceanic sagittae, 2 stations, 2–4 c.c., 1–2%; *Sagitta enflata*, 2 stations, 11–12 c.c., 10–10%; salps, 4 stations, 4–30 c.c., 4–27%; *Temora stylifera*, 2 stations, 4–7 c.c., 3–6%.

May. Calanus averaged about as important in the total community, for the area as a whole in May (30–50%) as in April (40–60%), in the years when the winter had been normally cool, i.e., 1929, 1930, 1931, but after a warm winter (1932), it was much less so (16%). In all years (1929–1932), however, it averaged much more important relatively in the offshore belt than inshore, though with considerable difference in this respect from year to year, and about twice as important in the north as in the south. On the other hand, while Calanus was the largest single item in April in both years of record, in May this was true in two years (1929, 1931) only, whereas in the other years (1930, 1932), it was surpassed by Limacina. And the percentage of Calanus in the rich (> 500 c.c.) hauls also averaged considerably lower in May (16–27%) than it had in April (33–77%) in the two years (1929, 1930) for which information is available for both these months. Conflicting evidence of this sort is perhaps more reasonably explained as due to the brevity of the observational series, and to the roughness of the methods, than to any definitely seasonal trend, one way or the other, from the one month to the next.

Centropages, contrasting with Calanus, declined greatly in relative abundance, between February, or April, and May in three of the four years of record (1929, 1930, 1932), as appears from its average volumes and percentages for the area as a whole (Table, p. 229), while in the fourth year (1931), this species was so scarce throughout the season that the calculated monthly values are not significant for it in this connection. Furthermore, Centropages, which formed more than 50% of the catch at five out of eleven winter stations where more than 300 c.c. of plankton was taken, equalled 30% at only one of the 60 "rich" (> 500 c.c.) hauls for April and May combined.

Corresponding to this vernal decrease in relative importance, the area where Centropages averaged as much as 10% of the total volume contracted considerably in the north from February to April in 1930, though expanding offshore in the south meantime, while in 1932, a decided contraction of the same sort had in any case taken place by May, showing that this copepod is on the average, only a minor element(<1–5%) in the northern sector by the end of spring. And it is not much more important then, in the southern sector(<1–8%) in normal years (e.g., 1929, 1930), though after a very warm winter (as in 1932), its percentage may average but little lower in May (15%) than in February (29%). A vernal decline in relative importance seems equally characteristic of *Sagitta serratodentata*, judging from the fact that its percentage in the total catches averaged only about 1/20 as great in May as in February of 1930, less than 1/15 as great in 1931, and 1/5 as great in 1932. In fact, only two out of ten spring cruises showed it as forming as much as 2% of the general community (Table, p. 229). And it seems that it usually declines to less than 5% by May, even in the southern sector, where a considerable percentage of it may persist until April in some years (e.g., 1929, 16%).

The vernal histories of other members of the group that are dominant at the end of winter are less regular, for they may show increases in some years, decreases in others, though these alterations have usually been of a smaller order of magnitude than for Calanus, for Centropages, or for *Sagitta serratodentata*. In some years, for example, Pseudocalanus shows an upward trend at first, but then a decline, as in 1930, when its percentage about doubled between February and April, but then fell to an insignificant figure by May. And it may have experienced a similar succession in 1929, when it formed less than 1% in May (no information for that February). But the alteration was of the reverse order in 1932, when its percentage more than doubled between February and May, while in the fourth year of the series, its relative standing was about the same in the one month as in the other.

The vernal cycle for *Metridia lucens* seems to have paralleled that for Pseudocalanus in 1930, when its average percentage about quadrupled from February (4%) to April (16%), with a corresponding expansion of the area where it averaged as much as 10%, but then fell again by about 1/3 to May (5%). But it is doubtful whether any significant alteration in its relative abundance took place during the spring of 1929, of 1931, or of 1932, because its percentage in each of these years averaged about the same in May as it had in February. Neither is there any evidence that notably rich centers ever develop for Metridia at this time of year, as happens frequently for Calanus, and at least occasionally for Pseudocalanus. Metridia, however, continues as definitely an "offshore" species through the spring, as it is in February, its percentage having averaged about 2–17 times as high offshore as inshore, both in April, and in May of each year of record, also about twice as high in the north (8%) as in the south (4%) for the April-May cruises combined.

The year (1930) that saw the most pronounced fluctuations for Metridia was, however, one of comparative constancy from February through April to May, for *Sagitta elegans*. But the area where this chaetognath was relatively important (> 10%),—even less extensive early in that April than it had been in February—then greatly expanded southward by May. And in 1929, its percentage in the catches about quadrupled from April (2%; no February data available) to mid-May (9%). Likewise in 1932 it averaged more important in May (6%), than it had in the preceding February (1%), while in 1931 (thanks to more rapid multiplication by Calanus), it was in only about half as great percentage in the one month (17%) as it had been in the other (38%), although it had meantime increased in average abundance from about 58 c.c. to about 84 c.c. Regionally, however, the picture for *S. elegans* is more consistent than the foregoing might suggest, for in all years of record, it ranked considerably higher in percentage inshore (5–34%) than offshore (< 1–10%) in April and May, as seems in fact to be the general rule for it; also higher in the northern sector (3–14%) than in the southern (< 1–4%) on seven of the ten spring cruises.

In the case of Limacina, a 3-fold increase in percentage was registered between April (4%) and May (12%) in 1929, a 15-fold between early April (3%) and mid-May (45%) in 1930, and an 8-fold between February (< 1%) and May (8%) in 1931, with corresponding wide southward expansion of the areas where it averaged as much as 10% of the total community (Fig. 12). On the other hand, its percentage decreased by nearly ½ between February (38%) and May (23%) in 1932 (all stations combined). Neither has the north-south or inshore-offshore relationship of Limacina proved any more consistent at this season, its percentage having averaged at least ½ greater in the north than south on four of the ten spring cruises, but the reverse on two others, and significantly greater inshore than offshore on five cruises, but greater offshore than inshore on two.

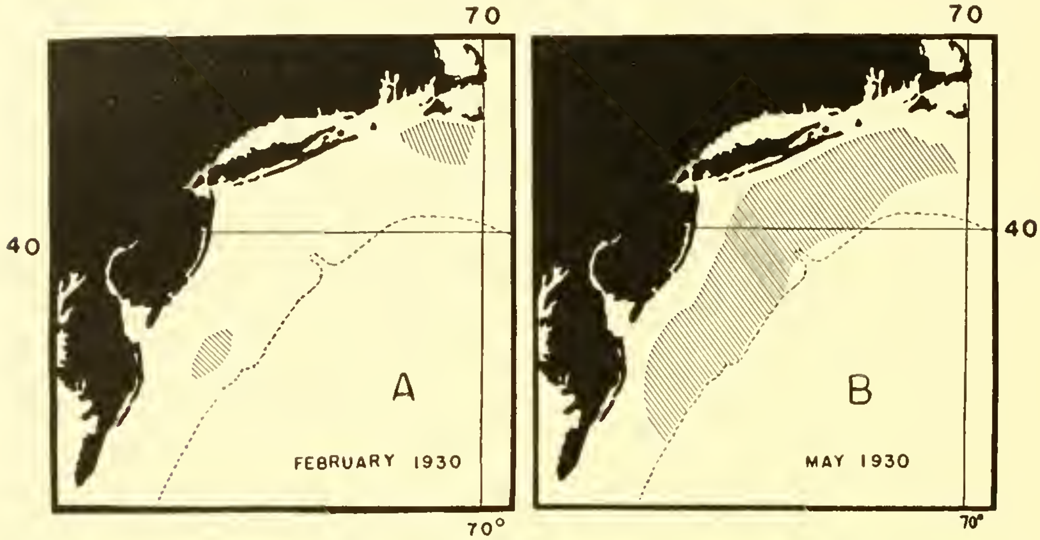


Fig. 12. Areas where *Limacina retroversa* made up more than 10% of the total volume of plankton: A, February 5–13, 1930; B, May 12–23, 1930.

The general result of these mutual fluctuations among the leading species is, that while the percentage of Calanus, for the area as a whole, has averaged about the same in May as a month earlier, its rank, relative to its nearest competitors has averaged lower in May than in April, but that of Limacina and of *Sagitta elegans* much higher. Consequently, if we name April the "Calanus" month, we might equally name May the "Calanus-Limacina-*Sagitta elegans*" month for the area as a whole, and for the offshore belt. But the average ranking for May in the inshore belt, and in the southern sector, is the reverse, i.e., "Limacina-Calanus." And the picture is not greatly altered, even if one very productive catch of Limacina (2666 c.c., midway out on the Corson profile, May 20, 1930) be omitted from the calculation.

Apart from fluctuations in the relative strengths of the leading species as just outlined, the most interesting alteration from April to May is increasing diversification in the general community made evident by the fact that the list, for the latter month, of other species that have averaged as much as 1% (Table, p. 229) includes larval euphausiids, and crab larvae (these had already appeared in significant proportions, locally in April), besides *Oikopleura labradoriensis*, *Aglantha digitale*, leptoline medusae, and salps. Analysis of the rich (> 500 c.c.) hauls points in the same direction, for while the eight leading species were responsible for 80%, or more of the catch in every rich haul in April, this was the case in 38, only, out of 46 such cases in May. We may also note that *Calanus hyperboreus* (which did not form as much as 1% of any April catch) constituted 2–11% of the 14 rich catches that were made in May, in 1930, occasionally also in 1932. However, the list of species, which—while never averaging 1% for any cruise as a whole—have reached that level at individual stations, is shorter for May than for April, as follows:

> *Acartia longiremis*, 4 stations, 5–16 c.c., 1–7%; amphipods, 2 stations, 4 and 23 c.c., 2 and 4%; anthomedusae, 1 station, 85 c.c., 36%; Arachnactis larvae, 1 station, 16 c.c., 9%; *Candacia armata*, 3 stations, 8–38 c.c., 3–22%; *Centropages hamatus*, 7 stations, 5–59 c.c., 2–26%; *Clione limacina*, 10 stations, 3–75 c.c., 1–13%; Doliolum sp., 2 stations, 53–80 c.c., 8–61%; *Euchirella rostrata*, 1 station, 3 c.c., 1%; Evadne sp., 1 station, 9 c.c., 2%; *Mnemiopsis leidyi*, 1 station, 8000± c.c., 90%; mysids, 1 station, 2 c.c., 1%; *Oikopleura dioica*, 1 station, 7 c.c., 7%; *Paracalanus parvus*, 1 station, 14 c.c., 7%; *Paraeuchaeta norvegica*, 1 station, 27 c.c., 15%; *Pleuromamma gracilis*, 5 stations, 6–18 c.c., 1–10%; *Rhincalanus nasutus*, 9 stations, 4–74 c.c., 2–24%; *Temora longicornis*, 1 station, 10 c.c., 4%; *Temora stylifera*, 1 station, 2 c.c., 4%; Tomopteris sp., 1 station, 2 c.c., 5%.

And the only rich centers for any member of this list in May was a swarm of lobate ctenophores off Currituck, on May 15, 1929 (p. 371).

It is especially interesting that the percentage of benthonic derivatives, of all sorts, combined, i.e., decapod larvae, gammarids, mysids, and leptoline medusae, was so low in May for the area as a whole (maximum, 8%, May 1931), even in the inshore belt, where the depth of water is less than 50 meters for most of the area included. The relative paucity of oceanic forms of any sort anywhere in May is also worth emphasis, for salps, representing this group, assume some importance locally later in the season (p. 240).

June. The percentages for the eight leading species have averaged about the same for June (72–97%, Table, p. 229), as for May (63–92%), and the list of dominant species includes only one member (Clione) on any June cruise, that does not appear in the list for May. Calanus, on the whole stands relatively somewhat higher in June than in May, ranking first, by far, in three of the years (1929, 1930, 1931) and about equalling its closest rival (Aglantha) in the fourth year (1932), whereas in May, it ranked second in two of the four years, first in two only. And a still more definite trend in relative importance, upward from May to June, appears, for Calanus, in the relative frequency with which it has formed upwards of 80% in the rich (> 500 c.c.) catches, for this happened in 3 out of

18 such cases in April, in 4 out of 40 cases in May, and in 17 out of 36 cases in June, but not at all in February. On the other hand, it appears that no significant alteration is to be expected from April through June, in the inshore-offshore and north-south gradients for *C. finmarchicus*, for it has averaged in about twice as great percentage offshore and in the north, as inshore and in the south, throughout this part of the year (Table, p. 229). And this last generalization is further supported by the fact that very strong dominance by Calanus (80%) is also much more frequent offshore in June (25% of the stations) than inshore (7% of the stations), whereas relative scarcity (less than 5%) was much less frequent offshore (12% of the stations) than inshore (26% of the stations).

Lest the reader gather the impression from the foregoing that Calanus (or any other species for that matter) is distributed with anything approaching relative uniformity over our area, at any season, we must, however, emphasize the fact that this is very far from the truth. Actually, a chart for any given cruise, whether for relative abundance, or for absolute, shows wide and irregular variations within short distances.

Sagitta elegans also increased appreciably in relative importance from May to June in three of the years (1929, 1930, 1932), in fact, doubled in one (1932), its trend being also upward, in the rich (> 500 c.c.) hauls, though this increase was not sufficient to bring it into rivalry with Calanus. In the fourth year (1931), it showed no definite trend in percentage, one way or the other, during this period. It has also averaged much more important inshore (about 27%, for all years combined) than offshore (about 7%), in June, just as in May but with no consistent contrast between north and south.

Limacina, contrasting with *C. finmarchicus* and *S. elegans*, decreased in importance from May to June, in each year, its average percentage for all cruises combined being only 1/3 as great in the latter month (8%) as in the former (20%) in the north, only 1/5 as great in June (5%) as in May (26%) in the south. Similarly, it formed 80% of the total catch in only one of 39 rich (> 500 c.c.) hauls in June, contrasting with 5 out of 41 such cases in May. It is thus evident that this pteropod has passed its peak in importance by the end of the spring, with a subsequent decline by about 2/3, in its percentage in the plankton, through June, as a reasonable expectation. As a result of this seasonal decline, Limacina, ranking first or second in May has only once ranked second in June (1930), and only fourth or fifth in the other years.

It is doubtful whether any very pronounced seasonal trend in relative percentage in either direction is characteristic for any of the other leading species from May to June. Thus, the percentage of Aglantha, which increased about 4-fold during this period in one year (1932), did not appreciably alter in any other year. The average percentage of Metridia, also, altered very little from the one month to the other in any year, ranging for the whole series only between 1–2% and 6%, though its percentage in the rich catches markedly declined in one year (1930). The period, May-June, also, appears one of relative constancy for the average percentage of Centropages, which did not alter then by more than 1–3% or so, in any year of the series. It is, in fact, during the period, May-June, that this copepod is least important, for it has then averaged only about 1–11% of the total plankton, for the area as a whole, or 1–14% in the inshore belt, contrasted with 1–49% in February. We may also point out that while Centropages monopolized (formed more than 80%) one out of 11 rich catches in February, this was not recorded at all in May and June. And euphausiids, as a group, have also averaged about the same in June as in May, i.e., 1–5%, whether for the area as a whole, or for rich (> 500 c.c.) catches.

Species, however, that rank low in average percentage, may rank high locally, or even dominate, in June, as at other seasons. Euthemisto, for example, which has averaged only 7%, in general, in that month constituted 19–84% in eight out of 48 catches in the year 1930, which ranks it among the leaders, at times. *Clione limacina* also formed 7–73% in 10 June catches in 1932 (bringing its average for that month as a whole up to 5% for the area as a whole), though it did not form as much as 7% at any station in June of the other years, and agalmids ranked high (about 42%) in one June haul of 220 c.c., *Centropages hamatus* formed 26% of another of 218 c.c., (both in 1932) while euphausiids made up 9% of one of the three rich catches (> 500 c.c.) that were recorded for June 1932. These rich spots may perhaps have been potential reservoirs for future local swarms of these species. And it is possible that the following instances where some particular species formed 1% or more of the June catch (listed below) may also be so considered:

Acartia longiremis, 6 stations, 2–15 c.c., 1–7%; *Aequorea aequorea*, 1 station, 11 c.c., 11%; *Agalma okeni*, 1 station, 13 c.c., 1%; agalmids, 4 stations, 4–94 c.c., 3–42%; amphipods, 6–35 c.c., 1–48%; Arachnactis larvae, 3 stations, 8–37 c.c., 1–17%; *Calanus hyperboreus*, 5 stations, 4–17 c.c., 1–6%; *Candacia armata*, 1 station, 6 c.c., 1%; *Centropages hamatus*, 6 stations, 2–189 c.c., 1–60%; Crago sp., 3 stations, 5–35 c.c., 3–13%; cumaceans, 1 station, 2 c.c., 2%; diphyid eudoxids, 1 station, 25 c.c., 4%; Doliolum sp., 3 stations, 19–82 c.c., 3–50%; Eucalanus sp., 16 c.c., 4%; Evadne sp., 7 stations, 2–25 c.c., 1–17%; *Lensia conoidea*, 2 stations, 6–13 c.c., 2–3%; *Mecynocera clausi*, 1 station, 4 c.c., 1%; *Neomysis americana*, 2 stations, 22–100 c.c., 9–83%; *Oikopleura dioica*, 4 stations, 7–17 c.c., 2–17%; *Pleuromamma gracilis*, 1 station, 4 c.c., 3%; *Sagitta enflata*, 2 stations, 2 c.c., 1%; *Temora longicornis*, 6 stations, 2–12 c.c., 2–11%; *Tomopteris catharina*, 1 station, 4 c.c., 4%.

It is especially interesting that benthonic animals of all sorts combined, have averaged no more important in June than in May, for the area as a whole (Table, p. 229), because they may then be the leading forms close in to the land, at localities where the more generally dominant species happen to be only in small amount. Cases in point are *Neomysis americana* (100 c.c.) and crab larvae (68 c.c.) forming 83% and 48% respectively of the total catches, at two stations near the mouth of Delaware Bay in June 1930; crab larvae (70 c.c. and 65 c.c.) forming 19% and 15% near Seagirt and Winterquarter, on two occasions in 1931; and leptoline medusae (120 c.c.) forming about half the catch midway out on the shelf off Martha's Vineyard on June 19, 1932; this last instance being particularly interesting because the source of supply in this case was probably Nantucket Shoals, i.e. to the eastward. On the other hand, salps of one species or another have appeared locally near the outer edge of the shelf in considerable aggregations in June, foreshadowing the much greater importance they assume a month later in the summer (p. 242). They may indeed constitute as much as 9% of the general June average for this belt as a whole, in some years (e.g., 1929, 1932), though in others, as in 1930 and 1931, they may not average more than 1% there, in that month. And in 1929 Doliolum (recorded at one May station, p. 270) had entered the southernmost sector in such numbers by June, that it was not only omnipresent then along the Hog Island and Chesapeake profiles, but constituted 21% of the average catch there, though not detected at all at any of the stations farther north, or anywhere within the confines of our area in any other June, for that matter. But the increase in the relative abundance of salps and Doliolum has not been accompanied by any corresponding increases in the number of oceanic species encountered. On the contrary, fewer of these species were detected in June than in May.

The combined annual tabulation for June (p. 267)—probably representing the normal ranking for the month better than the percentage distribution for any one individual cruise—shows Calanus so far in the lead offshore and in the north, that it outranks its closest competitor (*Sagitta elegans*) more than 2 to 1 for the area as a whole. *S. elegans* about equals Calanus inshore, however, and in the south. The lower rankings for June have shown wide variation from year to year, second for the region as a whole being either *S. elegans*, Limacina, or Aglantha, third, *S. elegans*, *Centropages typicus*, or Pseudocalanus, and fourth, *S. elegans*, *Centropages typicus*, Metridia, Limacina, Euthemisto, or euphausiids.

July. The data for July are confined to one general cruise in 1929, and two in the northern sector (north from Barnegat) in 1930 and 1931. But the results of these, added to previous information for the summers of 1913 and 1916 (Bigelow, 1915; 1922) give, at least, an indication of the seasonal succession, and of the orders of magnitude to be expected in normal years.

If we omit, from our calculations, one phenomenally rich catch of salps (67109 c.c.), at the edge of the continent off Cape May, July 18, 1929, the relative volumetric strengths of the leading species in the July catches have averaged as tabulated on page 229. In the year 1929, which may perhaps be accepted as representing the median condition, the most striking alterations from June to July, for the region as a whole (Fig. 11), were (A) that *Sagitta elegans* had forged ahead of Calanus throughout the inshore belt, though still lagging behind it offshore, (B) that *Centropages typicus*, which had fallen to a low rank by May and June (p. 229) had again tripled in relative importance by July, i.e., was then about 1/2–2/3 as abundant, volumetrically, as Calanus in the north (indifferently offshore-inshore) and ranked ahead of Calanus to the south.

Euthemisto compressa should perhaps be ranked higher in relative importance for July than might be suggested by its low percentage (1–6%) for the several years combined, because local centers of high abundance may develop for it. In 1929, for example, it formed 28% of a rather small catch (67 c.c.) on one occasion (St. 20556) near Cape May; in 1930, again, it formed 35% of the total at a station near Shinnecock, and it was found swarming midway out on the shelf off Martha's Vineyard and off Montauk in July 1913 (Bigelow, 1915, p. 281). The case is parallel for *Temora longicornis*, for while this copepod did not average as much as 1% on any July cruise, it formed 1–2% of the rich (> 500 c.c.) catches on three occasions in 1931, while in 1916, it swarmed near Martha's Vineyard (Bigelow, 1922, p. 146). *Clione limacina*, may, likewise, be relatively prominent locally in July, for it formed 9% of a 540 c.c. catch close in to New York on one occasion in 1930, though it did not average as much as 1% on any July cruise as a whole. It is also suggestive, on the negative side, that while euphausiid larvae formed 35% of one rich (> 500 c.c.) catch, offshore, off New York, in July 1929, euphausiids as a whole altered but little in importance from June to July, their respective percentages being < 1% inshore and 6% offshore for the former month, < 1% inshore and 6% offshore for the latter, in the year in question. And leptomedusae, which (in 1929) had formed 2–11% of the catch, at a few stations in the northeasternmost sector in June (p. 240), had practically vanished thence by the following month.

On the other hand, the siphonophores (*Muggiaea kochii*, *Lensia conoidea*, and unidentifiable agalmid fragments) may locally constitute as much as 8–10% midway out on the shelf in the southernmost sector as, for example, in 1929 off Chesapeake Bay and off Winterquarter. Ctenophores (*Pleurobrachia pileus* and *Mnemiopsis leidyi*), also may become the dominant group inshore and to the south in midsummer, even practically monopolizing the water there at that season in some years, e.g., 1913, as described below (p. 369, 370), though they are insignificant in importance in other summers, as in 1929, when only one rich center was recorded for them. And it appears that the case is similar for at least one category of visitors from offshore, namely, the salps, which were dominant close to New York and locally elsewhere well inshore by the first of August in the summer of 1913,[1] though curiously enough, they only occurred sparsely farther out on the shelf at the time (Bigelow, 1915, p. 270). But seemingly it is only in exceptionally warm years that this occurs, for while salps formed 24% of the average catch offshore in July 1931, and swarmed locally near the 200-meter line in that month of 1929, they were recorded only occasionally inshore at that season, in 1930 or in 1931, and not at all on the shelf in the cold summer of 1916, though locally abundant out beyond the continental edge at the time (Bigelow, 1922, p. 156).

The scarcity of salps inshore, in most summers, added to the facts that *Rhincalanus nasutus* showed no increase in relative importance from June to July in 1929, 1930, or 1931, although generally distributed in the latter month, that Doliolum did not increase relatively from June to July in 1929 (the only year when recorded at all inside the 200-meter line), and that other oceanic forms have been negligible volumetrically, in on the shelf, in all the summers of record is sufficient evidence that mass invasions of the northern part of our area by visitors from warmer waters offshore, are exceptional events, even at the warmest time of year. In fact the only "tropicals" ever likely to be of volumetric import there, are such as are capable of very rapid multiplication—e.g., salps. Contributions rom mid-depths along the slope, of the category represented by *Eukrohnia hamata* and *Paraeuchaeta norvegica* have also been insignificant inside the 200-meter curve, north of Delaware Bay, in every year of record (p. 250), at all seasons.

In normal years, in short, the waters in the northern sector are as strongly dominated in July as in June by the boreal assemblage, lead by Calanus, Centropages, and *Sagitta elegans*, whether judged by the fact that these three species

[1] No precise quantitative data available for that year.

together have averaged about 86% in all July hauls combined in that sector, or by their prominence in the rich (> 500 c.c.) centers, of which they have on the average constituted about this same percentage for the several years combined, in that month. In the southernmost sector, however, represented by the Winterquarter, Hog Island, and Chesapeake Bay profiles, a considerable invasion by warm water species was indicated in 1929, by the presence, in July, of 3% (on the average) of the southern appendicularian, *Oikopleura dioica*, 5% of *Muggiaea koehii*, 10% of Doliolum, 3% of *Lucifer typus*, 3% of the phyllosome larvae of Palinuridae, and 9% of sundry oceanic copepods in combination. And the occurrence of phyllosome larvae there is especially interesting as evidence of the infiltration of a neritic species from far to the southward, no doubt by the offshore route, because the northern boundary for their probable parent, the spiny lobster (Panulirus) is Cape Lookout in North Carolina in Latitude about 35° N.

Yet, even with this invasion of oceanic forms, the list of species, which, while not equaling 1% in any subdivision of the area on any July cruise, hence not discussed above, have formed 1% or more at particular stations, is considerably less extensive for July than for June or May, as follows:

Acartia longiremis, 2 stations, 4–9 c.c., 1–3%; agalmids, 1 station, 9 c.c., 8%; *Calanus hyperboreus*, 1 station, 6 c.c., 1%; *Candacia armata*, 6 stations, 3–22 c.c., 2–17%; *Eucalanus attenuatus*, 2 stations, 4–89 c.c., 4–36%; Evadne sp., 1 station, 4 c.c., 1%; Phronima sp., 1 station, 13 c.c., 1%; Podon sp., 1 station, 6 c.c., 7%; stomatopod larvae, 1 station, 4 c.c., 1%; *Temora longicornis*, 4 stations, 2–26 c.c., 1–2%; *Temora stylifera*, 1 station, 26 c.c., 9%.

Autumn. Quantitative information is lacking for August and September. But, if October data for the one year of record (1931) be representative, as seems probable, it appears that early autumn sees a notable decrease in the relative importance of Calanus, the percentage of which declined in the offshore belt[1] in that year from 61% in July to 8% in October in the northern sector, and from 41% in June[2] to 7% in October in the southern. In fact, the maximum percentage of Calanus in any of the richer (> 300 c.c.) October hauls, was only 16%, contrasted with frequent percentages of 80% or more in summer and spring, while there was one October haul without Calanus. The average percentage of salps also decreased in the northern sector, offshore, from 24% in July to less than 1% in October, though *Iasis zonaria* then formed 51% of the total catch of 112 c.c. at one station off Winterquarter in the south. On the other hand, *Centropages*

[1] The October cruise of 1931 was confined to the offshore belt.

[2] The July cruise was confined to the northern sector.

typicus, which had been negligible in June and July of the year in question, so greatly increased relatively (as well as absolutely) during late summer, or early autumn, that by October, it ranked far above its closest rival (Paracalanus) in the north (47%) and slightly so, in the south (14%). Perhaps even more striking in that year was the autumnal increase in the percentage of Paracalanus, which did not average more than 1% in any considerable subdivision of the area in any summer of record, but which formed 26% offshore in the north, and 12% in the south, in the October in question. *Metridia lucens*, also, increased in the north from 1% to 11% between July and October, but was in about the same percentage in the south in the latter month (2%) as it had been in June (1%). Other species showing smaller, or less regular increases from June or July to October are Pseudocalanus from less than 1% (June) to 4% (October) in the south, but with little change in the north; *Sagitta serratodentata*, from less than 1% in June to 2% in October in the north and from 2% in June to 9% in October in the south; while *Sagitta enflata*, *Oikopleura dioica*, and Penilia, which did not enter into the picture at all in the north in July or in the south in June, averaged 6%, 2%, and 8%, respectively, of the catch in the latter sector in October. However, none of the other members of the community that constituted as much as 1% of the average catch for that October had experienced any significant change in relative importance since June (in the south) or July (in the north). And the list of species forming 1% or more at individual stations had not lengthened appreciably in this same period:

Acartia sp., 2 stations, 1–4 c.c., 4–6%; agalmid, 1 station, 9 c.c., 4%; *Candacia armata*, 2 stations, 3–14 c.c., 3–11%; *Centropages violaceous*, 1 station, 1 c.c., 1%; Corycaeus sp., 1 station, 3 c.c., 3%; *Mecynocera clausi*, 4 stations, 1–4 c.c., 1–4%; Oncaea sp., 1 station, 9 c.c., 11%; *Pleuromamma gracilis*, 1 station, 2 c.c., 1%; *Scolecithrix danae*, 2 stations, 3–14 c.c., 2–12%; *Temora longicornis*, 1 station, 1 c.c., 1%; *Temora stylifera*, 2 stations, 1 c.c., 1%.

These mutual changes in relative abundance result in a reversal in relative ranking, from summer (Table p. 267) to mid-autumn, when Calanus ranked only fourth instead of first, but Centropages first instead of third, fourth, or fifth (Fig. 11), with second place falling to Paracalanus, the highest ranking of which was not above fifth on any July cruise, while it does not appear at all in the lists of dominant species for April, May, or June.

No data as to the relative abundance of the various species are available, for the three month period, November to January, of any year.

Annual Differences

It was a fortunate chance that so short an observational series should have included one year (1932) when the late winter was unusually warm in the waters of our area, one (1913) in which the summer was warmer than normal, and one (1916) in which it was colder, making it likely that such annual variations as were recorded cover the range commonly to be expected from year to year.

It is not astonishing that typically boreal species such as *Calanus finmarchicus* and *Sagitta elegans* were relatively less prominent at the end of a winter of the type represented by 1932 than in the other years. And the high percentage of Paracalanus in that same February may also have been associated with temperature. But temperature offers no apparent explanation for the facts that one of the two years when *Centropages typicus* ranked high (1930) is to be classed as cool, the other (1932) as warm; or that while *S. elegans* was the dominant form in one of the cool winters (1931), it was of only very minor importance in the other (1930). And we can merely note that annual variations in the relative ranking of the several dominant species were much wider in the offshore belt than inshore. No doubt the explanation for this lies in the fluctuations of conflicting water masses along the edge of the continent.

Following an abnormally warm winter (to judge from 1932), Calanus continues much less important relatively than usual, as well as less abundant, through May and June, even though the temperature anomaly may have entirely disappeared by mid-spring. On the other hand, Aglantha, Limacina, and *Sagitta elegans* ranked much higher in that June than in any other. The chief variation from year to year later on in the summer—and one of considerable significance from the standpoint of the fertility of our region as a pasture for plankton-eating fishes—is that Calanus and its companion species dominate much farther southward in cool and average summers, than in what may be classed as "warm," at least along the outer part of the shelf. On the other hand, ctenophores (Mnemiopsis and Pleurobrachia), combined with salps, play a dominating rôle to the southward, especially inshore, at least in some warm summers, but are not volumetrically significant over any extensive areas in cool. The one extreme in these respects may be illustrated by 1929, when *Calanus finmarchicus, Centropages typicus,* and *Sagitta elegans* formed even a larger percentage of the total catches for the southern sector as a whole in July (average, 58%) than they had in June (34%) or in May (27%),[1] except at one station close to the 200-meter

[1] 93% in April, 34% in May, 50% in June, and 64% in July.

contour off Cape May, where salps swarmed (p. 241). And Calanus was also the leading species, offshore, southward of New York in the summer of 1916—likewise a cold year—along a narrowing belt to the offing of Chesapeake Bay as described elsewhere (Bigelow, 1922, p. 139). The opposite extreme was illustrated by the summer of 1913, when copepods, which were in rich aggregations over the continental shelf south of Cape Cod, were "counted by individuals" south of New York (Bigelow, 1915, p. 285), instead of by hundreds of cubic centimeters, while in some of the southern hauls no copepods at all were detected. *Sagitta elegans* was, also, so scarce south of New York in that summer that none of the 19 subsurface hauls yielded more than odd specimens of it there, which applies equally to Limacina, to Euthemisto, and to euphausiids as a group.

It is an interesting question whether it is characteristic of warm summers that the poverty of the Calanus community, from New York southward, is compensated for—especially in the inshore belt—by swarms of ctenophores (Mnemiopsis and Pleurobrachia) and of salps, as happened in 1913 (Bigelow, 1915, p. 270). Unfortunately, no data are available for July for 1932, the year of the present series that seems the most pertinent in this connection. But the fact that ctenophores were found swarming locally in May (p. 237), in June (p. 369), and in July (p. 242), combined with widespread presence of salps in the offshore belt at that season, and occasionally in abundance (p. 242), makes it likely that our area is always sufficiently seeded with members of these groups throughout the vernal half year, for rapid multiplication to take place when circumstances favor.

No information is available as to annual variations in the relative abundance of different species for autumn or early winter.

Sources of the Local Plankton

The planktonic community of our area, like that of the Gulf of Maine, consists in great majority of holoplanktonic species. The only benthonic derivatives that have averaged as much as 1% of the total volume in either subdivision of the area at any season, have been small leptoline medusae, which may form up to 4% for the area as a whole in May (Table, p. 229), and the larvae of crabs or of hermit crabs, which may swarm locally next the land in July (p. 286), and form up to 1–5% offshore as well, in late spring and early summer in some years (Table, p. 229). Perhaps we should also so classify (because of winter eggs) the cladoceran, *Penilia schmackeri*, which formed 8% offshore in the south in the one October of record.

Indigenous species also greatly predominate, in volume, over immigrant, at all seasons, having (on the average) formed upwards of 92% of the total volume of plankton for the area as a whole in February, 95% in April and May, 89% in June, 84% in July (of the one year when the entire area was surveyed) and 89% on the one October cruise. Immigrant species were in fact negligible in February and April, except for salps which may appear in small percentage in the offshore belt, even this early in the year (p. 272). With the advance of the season, other immigrants enter, however, in small amount into the "dominant" list ($> 1\%$), some from the colder waters from the east, others from the continental slope offshore. The members of the first of these categories, represented in May and June by *Oikopleura labradoriensis*, by *Calanus hyperboreus*, and perhaps by the lobate ctenophore Bolinopsis, have never in our experience been of any volumetric importance even in the easternmost sector which is most open to their entry. And except for salps, visitors from offshore are equally insignificant in the volumetric total in the northern sector, even offshore, in spring. But they play a somewhat more important rôle by midsummer in the southern sector, where, in 1929, tropical decapods and copepods, Doliolum, salps, and siphonophores together formed about 15% of the average catch. And the state is similar in autumn, judging from the fact that in October 1931, offshore chaetognaths and oceanic copepods, in combination, formed 18% in the offshore belt in the south.

The lists also include a considerable variety of other immigrants, besides those just mentioned, which—if never plentiful enough to be of any volumetric importance within our limits—promise to be of such value as indicator-species that they deserve some discussion from that viewpoint, even though this be somewhat foreign to the main thesis of the present report. Indicator-species, from whatever source, may be grouped for convenience into two categories. The one group comprises those species that either fail to breed in exotic surroundings, so that their presence there endures only for the span of life of the entrant individuals, or which—if they do succeed in breeding—vanish shortly after the immediate effects of active invasion by exotic waters have ceased. The localities of occurrence of the members of this group yield direct evidence as to short term intrusions of waters of one or other origin into our area. The second category comprises the considerable variety of species that, while regularly indigenous, vary periodically in abundance as water of one or another origin is in the ascendency. In the long run, it is from this group that we may expect the more reliable information as to the secular variation in the proportionate amounts in which the different waters mingle. For an excellent example of this we may refer to the information that the mutual fluctuations in abundance of *Sagitta elegans* and *Sagitta setosa* have yielded as to variations in the proportionate amounts of Atlantic and of Coastal waters in the English Channel (Russell, 1935; Kemp, 1938; Furnestin, 1938) and of oceanic and "Bank" water off the east coast of England (Wimpenny, 1937). But trustworthy inferences in this regard must await much more detailed knowledge of the ecological relationships of the animals concerned, than our studies can yet provide.

In the particular part of the sea with which we are concerned, the waters that mingle over the shelf, to maintain the comparatively stable state (as regards temperature and salinity) that exists there, draw chiefly from land drainage on the one side, from the highly saline band along the continental slope on the other, and from intrusions past Cape Cod, of shelf water from the east, which come chiefly in the spring. The planktonic animals that these waters bring with them are subject to a similar classification. But it is doubtful whether any considerable volume of water of shelf origin enters our area past Cape Hatteras from the south, for no direct evidence of this has been detected in the distribution of temperature or of salinity (Parr, 1933; Bigelow, 1933; Bigelow and Sears, 1935).

Within our limits—even in the most southern sector—immigrants from shelf waters further south have been negligible, as was to be expected from the insignificance of water increments from this source that might convey them. In fact, the only species, palinurid larvae, certainly belonging to this category that has been detected in such examination of the catches as has yet been made, may actually enter our boundaries *via* the offshore route, i.e., from the continental edge, for these phyllosome larvae are notoriously subject to extensive northerly drifts along the American slope. Immigrants of the opposite category, namely from more easterly shelf waters, play a much more important rôle, due to the considerable amounts of water from that source, that may enter the eastern sector in the spring in some years, and perhaps to some extent every year. *Calanus hyperboreus* is especially interesting in this respect, its existence being so brief in our area that the fluctuations in its local status very closely follow the waxing and waning of the drifts that bring it past the offing of Cape Cod. *Oikopleura labradoriensis* appears to be slightly more successful as a colonist, for it may breed to some extent, as it drifts westward and southward. But its annual presence within our limits is sufficiently brief for it, too, to serve as a reliable indicator of a more boreal source. So, too, for *Thysanoessa longicaudata* and perhaps for Erythrops. The incidence of the species belonging to this category may indeed prove more reliable as drift-indicators in this particular case, than is the distribution of temperature, because the latter is so nearly alike on the two sides of Cape Cod at the critical season, that it is not easy to follow east-west movements of water there, by their thermal effects.

We can already say that the combined records for these species show the effects of such indrafts as extending widespread over the shelf down at least to latitude 38°, and occasionally to 36°, in one year or another in the months of April, May and June, but that they give no evidence of any significant increment from this source in the later summer, in autumn, or at the end of winter.

Comparison with the plankton of the Gulf of Maine brings out the interesting difference that none of the hauls in our area have yielded so much as a single specimen of the typically subarctic forms, *Ptychogena lactea*, *Mertensia ovum*, *Limacina helicina*, or *Oikopleura vanhöffeni*. Neither has *Metridia longa* ever been detected west of Cape Cod, although it occupies much the same faunal niche in the Gulf of Maine to the east that *Oikopleura labradoriensis* does in our area, becoming widely distributed there, and perhaps succeeding in breeding to some extent, in years when it passes Cape Sable in greatest number (Bigelow, 1926, p. 61). The offing of Cape Cod thus appears to mark as definite a transition-zone (probably thermal) for some of the northern planktonic animals as it does for many benthonic forms. Another interesting regional contrast is that while our area and the Gulf of Maine both receive immigrants from the east, these tend to disperse much more generally over the shelf west and south from Cape Cod, than is the case in the Gulf, where the shorter-lived, subarctic immigrants have been most frequently encountered either in the eastern side or—if further west—within about 30 miles or so of the land; in other words in the track of the peripheral anticyclonic drift (Bigelow, 1926, p. 59; Fish and Johnson, 1937, p. 248).

Little can be said as to the magnitude of the contribution that waters coming from the east—i.e., from George's Bank or the Gulf of Maine—makes to the volume of plankton in our area, because much the same assemblage of species usually dominates the community to the east as well as to the west of Cape Cod; the few that are sure indicators, within our limits, of this eastern source are relatively unimportant in the Gulf also, so far as volume is concerned.

The basin of the Gulf of Maine, at depths greater than about 150 meters might be described—without much exaggeration—as a lateral extension of the slope water habitat *via* the Eastern Channel, so far as temperature and salinity are concerned. And this is reflected in the fact that its deeper strata constantly support a considerable endemic population of the boreal mid-water copepod, *Paraeuchaeta norvegica,* and of the decapod genus, Pasiphaea, with a sparse but generally distributed immigrant population of *Eukrohnia hamata*. A scattering of *Dimophyes arctica* of similar origin also occurs there, while *Sagitta maxima* and *S. lyra*, (perhaps the most useful animal indicators of water entering the Gulf of Maine at lower levels) have been taken repeatedly in the deep hauls in the basin. No topographic parallel to this particular situation exists west or south of Cape Cod, for while the submarine gorge off the Hudson River, and the others farther south that have recently been mapped by the U. S. Coast and Geodetic Survey (Rudé, 1938) furrow the edge of the continent to a depth much greater than that of the basin of the Gulf of Maine, the extent of area occupied by their troughs is so small that movements of water up their slopes would not be expected to contribute much to the communities existing over the neighboring shelf. On the other hand, the whole frontage of the latter is open to direct influences of this sort from the continental slope.

Actually, *Paraeuchaeta norvegica*, *Sagitta maxima*, and *Eukrohnia hamata* complete the list of immigrants from offshore that are reliable indicators of water from the deeper levels within our area, for we have no record at all of *S. lyra* or of *Demophyes arctica* within our limits, nor did the towings for the period, 1929–1932, yield a single representative of the bathypelagic community of black fishes that Beebe (1929) found so abundant in the mouth of the Hudson Gorge, of red prawns, or of deep water medusae. The very paucity, however, of what we may name the "Paraeuchaeta" community makes them (when they do occur on the shelf), the more reliable indicators of highly saline water, expanding shoreward up the bottom slope. By this evidence, water movements of this sort have no significant effect as agents of mass transport beyond the 100-meter contour.

Monthly ratios of records of Paraeuchaeta, Eukrohnia, and *S. maxima* combined, to total number of offshore stations, of 1.1 to 1 for February (32 records); 0.6 to 1 for May (55 records), 0.1 to 1 for June (8 records), and 0.1 to 1 for July (4 records), with no records at all for October, point to such indrafts as decreasing somewhat either in frequency or in volume from late winter through spring to summer, seemingly to cease entirely in early autumn.

The great majority of the records for this group lie within 20 miles or so of the edge of the continent, though occasionally dispersed farther inshore, as discussed under the individual species concerned. But they are scattered all along this offshore belt, from the one boundary of the area to the other, without apparent concentration in any particular sector.

The records inside the 200-meter contour for species which (while equally surely of offshore origin) may have come in with the upper strata of water, are not only much more numerous (Fig. 13), but this group is qualitatively much more varied for it includes salps and Doliolum; the decapod, *Lucifer typus*; the amphipod, Phronima; the euphausiids, Stylocheiron, Thysanopoda, and Euphausia; the copepods, Eucalanus, Euchirella, Pleuromamma, Rhincalanus, *Centropages violaceus, Mecynocera clausi,* Sapphirina, *Scolecithrix danae, Calanus minor, Undinula vulgaris*; the pteropods, *Corolla calceola, Crescis acicula, C. conica,*

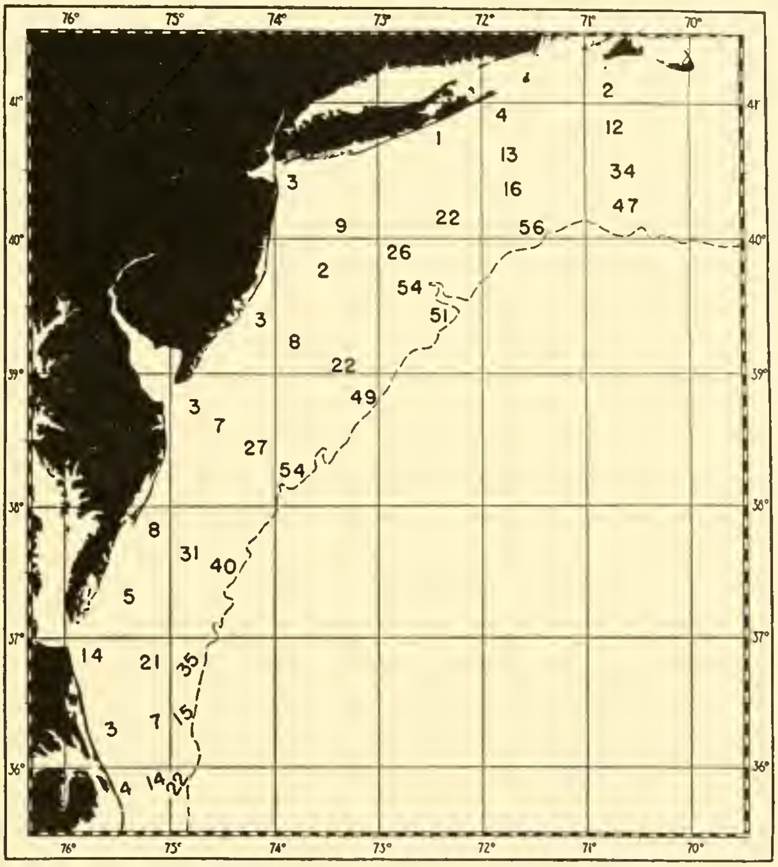


Fig. 13. Numbers of records at different localities, for tropical oceanic species listed on this page.

C. virgula; the heteropod, Firoloida; the chaetognaths, *Sagitta hexaptera, Pterosagitta draco,* and *Krohnita subtilis*; the medusae, Niobia and Aglaura (Bigelow, 1915); and the siphonophores, Abylopsis, Bassia, *Agalma okeni, Ceratocymba sagittata, Eudoxoides spiralis, Chelophyes appendiculata, Lensia fowleri, Vogtia pentacantha,* Physophora, and Physalia. *Candacia armata* and *Sagitta enflata* also depend on immigration, from the continental slope, for their continued existence on the shelf, though perhaps breeding there to some extent locally (pp. 318, 356), while the palinurid larvae may also reach our southern sector via the offshore route (p. 243). The localities of capture, for this group as a whole, have been most numerous at the outermost stations, i.e., within 10–15 miles of the 200-meter contour, progressively less and less so in toward the land (Fig. 14), as distance from their source of origin increases, though occasional members of the group have been taken even close in to the coast here or there as noted elsewhere. The most interesting feature of the distributional chart is, however, that the records for the category as a whole have been about as frequent, relatively, off one sector of the coast as off another (apparent concentrations on the chart result from the geographic locations of the several profiles and the number of stations on each), corresponding to the fact that the slope water with its oceanic fauna, not only fronts the entire length of our area, but lies as close to the 200-meter line in one place as in another, and with successive isotherms tending on the whole to parallel the trend of the continent. In fact, a majority of the species here used as indicators of that source have long been known to occur in this belt much further to the north and east.

The obvious implication is that the mixture of offshore oceanic water with inshore shelf water takes place all along the outer edge of the shelf westward and southward from the offing of Martha's Vineyard past that of Chesapeake Bay. This contrasts with the situation in the Gulf of Maine, where indrafts of this sort enter chiefly in the eastern side, and where records of oceanic indicators have not only been far less numerous than is the case west and south of Cape Cod, but confined for the most part to the peripheral belt, just as are those for arctic indicators (Bigelow, 1926, Fig. 31).

The average number of records for this category of species (omitting *Sagitta enflata* and Candacia which may reproduce to some extent within our limits) was 2.4 per offshore station in February, 2.4 in April, 3.1 in May, 2.6 in June, and 2.7 in July, but 4.6 in October, for the period 1929–1932. This seasonal distribution suggests that immigration is as active in one month as another from the end of winter through spring and summer, but somewhat more so in autumn. In this connection, it is perhaps appropriate to point out that averages of about 3.4 records per offshore station for species of this category for all months combined in 1930, 3.4 record in 1931, and 3.6 record in 1932 do not suggest any wide difference from year to year, during the three year period. And while the average for 1929 was somewhat smaller (about 1.5) it may not have been significantly so, in view of the roughness of the methods employed.

The catches have yielded but few species the production of which is known to be closely confined to the immediate vicinity of the land, and which can consequently be classed as reliable indicators of drifts of water seaward from the coast-line out over the shelf. Among such are the larvae of the blue crab (Callinectes); the mysid, *Neomysis americana*; the copepods, *Acartia clausii* and *A. tonsa*; and the cladoceran genera, Podon and Evadne. Stomatopod and palinurid larvae also fall in this same category, but may more immediately be indicators of offshore water in the particular region in question (p. 243). And the bottom habitats of other benthonic derivatives so far detected in the catches, such as the larvae of other species of crabs, the decapod-shrimp, Crago, and the various leptoline medusae, extend to depths so great that the contribution of their pelagic stages to the plankton of the overlying waters may take place well out on the shelf. We may refer in this connection to the hydroids that have been found floating—and apparently growing—near the surface over George's Bank in spring and summer (Bigelow, 1914, p. 414; 1926, p. 379; Fraser, 1915, p. 306).

In the case of the blue crab larvae, the captures extended 50 miles out, off Chesapeake Bay (Bigelow, 1915, p. 271). Captures of *Acartia clausii* and *A. tonsa* (the latter for 1916 only) were however coastwise (p. 303). Most of the records of Neomysis likewise lie within a few miles of land. In short, the contribution, from this general source, to the planktonic community of the continental shelf, even in the inshore belt—has proved negligible, except locally and temporarily, close in to the land, which parallels the situation in the Gulf of Maine. Neither have we any record out at sea of the scyphomedusan genus Aurellia, anywhere west or south from the Martha's Vineyard profile, though it is plentiful at Woods Hole at the one boundary of our area, and in Chesapeake Bay at the other (Cowles, 1930), or of Dactylometra, which swarms in summer in estuarine situations along our middle Atlantic coast. But since no particular watch was kept for large medusae (as has been done in the Gulf of Maine), the inference to be drawn from their failure in the collections, is only that they were not dispersed seaward, in any summer of record, in sufficient numbers to be picked up in the nets.

On the other hand, the records for Evadne were widespread across the whole breadth of the shelf, with those for Podon also extending well out (p. 346), which suggests considerably wider dispersal offshore for these cladocerans within our limits than in the Gulf of Maine (Bigelow, 1926, p. 307; Fish and Johnson, 1937), where the dominant drift is more definitely peripheral.

THE AREA AS A FEEDING GROUND FOR PLANKTON-EATING FISH

It is common knowledge that the groups of animals ordinarily dominant in the plankton of our area are staple food for fishes in boreal seas generally, and that the particular species of copepods, pteropods, amphipods, and sagittae, with which we are here concerned, are leading items in the diet of the mackerel within our limits (Bigelow and Welsh, 1925, p. 201), as well as in that of the herring in higher latitudes.[1] In fact, the only occasions when any considerable fraction of the animal plankton of our area is not what we may term "nutritive" fish food, are when ctenophores, medusae, or salps may temporarily dominate the local community.

The various analyses that have been published of the chemical composition of planktonic animals show considerable differences in the percentage of proteins, carbohydrates, and fats, not only between different groups and species, but even for the same species at different times and localities. Brandt (1898), Rosenwald (1904), and Delff (1912), for example, long ago showed that the fat content of the dry matter in copepod plankton at different localities in North European waters, may be as high as 12.5% or as low as 5%, while Wimpenny (1929, p. 19) records 9.3%–36% of fat in the dry matter of different samples of plankton dominated by various species of copepods, sagittae, Oikopleura, and other organisms. Especially pertinent in the present connection is Orr's (1934) observation that adult Calanus may have from 10.5–29.6% of fat in the female and 18–33.7% in the male, at a given locality at different seasons.[2] And the presence of about 30% of ether extract in dried Calanus collected off New York in May 1929, as determined by Dr. Th. von Brand at the Woods Hole Oceanographic Institution, even after long preservation in formalin, shows that this copepod may be at least as rich in fat in the western side of the North Atlantic as it is in the eastern. Five per cent of ether extract in the dry matter of Limacina preserved in formalin, similarly, confirms Rosenfeld's (1904) early report of 7.3% fat for this pteropod. So far as we are aware, sagittae have not previously been studied from this point of view, although they enter largely into the dietary of various fishes. But recent analyses by Dr. von Brand of the dry matter of freshly caught *Sagitta elegans* showed about 16% of ether extract (fats plus lipoids). Dr. von Brand also informs us that in samples preserved in formalin (and hence comparable to the plankton volumes with which we are dealing), the dry weight is about 12% of the wet weight in *Calanus finmarchicus*, a value falling well within the range reported by various authors for copepod plankton, and about 11% of the wet weight in Limacina,[3] but only about 7% in *Sagitta elegans*.

[1] For a recent study of the relative importance of the different species in the diet of the herring in the North Sea, see Savage, 1937.

[2] For summaries of early analyses, see Steuer, 1910, pp. 656–659.

[3] No doubt the shells of the latter had lost some of their lime in the preservative.

The foregoing suggests that while Calanus in good condition ranks far above most of the other dominant species, if judged by fat content, the other crustaceans may be grouped with Limacina and with *Sagitta elegans,* while the high ratio of wet weight to dry in the latter is perhaps balanced by the high percentage of chitin in crustaceans, and of lime in Limacina. Comparisons of this sort fail, however, to include any estimate of the relative digestibility of these different groups, which no doubt differs for different species of marine fishes, a vital matter as to which we still remain wholly in the dark. Lacking information in this regard, we base the following discussion on the assumption that the crustacean, molluscan, and chaetognath fractions can be justly combined as being of high nutritive value, leaving the salps and the watery ctenophores and medusae out of account altogether, as being of low. Subtraction of the latter does not appreciably affect the picture for February or for April, when medusae, ctenophores, and salps combined, formed less than 1% of the total catch, in each year's record. And these may continue negligible (not more than 1%) right through the later spring and summer, as happened in 1930. But they formed, on the average 9% of the total plankton in May and June, and 10% in July of the other years combined, with a maximum of 22% for the area as a whole in June 1932, percentages large enough to be of some significance in relation to the nutritional value of the general community.

The distributional pictures for the volumes of plankton surface to bottom after omission of the non-nutritive group, would represent what may be termed the potential richness of the area as a feeding ground for fishes. But it is obvious that some levels will be richer than others, some poorer, unless the vertical distribution of the plankton be uniform. Average volumes as calculated for the water column as a whole may therefore be a considerable understatement of actual richness as this affects the fish population. For example, a given locality might well be much richer, at some one level, than might be suggested by an average volume derived from the combination of a poor catch shoal, with a large catch deep, or vice versa. The ratios of the richest catches (irrespective of depth) to the average volumes for the column as a whole, in the months when tows were made at two or more levels, do, in fact, show that such averages considerably minimize the actual richness, at the most productive depth. This is true even at the end of winter when the plankton is most nearly uniform vertically, while in midsummer, the ratio has approached the maximum that is possible for cases where an average has been derived from two values only.

Ratio of volume at level of maximum abundance to average volume for the water column as a whole, for the more nutritive plankton

Month and year	North	South	Inshore	Offshore	General average
Feb. 1932	1.4 to 1	1.4 to 1	1.2 to 1	1.4 to 1	1.35 to 1
Apr. 1929	1.5 to 1	1.6 to 1	1.5 to 1	1.4 to 1	1.5 to 1
May 1929	1.3 to 1	1.7 to 1	1.6 to 1	1.5 to 1	1.38 to 1
1931	1.3 to 1	1.2 to 1	1.4 to 1	1.3 to 1	
1932	1.4 to 1	1.2 to 1	1.2 to 1	1.4 to 1	
June 1929	1.6 to 1	1.4 to 1	1.3 to 1	1.7 to 1	1.5 to 1
1931	1.5 to 1	1.4 to 1	1.5 to 1	1.5 to 1	
1932	1.5 to 1	1.6 to 1	1.6 to 1	1.5 to 1	
July 1929	1.8 to 1	1.7 to 1	1.7 to 1	1.7 to 1	1.8 to 1
1931	1.9 to 1		1.9 to 1	1.74 to 1	

Discussion as to the relative richness of different parts of the area, at different seasons should therefore be based primarily on the volumes existing at the level of greatest abundance. Information in this respect is available for the great majority of the stations of 1929, likewise for most of the offshore stations of 1931 and 1932. But the hauls at many of the inshore stations in the two latter years extended from near the bottom to the surface, hence yielded minimal values only. And these have been adjusted, in the following tabulation, according to the particular ratio that prevailed at the time in the general subdivision in question.

Average volumes at level of maximum abundance, observed or adjusted as above, for the more nutritive plankton

Month	Year	Inshore	Offshore	North	South	Total area surveyed
February	1931	264	153	74	220	199
	1932	660	116	74	519	478
April	1929	304	479	440	324	376
May	1929	265	441	439	178	329
	1931	522	801	640	481	608
	1932	299	497	371	365	361
June	1929	232	447	379	26	312
	1931	784	1124	981	809	908
	1932	251	431	264	410	301
July	1929	480	347	730	313	415
	1931	1294	1178	1322	—	—

If the ratio averaged about the same in 1930 (when only one haul was made at each station), as it did in the other years combined, the volume of nutritive plankton at the level of maximum abundance may be assumed to have been about as follows, in that year:

Month	Inshore	Offshore	North	South	Area surveyed
February	299	59	144	193	187
April	362	451	594	390	279
May	607	1436	896	970	928
June	645	467	630	363	512
July	1080	580	787	—	—

At the end of the winter, according to these tabulations, the amount of nutritive plankton averages smallest in the north and along the offshore belt, where, in fact, the supply may be so poor (less than 75 c.c.) as to make it doubtful whether any considerable population of plankton-eating fishes could subsist, if actively feeding. And while volumes have averaged somewhat larger in the south near shore, the only winter (1932) when even that subdivision could be classed as "rich" (more than 400 c.c.) was one when the water was abnormally warm.

In every year, the volume of nutritive plankton considerably increased in the northern sector by April (1929) or by May, at latest. This vernal augmentation on a broad scale involved the area as a whole, in one year (1931), but it was confined to the northern sector in each of the other two years with average volumes decreasing somewhat in the southern sector in each of these cases from February or April to June or July, resulting in a roughly stationary or slightly downward trend for the area as a whole (Table, p. 229). It follows, in most years, that when volumes reach their peak in the northern sector, which may be as early as May (1930) or not until July (1929, 1931), they average considerably larger there than they do in the southern sector at any time of year, a regional contrast illustrated graphically by the concentration of very large (> 1000 c.c.) catches north of the Cape May profile, irrespective of the season (Fig. 15B). And while the center of summer abundance may, on the contrary, lie in the south after an abnormally warm winter, (e.g., 1932) when large amounts of nutritive plankton exist there in February, the combined evidence of the series as a whole is that the richest pasture for fishes usually develops somewhere within the area outlined in Figure 15; and in July, by which month the average volume of nutritive plankton at the levels of greatest abundance had risen there to about 1300 c.c. in 1931, to about 800 c.c. in 1930, and to about 700 c.c. in 1929, with occasional concentrations as rich as 2000 c.c.

The familiar fact that the mackerel are thin when they first appear near our coasts in spring, but soon gain fat on the diet afforded by the local plankton, is sufficient evidence that average volumes of this general order of magnitude, at the level of greatest abundance, corresponding to 1.2–2.2 c.c. per cubic meter of water, are more than sufficient for the maintenance and growth requirements of this particular fish. They contrast with an average of only about 300 c.c., and maximum of 914 c.c. for June and July, inshore in the southern sector.

By the evidence of 1931, the amount of nutritive plankton—however estimated—greatly decreases all along the offshore belt between July and October, to an average so low (perhaps 200–300 c.c.) that autumnal feeding conditions must be classed as moderate at best. But we have no information, under the present heading, for the late autumn or early winter.

Consideration of the relative frequency with which the plankton averaged more than twice as voluminous shoal ($<$ 10 meters) as deep ($>$ 18–20 meters) or the reverse, in different months, shows that mackerel, or other fish would find the best feeding conditions as often at one depth as at another during February, April, and May, while more often still, there is no strong gradient of either order at this season. By July, however, when the plankton as a whole averages most abundant in mid-depths (p. 218), the best feeding conditions would be found 15–20 times as often at some depth greater than 20 meters as between 10 meters and the surface. And on the few occasions (total cases, 24) when a very strong concentration was recorded at any particular depth (volume more than 10 times as great at one level as at another), this occurred about 5 times as often deep as shoal, for the months, February–June, but at least 20 times as often deep as shoal in July. Thus, there is nothing in the vertical distribution of the more nutritious plankton that might tend to hold the fishes subsisting upon the latter at any one depth more than at any other, from the end of winter through spring and into the first month of summer. But if plankton-eating fishes are able to find their way to the zones where food is most plentiful—which it is likely that they can vertically—they would naturally tend to desert the superficial 10–20 meters of water in midsummer (with corresponding effect upon the fisheries), unless this descent were to bring them into temperatures unfavorably low. And this would hardly be the case for the mackerel, commercially the most important fish that subsists on the larger zooplankton in our region, for water of 12–14° appears to be entirely suitable for it.

The frequency with which the hauls have yielded odd specimens of mysids (chiefly *Neomysis americana* and *Erythrops erythophthalma*), bottom living shrimps (Crago), gammarids, and cumaceans, occasionally in volumes as great as 20–25 c.c. or more, further indicates that recruitment of the plankton near the sea floor from this source provides an important additional food supply for any plankton-eating fishes that may forage close to the bottom, a category to which the local species of hake (Urophycis)—well known "shrimp eaters"—doubtless belong. And we find a still more arresting example of this sort in the Gulf of Maine in a great abundance of the edible shrimp, *Pandalus borealis*, over muddy bottoms (Hjort and Ruud, 1938; Bigelow and Schroeder, 1939).

There has been much discussion (with wide disagreement) of the extent to which fishes of various species that subsist on animal plankton direct their wanderings to follow the richest aggregations of available feed. The opportunity afforded by the records of 1930 to compare the location of the chief mackerel fishery from month to month (supplied by Mr. O. E. Sette, of the U. S. Bureau of Fisheries), with the areas where nutritive plankton was most abundant is, therefore, timely, this having been a season when both mackerel and plankton were at least moderately abundant, and when the latter was composed almost entirely of the more nutritious groups. In that particular year, mackerel were first caught in abundance in the last week of April, off Delaware Bay and southward, where the average amount of plankton had recently risen from about 180 c.c. to about 500 c.c. for the water column as a whole (Fig. 14). Prior to the first of that May, the northward extension of the rich belt of plankton seems to have been barren of mackerel or nearly so. But the fishery (following the schools of mackerel sighted at the surface) shifted northward by the middle of May to a belt extending all along from New York, eastward to Nantucket, suggesting that the mackerel that had first struck in well to the south, had migrated northward and eastward along the belt of rich feeding ($>$ 500 c.c. of plankton), leaving behind the richest pool of all. And by July, the main body of mackerel—or at least that supporting the seine-fishery—had moved still farther east, to the region of Nantucket Shoals and the neighboring parts of the Gulf of Maine, although volumes of 1100–1600 c.c. of plankton for the water column as a whole still existed locally, in the region which they had recently deserted, with a strong probability that the whole sector between the New York and Martha's Vineyard profiles still supported an average volume of at least 700 c.c. at the most productive level.

At this point, we should remind the reader that the purse-seine fishery for mackerel, to which the present discussion is limited, draws only from such schools as are close enough to the surface to be seen, which leaves open the possibility that considerable bodies of mackerel may have remained in the eastern sector of our area that summer, after the surface schooling fish had moved farther east-

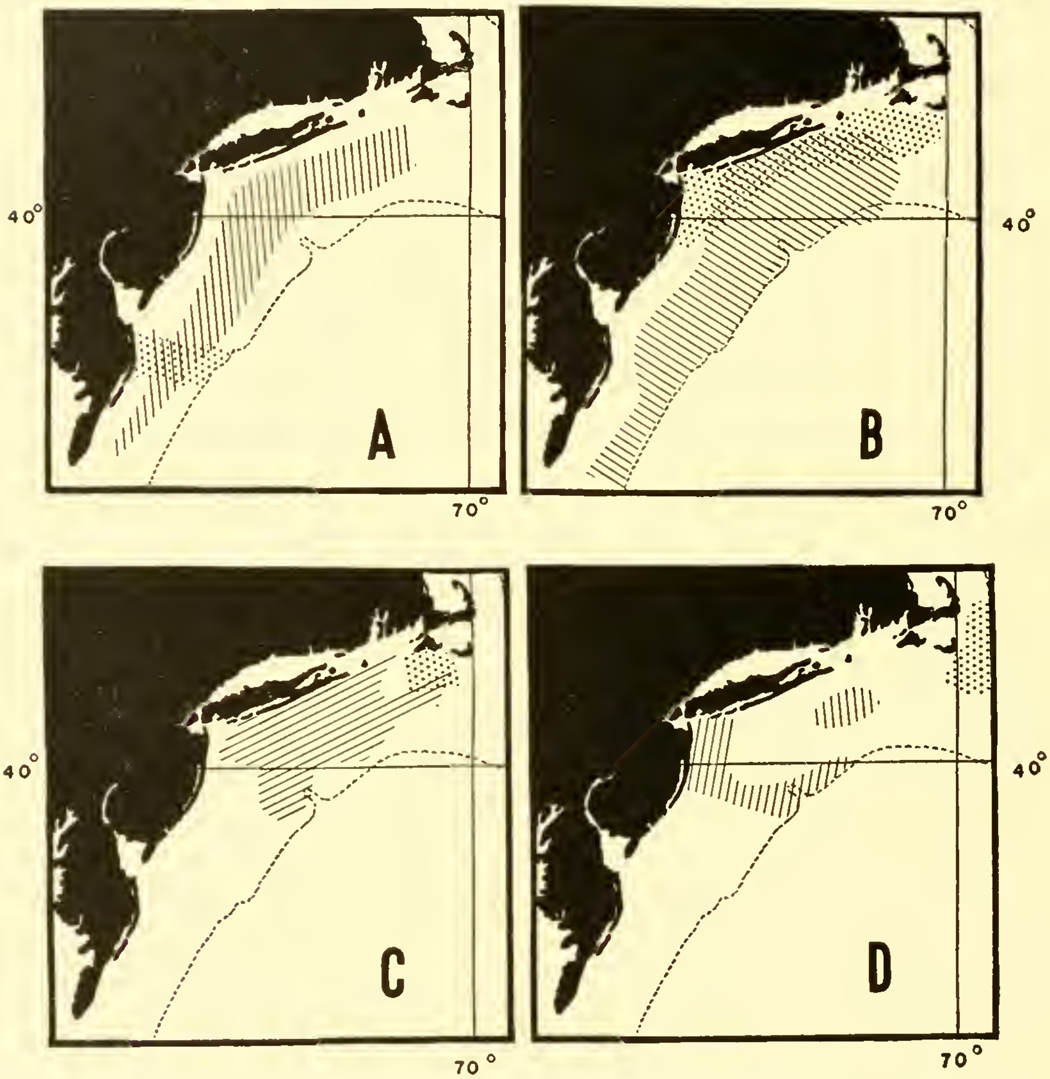


Fig. 14. Locations of areas where plankton was most abundant (hatched); and where the mackerel fishery was chiefly concentrated (dotted), in 1930: A, April 22–May 1; B, May 12–23; C, June 24–July 1; D, July 10–18.

ward, but living deep down in the water where we have good reason to believe that the plankton was most abundant. Nevertheless, the evidence outlined above seems to us strong, that at least a large proportion of the mackerel stock travelled horizontally along the belt of abundant plankton, seemingly without reference to the precise localities where the latter was richest, to waters where we have no reason to suppose that feeding conditions averaged any better; a movement for which the quantitative distribution of the plankton does not offer any apparent explanation and which must therefore be credited to some impulse to migration of a different sort.

In this respect, the mackerel may differ from the herring, for Wimpenny (1929, p. 10) remarks that the "view that herring seeks and perhaps depends upon, the fattest food seems to me to have much to commend it."

CONCLUSIONS

The Plankton as a Whole

Horizontal Distribution

The preceding discussion may be summarized as follows:

In years when the shelf waters as a whole experience a pronounced winter chilling, the zooplankton is volumetrically at a low ebb in February, though we have yet to learn whether the annual minimum falls in that month or earlier in the winter. The plankton then averages richest next the coast, and in the south, poorest in the northeastern sector and along the edge of the continent. Experience in 1930 and 1931—presumably the situation was essentially similar in 1929—suggests, as a reasonable expectation for a normal February, volumes ranging from about 100 to 500 c.c., for the water column as a whole (occasionally as rich as 1000 c.c.) in the belt marked A on Fig. 2, with averages of 150–200 c.c., of 50–100 c.c., and of 10–120 c.c. in the belts B, C, and D, respectively. And available data show that the water is notably barren, then, along the continental slope—a maximum of only 35 c.c., a minimum of 13 c.c., for all years combined.

After a warm winter, however, such as that of 1932, the late February plankton may average from two to three times as plentiful in the southern sector as in cooler years, but not significantly richer in the northern sector, so that the regional contrast at this season is widest in years of that type.

A marked augmentation in the volume of plankton takes place during the spring in some years (illustrated by 1930 and 1931), but not in others, e.g., 1929, 1932, but we still lack a convincing explanation for the existence of these two contrasting states. In years when this augmentation does occur, it appears first at scattered rich centers, as a result of which the plankton may vary widely in amount between neighboring localities. These centers may soon merge, so that the productive areas become rather sharply demarked from the less productive, as in 1930, or they may continue more or less independent, resulting in a decidedly complex areal pattern, as in 1931 (Fig. 4).

In years when vernal augmentation occurs, it is first centered chiefly in the northern and northeastern sector, expanding eastward at some time during the spring to the limit of our area (Martha's Vineyard profile) in years of high production (e.g., 1930, 1931). And it also tends to spread progressively from north to south with the advance of spring, most markedly along the mid-belt of the shelf, but also involving the waters seaward to some extent out beyond the continental edge. Vernal augmentation of this type may either culminate in May, followed by some decrease in early June, with little further alteration through July (as in 1930), or the plankton may continue to increase slowly in amount through June and into July, as in 1931. Contrasting with this enrichment to the north, and offshore to the south, the plankton of the coastal belt south of New York, at most increases slightly during the spring, as happened in 1931, or it may even decrease somewhat, as in 1930. Neither have rich pools such as may exist close to the mouth of Chesapeake Bay or southward of the latter in February or in April, ever been found there in May or later.

Various lines of evidence indicate that vernal augmentation in our area results chiefly from local reproduction, with mass immigration from the east contributing very little; indrafts of water from that source may even tend toward impoverishment.

In years of the opposite type (e.g., 1929, 1932), the plankton alters but little in average volume (continuing relatively poor) from late winter or early spring through June, as in 1932, or even through July, as in 1929. Conditions in 1932 suggest that a poor production of plankton is to be expected after an abnormally warm winter—even if this thermal abnormality be obliterated during the spring, and if summer temperatures be about normal. But—by the evidence of 1929—production may also be poor after a normally cold winter.

Since the observational series included as many years of the one type, as of the other, so far as production of plankton is concerned, the following monthly averages, for all years combined, are probably a fair representation of the characteristic state. On this basis, the volume of plankton may be expected perhaps to double over the area as a whole between February and May or June, and to multiply more than six-fold in the northern sector between February and July, in an average year, while in a year of good production, it may multiply nearly four-fold over the area as a whole, and more than 14-fold in the north, between the end of winter and the date of the summer peak. Peaks of equal abundance may perhaps develop locally in August and September when quantitative data are lacking. But the plankton then decreases again by October, to a volume about equalling the average for April.

Average volumes, c.c. per standard haul

Month	Inshore	Offshore	North	South	Area surveyed
February	339	80	75	282	222
April	252	335	354	234	231
May	342	576	451	425	443
June	343	421	388	330	372
July	551[1]	492[1]	505	—	—
October 1931	—	234	236[2]	231[2]	—

[1] North only. [2] Offshore only.

The tabulation further shows, first, that regional contrasts are much the widest in February, when the plankton has averaged some four times as rich inshore and south, as offshore and north, and, second, that a reversal tends to take place

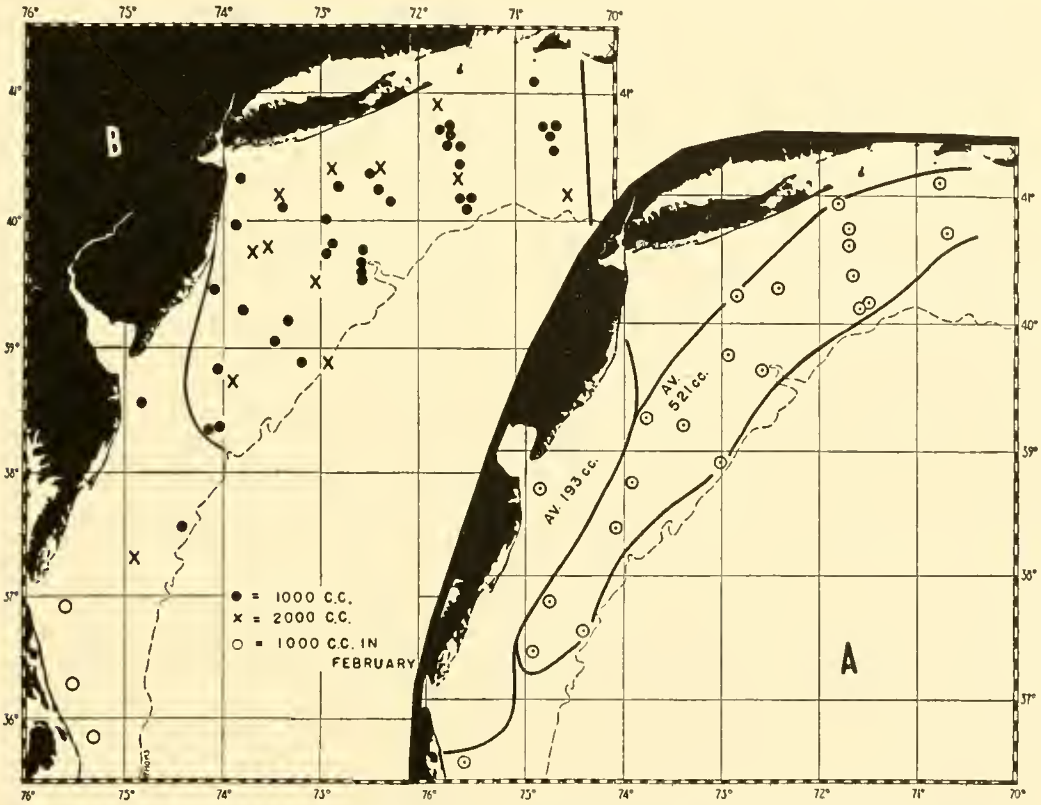


Fig. 15. Volumes of plankton: A, averages in different areas, mid-May to mid-June, of all years combined; with locations of volume greater than 900 cc.; B, stations where the volume of Plankton was larger than 1000 cc. at the richest level, after subtraction of medusae and salps.

early in the spring, from the winter state, to a slight contrast of the opposite sense (richest offshore and north), which prevails generally through April, May, and June. And the majority of the chief centers of abundance (> 900 c.c.) have similarly been concentrated on the outer part of the shelf to the north and east of the Hog Island profile (Fig. 15A). But there have been considerable variations in this respect among individual cruises.

It is probable that the average volume of plankton existing in the offshore belt in the north in July 1931 (912 c.c.) approximates the maximum that is to be expected over any considerable part of our area, at any season, in normal years, though the richest catch of all (67109 c.c., mostly salps off Delaware Bay, July 18, 1929) was made at the edge of the continental shelf. At the other extreme, the region that has proved least productive in late spring and summer is the coastwise belt southward from Barnegat, where volumes from mid-May to June have averaged only about 193 c.c. Very rich centers (> 900 c.c.) may, however, develop locally, in this barren zone, as they do elsewhere (Fig. 15A).

In October, to judge from 1931, volumes average about as large north as south.[1] But we have no information as to the regional gradients later in the autumn, or in early or mid-winter.

Vertical Distribution

At the end of the winter, the plankton averages considerably richer in the upper 25–30 meters than deeper, but it is distributed with comparative uniformity, vertically, within that stratum, nor do diurnal migrations greatly affect the mass distribution at that season, when turbulence is still active, and illumination relatively weak. Migrations of this type, of the community as a whole, upward by night and downward by day have, however, proved widespread from April through June. The center of population also tends—though quite independent of this phenomenon—to sink to the mid-depths by April, there to continue through the later spring and summer. And this type of vertical stratification greatly intensifies from June to (probably) a maximum in July, when the 20–30 meter level stratum has averaged from 10–26 times as productive of plankton as the superficial 10 meters in different years. This enrichment of the deeper waters, relative to the surface, which is confined to the upper 40 meters or so, until June, also extends downward below 60 meters by midsummer.

It is probable that the development of this type of vertical stratification in spring results chiefly from the alteration usual at this season from dominance of the community by Centropages and Limacina, to dominance by Calanus. But the intensification of stratification that takes place from June to July results from the fact that by midsummer, the surface stratum warms to a temperature

[1] The one October cruise was confined to the offshore belt.

that is unfavorably high for the members of the boreal community that are the most prominent relatively at the season.

Annual Differences

The fact that the plankton, over the region as a whole averaged about twice as voluminous in the richest year as in the poorest in February and about three times as voluminous in midsummer, within a period of only four years, marks our area as one subject to fluctuations in this respect, perhaps wide enough seriously to affect the welfare of plankton-eating fishes. At the end of the winter, the plankton was richest in the year (1932) when temperatures were highest, but subsequent production poor, whereas vernal augmentation was most pronounced and summer volumes largest in a year when the plankton had been very scarce in February and when winter temperatures had been normally low. But it is clear that this is not a case of simple control by temperature, for one of the years of this same thermal type (1929) was one of poor plankton production.

Comparison With Other Areas

By available data our area on the one side of the Atlantic and the southern part of the North Sea, on the other, rank together in volume of plankton, with averages of about 0.5–0.8 c.c. per cubic meter (as estimated by the displacement method) at the season of maximum production, somewhat surpassed by more northerly European waters, but in turn ranking ahead of the Gulf of Maine, the Gulf of St. Lawrence, the Nova Scotian shelf waters, the English Channel, and the Baltic.

Relative Importance of Different Species

Recent data corroborate earlier observations that the planktonic community of our area, though quantitatively varied, is dominated by a small number of boreal species, among which the only ones that have individually formed as much as 15% of the total catch over the area as a whole in any one month have been *Calanus finmarchicus*, *Centropages typicus*, *Sagitta elegans*, *Sagitta serratodentata*, and *Limacina retroversa*. Inclusion of species that have formed 15% for one or other subdivision (though not of the whole area) on at least one survey, would add to this list euphausiids as a group, Euthemisto sp., *Metridia lucens*, *Paracalanus parvus*, *Pseudocalanus minutus*, *Aglantha digitale*, ctenophores, and salps, the latter being the only warm water derivatives that have been found to form any considerable part of the total catch, in either subdivision as a whole, on any cruise. The members of these categories (combined) have formed 89–93% of the total volume in February, 91–95% in April, 80–93% in May, 81–91% in June, and 80–95%, and 78% in October.

At the end of winter, either *Centropages typicus, Sagitta elegans,* or Limacina may be the leading item in the community (Table, p. 229). Centropages, however, and *Sagitta serratodentata* then decline so greatly in relative abundance, that they are of but minor importance in the community in late spring and early summer, while Limacina, which ranks high as late as June in some years (1930, 1932), is negligible later in the summer. On the other hand, Calanus which occupies a minor, or at most an intermediate position in February (8% on the average) so greatly increases in importance shortly thereafter that it was by far the most prominent species in each April of record, ranking also first or second (in which case it closely rivalled the leader) in May, in June, and in July of each year. Since the observational series included one year (1932) when Calanus was relatively scarce, but others (1930, 1931) when it was abundant, its combined monthly ranking for the series as a whole may be accepted as approximately representative of normal years. On this basis, Calanus with a combined percentage of about 35% for all cruises combined (for the regions surveyed), is on the whole responsible for the production of a larger volume of plankton than any other one species, its closest rivals being *Sagitta elegans*, Limacina, and *Centropages typicus*, each with 11–12%. Calanus may, in fact, be expected to form nearly, or quite ½ of the total volume of plankton, whether for the area as a whole (47%), for the northern sector (50%), or offshore (50%), from April through July. In the south, however, it reaches its maximum importance in April (47%), declining thereafter through May and June (18–22%) to July (9%) in 1929 (perhaps 10–20% in 1916 and negligible in 1913). Calanus also decreased greatly in relative importance during the early autumn—at least in the offshore belt—in the one year of record (1931), whereas Centropages so increased that it ranked first in that October, and Calanus only third or fourth (see Table, p. 229), which taken with conditions in February, suggests that Centropages probably continues much the more important of the two through later autumn and winter. The salps and ctenophores, Pleurobrachia and Mnemiopsis,—insignificant in amount earlier in the season—may practically monopolize the water over considerable areas in the mid-sector, in warm summers such as that of 1913, and be abundant there locally, even in cool (e.g., 1916, p. 370).

In the cases of the other members of the dominant group, the trend in relative importance is upward through the spring and summer in some years, but downward in others or alternately up and down.

The following tabulation of monthly percentages for the dominant species in the total community for the series as a whole may be taken as representative of the relative rankings to be expected in normal years.

Month	Calanus finmarchicus	Centropages typicus	Metridia lucens	Paracalanus parvus	Pseudocalanus minutus	Limacina retroversa	Sagitta elegans	Sagitta serratodentata	Ctenophores	Salps
February	8%	25%	7%	3%	5%	13%	15%	13%		
April	51	8	9		5	9	5	6		
May	32	4	5		4	22	20	1	3%	<1%
June	42	4	4		2	7	15	<1		2
July[1]	51	17	2		1	1	13	1		5
October[2]	7	34	7	17	2	<1	5	5		<1

[1] North only. [2] Offshore only.

The chief seasonal contrasts, apart from the ups and downs for individual species as just outlined, is that monopolization of the waters of our area by the regularly dominant community is most nearly complete in April, May, and June; least so in February, on the one hand, and in October, on the other; also in the south in July.

Previous explorations had shown that one need journey out only a few miles from the continental edge to encounter the typical warm-oceanic communities in full strength. And occasional representatives of a considerable number of species of warm water tunicates, copepods, pteropods, amphipods, etc., were reported widespread, here and there, over our area in the summers of 1913 and 1916 (Bigelow, 1915; 1922), as well as on most of the cruises for the period, 1929–1932, most frequently in the offshore belt, as was to be expected. But it appears that a definite barrier exists—perhaps in low salinity—to mass invasion of the shelf from offshore, anywhere to the north of the latitude of Delaware Bay, for oceanic species of all species combined, have never formed as much as 1% of the plankton in the northern sector, at any season, even in the offshore belt, with the exception of salpae, which may multiply so rapidly in the high temperatures of summer that the volumes that may be found on the shelf on any particular occasion give no indication of the numbers that may previously have drifted thither. And the dominant boreal community equally monopolizes the southern sector down past the offing of Chesapeake Bay, in April, May, and June. But it becomes relatively less important in the southernmost sector by July of normal summers, and a wide variety of oceanic and southern species considerably more so there, at that time of year. This, in fact, and the north-south gradient for Calanus are the most striking regional contrast that exists within our limits at any season. And the situation in the late winter of 1931 suggests that tropical communities may be expected to dominate the shelf waters from Cape Hatteras southward, the year around.

It is difficult to determine to what extent the plankton of our area may draw from the shelf waters to the eastward—George's Bank and the Gulf of Maine—with the invasion of the cold water that often comes from that direction in spring, because the qualitative composition of the dominant communities is much the same, west as east of Cape Cod. But the distributional pictures for the leading species lead to the conclusion that even if there be some recruitment from this more eastern, and more strictly boreal source, the maintenance of the local plankton depends chiefly on local production. It is especially instructive in this connection that species definitely to be classed as northern indicators in our area, such as *Calanus hyperboreus* and *Oikopleura labradoriensis*, have invariably formed a small part of the catches (an average of 6% at most) even on occasions when they have become dispersed far and wide. And with visitors from the coastwise water to the south equally negligible in average amount even in the southern sector at all seasons, with the unique exception of the invasion of Palinurus larvae in July 1929 that is described elsewhere (p. 243), our area is primarily self-contained so far as its plankton is concerned.

Feeding Conditions for Plankton-Eating Fishes

It has long been known that the major items in the diet of the local mackerel and probably of other fishes feeding on zooplankton, are the species of crustaceans, of pteropods, and of sagittae that dominate the plankton of our area. These differ in chemical composition as discussed on page 254. But it is not possible to assign relative weights to them, as fish food, without knowledge of their relative digestibility, for different fishes. The present discussion of the richness of the area as a feeding ground is therefore based on the assumption that they can be grouped together as "nutritive," the medusae, ctenophores, and salpae being left out of consideration as of low food value.

A better index to richness from the feeding standpoint, is afforded by the volume at the richest level, than by the average for the water column as a whole, because the former to some extent expresses the relative accessibility for fishes of the available supply. Information in this regard, obtained in 1929, 1931, and 1932, when two or more hauls were made at most of the stations, combined with adjusted values for 1930 (see p. 257 for the method of adjustment) yields the following monthly volumes of the more nutritive plankton at the richest level, for all years combined:

Average monthly volumes (c.c.) of the more nutritive plankton in the different subdivisions at the richest level

Month	Inshore		Offshore		North		South		Area Surveyed	
	Per Tow	Per M^3	Per Tow	Per M^3	Per Tow	Per M^3	Per Tow	Per M^3	Per Tow	Per M^3
February	408	0.7	109	0.2	114	0.2	311	0.5	288	0.5
April	333	0.6	465	0.8	292	0.5	258	0.4	327	0.6
May	423	0.8	794	1.3	586	1.0	498	0.8	556	0.9
June	478	0.8	617	1.0	563	1.0	447	0.8	508	0.9
July	951	1.6	701	1.2	791	1.3	—	—	—	—

This tabulation (and the data for the separate years on which it is based, Tables pp. 256, 257) shows the northern sector, offshore, as averaging poor in fish food at the end of winter (in some years very barren indeed), but the southern sector, inshore, as moderately productive, especially if winter chilling has been less extreme than usual (e.g., 1932). In years of this latter type, the center of abundance may even continue in the south until early summer. Usually, however, the volume of nutritive plankton so greatly increases in the northern sector during the early spring as to make this the richest part of the area by May, at latest, so to continue through July. In some years—those of high production—the vernal augmentation involves the other parts of the area as well, but in others (represented with equal frequency in the observational series), it is confined to the northern sector. The volume in the richest area at the peak season has been found to average nearly two to three times as great in a rich year (1930) as in a poor (illustrated by 1932). But these annual differences are not wide enough to obscure the general rule that the largest volumes usually develop within the area outlined in Fig. 15 and in July, when the average there has been about 1300 c.c. for the richest year and about 900 c.c. for all years combined, with local centers of abundance as rich as 2000 c.c.

A decided decrease is then to be expected—by the evidence of the one year of record—from this peak, to perhaps ½ as much nutritive plankton in the offshore belt in October. But we have no corresponding information for the inshore belt for that month, or for any part of the area in later autumn or winter.

In winter, in spring, and in the first month of summer, the most productive level for the nutritious plankton is about as often shoal as deep, while more often still there is no pronounced stratification of either order at this season. But by July, much the largest volumes occur about 15–20 times as often at depths greater than 20 meters as within 10 meters of the surface, so that feeding conditions average much the best then in the mid-depths. But we have no evidence as to the extent to which mackerel or other fish are able to profit by the opportunity provided by this type of stratification.

In the one year (1930) when the location of the chief mackerel fishery, from month to month was compared with the volumetric distribution of the more nutritious plankton, it appeared that the fish first struck in at the southerly end of the productive belt, and then moved northward and eastward along the latter (apparently indifferent to the precise localities where plankton was richest) until by July, the surface schooling portion, at least, of the mackerel stock had passed out of our area, leaving behind feeding conditions probably as rich as those of the Gulf of Maine, Nantucket Shoals, and George's Bank, to which they had repaired. But it is possible that a part of the mackerel may have remained west of Cape Cod, but living deep.

PART II. VOLUMETRIC DISTRIBUTION OF INDIVIDUAL SPECIES

CHORDATES

Doliolum sp.

Doliolum was taken in abundance midway of the shelf off Delaware Bay in the summer of 1913, with occasional specimens near land to the southward and at scattered stations along the continental edge (Bigelow, 1915). In 1929, a large catch (80 c.c.) was made off Currituck in May, and Doliolum had become generally dispersed through the southern sector by that June, so to continue through July (50% of the stations, Fig. 16A), in quantity varying from less than 1 c.c. to 82 c.c., or sufficient to make it of some importance locally in the plankton. But the most northerly record for it on the shelf during this period was off Atlantic City, proving that it was almost entirely confined to the southern sector at the time. Unfortunately, we have no information as to how late into the autumn Doliolum may have persisted on this occasion, other than that it

Fig. 16. Locality records:–A, Fritillaria, and Doliolum contour marking southern limit of Fritillaria; B, *Oikopleura dioica;* C, Salps; D, volumes of *Clione limacina* larger than 4 c.c.

had disappeared at some time prior to the following February. But the fact that we have no other record of Doliolum within our limits during the four year period, 1929–1932, shows that invasions by it on a broad scale are rather unusual events, the effects of which are limited for the most part to the southern sector.

During the height of vernal invasion in 1929 (May–July), the average volume of Doliolum was about 9 c.c. for the southern sector as a whole, the maximum about 82 c.c. And it is interesting that catches should have averaged rather higher inshore (4–5 c.c.) than offshore (1 c.c.), for Doliolum undoubtedly comes to our area from the continental slope.

Salps

It has long been known that salps of one species or another are plentiful along the continental slope abreast of our area. And the records for 1931 show that they are to be expected in small numbers close in to the coast south of Cape Hatteras, even at the coldest time of year, while they may also occur here and there well inshore considerably farther north at the end of a warm winter, such as that of 1932, when *Iasis zonaria* was taken at three stations on the Cape May profile. But salps are either wholly wanting on the shelf north of Latitude 36° at this season in more normal years (e.g., 1930), or at least confined then (and in small volumes) to the immediate vicinity of the 200-meter contour as in 1931. And by available evidence, their status is essentially the same in April, when the only inshore record was south of Latitude 36°, though we have record of them at 10 April stations near the 200-meter line in 1930, in volumes ranging from 1 c.c. to 30 c.c., with one catch of 5000 c.c. off Montauk on the 23rd of the month in 1929. But the records for May, while equally closely confined to the continental edge in the south, are dispersed well in on the shelf in the east (Fig. 16C), in amount up to 150 c.c. By June, they have been recorded widespread in the offshore belt, south as well as north, on one cruise or another, averaging about 14 c.c. in the offshore belt (all years combined) with a maximum of 261 c.c. And by July salpae may not only occur in enormous quantities along the edge of the continent —witness a volume of some 66 liters (by rough estimate), just inside the 200-meter contour on the Cape May profile, in 1929, and another of 1046 c.c. at about the same relative situation on the Martha's Vineyard profile in 1931—but may also invade the inshore belt as well at this season, to the southward of New York in great abundance, if the summer be a warm one. This, for example, happened in 1913, when they were in swarms, along the coasts of New Jersey, Maryland, and Virginia (Bigelow, 1915, p. 275, Fig. 67), and were recorded at every station westward and southward from the Montauk profile. Small numbers of salps were even taken close in to New York in the cold summer of 1916—when tropical immigrants were at a minimum—as well as at several stations offshore, in the south (Bigelow, 1922, p. 156, Fig. 52). Conditions vary widely, however, from year to year, in this respect, apart from temperature, for the record of salps, inshore for 1929 is confined to scattered specimens at three stations, all south of New York (maximum, 5 c.c.). And we have no reason to suppose that they ever occur in abundance inshore, east of New York, even in a July when they are general and abundant farther out at sea, as they were in 1931, when the average catch of salps offshore in the north was 167 c.c. (maximum, 1046 c.c.).

Salps may persist in small or moderate numbers here and there, well in on the shelf, until October (maximum, 103 c.c.) in some years, as exemplified by 1931, most abundant and most frequent in the south as was to be expected—or even until November, when many *Iasis zonaria* were taken at two stations off Martha's Vineyard in 1916 (Bigelow, 1922, p. 157). But their status in February (p. 272) makes it likely that they vanish wholly from the shelf, to the north of Lat. 36°, with falling temperatures, at the onset of winter.

Salps may be regarded strictly as oceanic immigrants in our region, sometimes developing local swarms there under the favorable conditions of summer, but unable to maintain themselves anywhere inshore from the 200-meter contour through the cold season.

Fritillaria sp.

Representatives of Fritillaria were recognized at localities widely scattered across the whole breadth of the continental shelf in the northern sector, and southward along the edge of the continent as far as the Currituck profile (Fig. 16A). And while the condition of the material did not allow specific identification, i.e., whether belonging to the wide-ranging *F. borealis* or to the warm water *F. venusta* (Lohman, 1901; 1911), this distributional picture at least suggests a more northern source of supply. The seasonal distribution of the catches (11% of the stations for February, 2% for April, 7% for May, 0% for June, 3% for July, and 0% for October) would not of itself suggest any relationship to the vernal indrafts of water from the east. But the fact that the only catch of measurable volume (9 c.c.) was made in May, is at least compatible with temporary recruitment from the region of the Gulf of Maine, where Fish and Johnson (1937) found *F. borealis* in considerable frequency. Neither have we any evidence of reproduction of appreciable magnitude anywhere within our area, for all the other local records of Fritillaria were of occasional specimens only.

Oikopleura dioica

Records for this appendicularian have been confined to the months of May (2 stations), June (4 stations), July (7 stations), and October (4 stations), and so strictly limited to the south (Fig. 16) that it can be as safely regarded as a warm water indicator in our area, as is *O. labradoriensis* of water from the east and north. In the southern sector, however, the localities of capture have been widespread, from close inshore out to the continental edge. And the fact that the catches ranged from 1–14 c.c. (average, about 8 c.c. for the stations of record) makes it likely that some local reproduction of *O. dioica* takes place as far north as Delaware Bay during the warm half of the year. But it is unlikely that this is ever on a scale large enough to make it an important item in the plankton. And we have yet to learn whether it vanishes from within our limits during the cold half of the year as completely as our failure to find it in February or in April would suggest (implying that reestablishment later in the spring depends on renewed invasion), or whether a scattering of the species actually survives the winter.

Oikopleura labradoriensis

Oikopleura labradoriensis deserves attention, among the species that are usually of minor importance, both because of the wide variation in its abundance from year to year, and as an indicator of water from the north and east. It has been recorded at only three stations in February, at five in April (all in 1930), always in minimal numbers, and it may continue very scarce in some years right through the spring and early summer, as in 1930, when it was recorded at only one of the 27 stations for May, not at all in June and July. But it may increase considerably in abundance, in spring, in other years as in 1931, when (not found at all in February) it was widespread in May, over the outer parts of the shelf as a whole, southward to the offing of Delaware Bay, averaging 5 c.c. in volume, for the whole region, with a maximum of 67 c.c. And it was still more abundant in 1932, when—similarly lacking in February—it had become general throughout all but the southern part of the region by the beginning of May, averaging about 29 c.c. by the second week of the month, with a maximum of 122 c.c. This, however, represented the peak for *O. labradoriensis* in each case, for its southern boundary shifted, in 1931, from the offing of Cape May to (roughly) the offing of New York between mid-May and mid-June, while in 1932, the percentage of stations at which it occurred declined in the northern sector from 95% at the end of May to 53% by the first week in June, and to 15% by the third week of that month, by which date it was entirely confined to the extreme northeastern corner of our area, while its average volume similarly decreased in the northern sector, to an average of 4 c.c. by the end of May, and to 1 c.c. in June. We have occasional record of it only in July (8 stations, all years combined) and none at all in autumn.

Its status, thus, appears primarily to be that of an immigrant entering our area in spring, to multiply there temporarily, if conditions favor, which happens most often in May, but disappearing altogether by mid-summer.

MOLLUSCS

Clione limacina

Frequency. The records for individual cruises have shown that Clione may appear anywhere on the shelf, from the coast line out to the edge of the continent, at any time between February and October, but so irregularly and sporadically that no dependence can be placed on its presence or absence in any particular region, or at any particular time of year. Combination, however, of the records for the several cruises suggests that it is usually least frequent at the end of winter and in early spring, and that it tends to become much more so with the advance of the season, for it was taken at 11% only of the stations for February and April, but at 46% in May, 53% in June, and 32% in July, with maximum frequencies of 84%, 78%, and 50%, respectively for the last three months. And this is in line with Rathbun's (1889) report of it in about 30% of his towings between the offings of New York and of Chesapeake Bay in late April, and May of 1887. An increase in frequency through the spring was even recorded in the year (1932) when Clione was most common in February, namely from 48% of the stations in that month to 54% in May and 70% in June. And the data for 1929, when it was not taken at all in April, but at 15% and 21% of the stations in May and June, respectively, and for 1931, when it was lacking in February, but was at 37% of the stations in May, similarly suggest that in some years it may not exist at all in our area until late in the spring.

These lines of evidence mark May and June as, on the whole, the months in which Clione is most frequent, with July falling but little behind. If 1931 can be taken as representative, the species then tends to decline in frequency during the autumn, and perhaps to disappear altogether before the beginning of winter, for it was taken at 15% only of the stations in that October and not at all in November 1916.

On one cruise or another, Clione has been found most frequent inshore, offshore, in the north, and in the south, apparently independent of the time of year. It tends, however, to be somewhat more frequent offshore than inshore, for this was not only the case in eight individual months with the reverse true in five only (February, 1930, 1932; June, 1929, 1930; July, 1929), but it was also recorded at a slightly greater percentage of stations offshore (33%) than inshore (25%) for the series as a whole.

We might perhaps have reasonably expected to find a species of presumably boreal origin—such as Clione—occurring more frequently in the northern sector of our area than in the southern. Actually, it was taken at 38% of the stations in the south, but at 34% only in the north, on all cruises combined. The fact that it was wholly lacking in the northern sector in five of the individual months (February, 1931, 1932; April, May, June, 1929; October, 1931), but only in two months (February, 1930, 1931) in the southern, is in line with the foregoing. It was, again, most frequent in the south in ten of the months when both sectors were surveyed, but in two only (April, 1930; May, 1931) was it most frequent in the north. And the maximum frequency in any one month has been considerably higher south (90%, May 1930 and June, 1932) than north (66%, June 1932). Thus, there seems no escape from the conclusion that in our area, Clione must be classed as a southern species, even though this places its center of frequency close to the southern boundary to its regular occurrence. And the distribution of the richer catches is in line with this, volumes larger than 4 c.c. having been entirely restricted to the sector southward from the New York profile (Fig. 16, D), with some slight concentration of the largest volumes off Virginia and off Chesapeake Bay, while Rathbun (1889) found it "common" and "abundant" to the south, only, of Lat. 39° N., in the spring of 1887.

Percentage of stations at which *Clione limacina* was taken

Month	Year	Offshore	Inshore	North	South	Area Surveyed
February	1930	0%	9%	10%	0%	5%
	1931					
	1932	44	67	0	75	48
April	1929					
	1930	20	6	19	9	16
May	1929	15	7	0	22	15
	1930	91	66	66	91	77
	1931	70	13	50	13	37
	1932	62	45	45	71	54
June	1929	0	16	0	33	21
	1930	10	25	24	0	19
	1931	63	54	48	83	67
	1932	90	60	66	90	70
July	1929	0	25	10	22	14
	1930	20	28	23	—	23
	1931	75	23	38	—	38
October	1931	15	—	0	20	—

Average volumes of *Clione limacina*

Month	Year	Inshore	Offshore	North	South	Area Surveyed	Maximum
February	1930	<1	0	<1	0	<1	<1
	1931						
	1932	<1	<1	0	<1	<1	<1
April	1929						
	1930	<1	<1	<1	<1	<1	<1
May	1929	<1	<1	<1	<1	<1	6
	1930	<1	<1	<1	<1	<1	<1
	1931	<1	<1	<1	<1	<1	4
	1932	<1	2	<1	3	1	75
June	1929	5	<1	0	8	3	79
	1930	<1	<1	<1	0	<1	2
	1931	3	2	<1	6	3	50
	1932	5	21	3	31	12	235
July	1929	<1	0	<1	<1	<1	<1
	1930	7	<1	3	—	3	50
	1931	<1	<1	<1	—	<1	<1
October	1931	—	<1	0	<1	<1	<1

Abundance. The records of Clione in February and April, have, in every case, been based on volumes smaller than 1 c.c. And even in May, when this pteropod is approaching its maximum frequency, the average catch for the area as a whole still continued less than 1 c.c. in three of the years (1929, 1930, 1931), and was only 1 c.c. in the fourth (1932). But the maximum had risen to 4–6 c.c. by that month in 1929 and 1931; 1932 yielded six May catches of 5–10 c.c. with one of 75 c.c., while the average volume of Clione was about 5 c.c., for the area as a whole in June of the several years combined, with maxima of 50 c.c. in 1931, of 79 c.c. in 1929, and of 235 c.c. in 1932. Thus, it appears that this pteropod may be expected to experience a considerable vernal augmentation in our waters in most years, either accompanying or briefly succeeding the seasonal increase in its frequency of occurrence. If it be scarce in June, it may considerably increase soon after, as happened in 1930, when the averages and maxima rose from less than 1 c.c. and 2 c.c. in that month to 3 c.c. and 50 c.c. in July. It may even be rather numerous locally, as late as August in cool summers—e.g., 1916 (Bigelow, 1922, p. 156). It seems more usual, however, for it to be in very small volume, anywhere west or south from Cape Cod by midsummer, even if widely dispersed then, as was the case in 1931; or even lacking altogether, as seems to have been the case in 1913. And the fact that the maximum catch for October was less than 1 c.c., added to our failure to find it at all in November (1916), suggests that this is equally true in autumn.

The rapidity with which the volume of Clione may alter, emphasizes the danger of generalizing, as to what is to be expected in the oft quoted "normal" year. In 1932, for example, the average fell from 27 c.c. in the first week in June, to less than 1 c.c. a few days later, but then rose to 8 c.c. in the third week of the month, with a corresponding fluctuation in the maximum catch. But the data suggest that a maximum catch of, say, upwards of 200 c.c. may be regarded as exceptionally rich for Clione, at any season, or an average of more than 20 c.c., whether for the area as a whole, or for any considerable subdivision of the same.

Source of the local stock. The abruptness with which fluctuations take place in the abundance and frequency of occurrence of Clione, added to the fact that one year may be richest in this pteropod in one month, another year in another, introduces the question, whether maintenance in our area depends more on local reproduction or on waves of immigration. The probability has already been mentioned (Bigelow, 1922, p. 174), that local centers for this species are the result of temporary breeding activity "of such few specimens as from time to time stray southward past Cape Cod." And if this pteropod does actually vanish as completely from our scene in autumn as now appears to be the case, this early suggestion is no doubt correct. Failure to detect any larvae, on the February or April cruises, makes it unlikely that breeding takes place in our area in winter, or in early spring. It is certain, however, that widespread reproduction may occur in late spring and early summer, because larvae were taken at 27% of the stations for May and 38% for June in 1929, 75% in May in 1930, and 50% in May and 28% in June in 1932. But the situation in this respect evidently varies widely from year to year, for larvae were detected at three stations only (all in May) in 1931. Nor have we any evidence,—in the occurrence of larvae—of reproduction later than June in any year, anywhere west of Cape Cod.

In good breeding years, such as 1929, 1930, and 1932, the production of larvae is widespread over the area as a whole, at the height of the season, without apparent concentration in any particular region, except perhaps, from the New York profile southward, as contrasted with the sector farther to the east. But it appears that the offing of Chesapeake Bay is roughly the southern boundary to their presence.

In most instances, the records for larvae have been based on less than 1 c.c. per catch, except during the first June cruise of 1932, when half a dozen catches were made larger than 15 c.c., with a maximum of 73 c.c. bringing the general average for the area up to 27 c.c. It is particularly interesting—if difficult to explain—that the largest catch for this cruise (for the entire series for that matter) was made in the south, off Chesapeake Bay.

Limacina retroversa

Frequency. It seems that the southern boundary to the regular occurrence of this well known boreal pteropod is not far from Latitude 36° N., for it was not found near Cape Hatteras, on the one cruise (February 1931) that extended so far in that direction. But it has been taken widespread throughout our area to the northward of Chesapeake Bay, on one occasion or another. At any given time, its range may cover all parts of the area indifferently—as was the case in May 1932—it may be confined to a definite pool or pools, leaving other extensive areas bare, as in that same month in 1929, or it may fail altogether at one station, but prove extremely numerous at another, only a few miles distant, with rich and barren centers complexly intermingled. But its presence at 58% of the stations inshore, 50% offshore, 56% in the north, and 59% in the south, shows it as about as frequent (relatively) in one subdivision as in another.

Seasonally, however, a rather definite succession has appeared from highest frequency in February (81% of the stations) through April and May (70%), June (66%) and July (21%), for all years combined. In each year of record, furthermore, Limacina was either lacking in the easternmost sector throughout the season of observation (e.g., 1929), or showed a general tendency to disappear thence during the spring, either locally (1931, 1932), or completely (1930). It also disappeared from the south between February or April and May or June, in three of the years of record, either from the inshore belt alone (1929, 1932), or across the whole breadth of the shelf, although in the fourth year (1930), it continued general in the southern sector right through June.

The general implication of the foregoing is that in the case of Limacina, throughout the spring and early summer, a comparatively barren belt usually separates one distributional center in the Gulf of Maine, from another in the waters west of Cape Cod, centering chiefly in the general offing of New York.

If the data for October 1931, and for November 1916 can be taken as representative, two alternative explanations are open: either that adult Limacina vanishes entirely from the offshore belt—hence presumably from the area as a whole—in late summer and early autumn (it was not found at all in October), to reappear widespread as far south as Delaware Bay by November, much as Redfield (1939) reports for the Gulf of Maine, or else that a stock of adults persists right through the autumn in some years, but not in others.

No information is available in our area through the first two months of winter.

Average volumes of Limacina

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	2	4	5	1	3	33
	1931	<1	<1	<1	<1	<1	2
	1932	228	7	1	195	138	1833
April	1929	18	2	12	11	12	138
	1930	29	43	49	25	36	409
May	1929	44	20	49	17	35	969
	1930	111	577	243	411	318	2666
	1931	48	27	18	91	39	400
	1932	77	54	74	35	68	887
June	1929	13	9	13	8	12	220
	1930	84	16	74	<1	59	1296
	1931	6	4	<1	16	6	63
	1932	12	40	19	42	26	221
July	1929	6	<1	2	5	3	55
	1930	18	13	13	—	13	128
	1931	24	0	15	—	15	233
October	1931	—	<1	<1	<1	<1	<1

Abundance. The great irregularity of distribution just emphasized, for Limacina, shows the danger of generalization, as to the normally seasonal cycle of abundance, or as to the average volumes of this pteropod that may be expected in different months. As an extreme illustration of variation in abundance, at a given season, we may cite February, when Limacina averaged less than 1 c.c. (maximum, less than 2 c.c.) in any subdivision of our area in 1931, but when it averaged 138 c.c. for the area as a whole, in 1932, with a maximum catch at the rate of 1833 c.c. A rather definite progression does, however, appear in the fact that the volumes of Limacina for the area as a whole averaged definitely higher in May of three of the four years (1929, 1930, 1931) than either earlier in the season or later, this seasonal peak being most clearly outlined in 1930, when it averaged five or six times more abundant in May (318 c.c.) than in April (36 c.c.), on the one hand, or in June (59 c.c.) on the other (Fig. 17). Again, in 1931, the average May catch (39 c.c.) was more than 39 times that for February, six times that for June (6 c.c.) and more than twice that for July (15 c.c.). Rich (> 100 c.c.) catches have also been made most frequently in May (17% of the stations), much

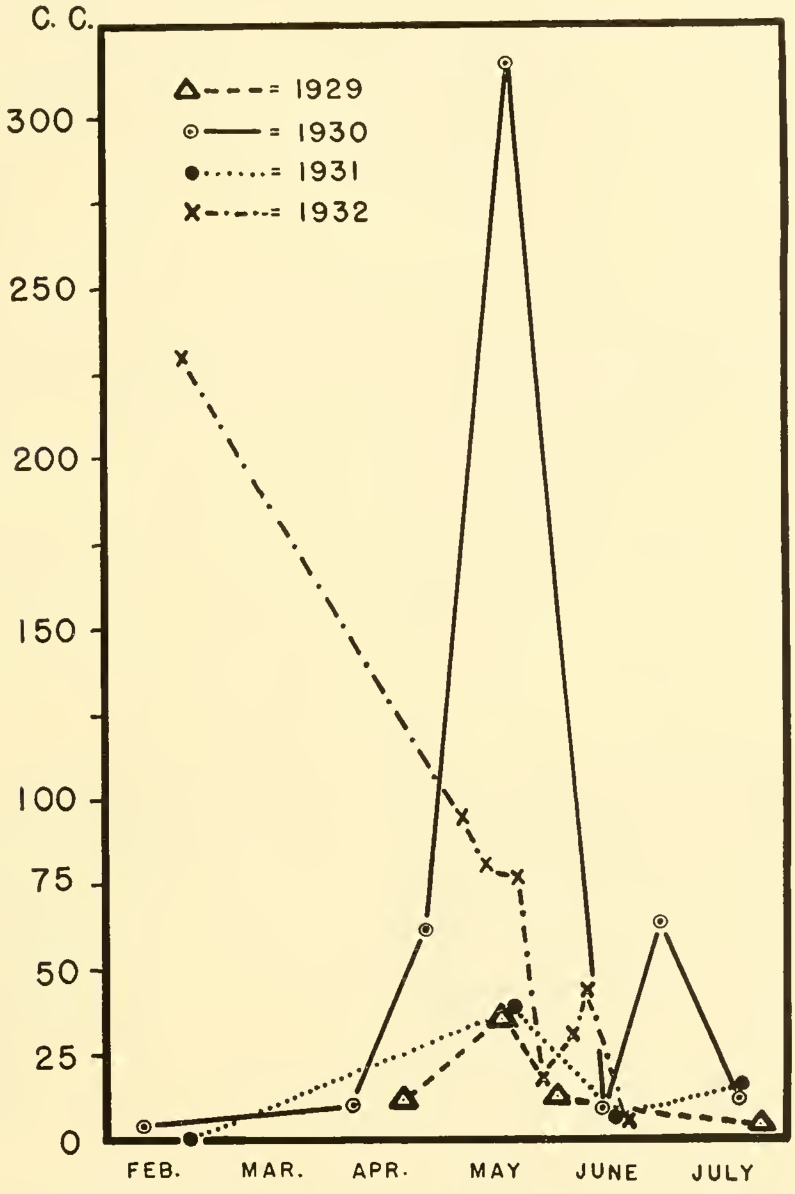


Fig. 17. Average monthly volumes of *Limacina retroversa*, in different years, for the area as a whole.

less so in February (6% of the stations), April (10%), June (6%), or July (3%), while mid- and late summer scarcity has also been recorded for 1913 and 1916 (Bigelow, 1915; 1922). But a different succession is illustrated by the data for 1932, when one very large catch (1833 c.c.) near Currituck was responsible for an average of 195 c.c. in the south, and of 138 c.c. for the area as a whole in February, but when the general average fell to 68 c.c. for May and to 26 c.c. for June.

Thus, it appears that it is usual for Limacina in our area to multiply after a normally cool winter to a pronounced vernal peak of abundance in May, then to decline as rapidly, through the summer, but that the peak may fall as early as February, after an abnormally warm winter, to be followed by progressive decrease through the spring and early summer. Present indications are that Limacina either disappears altogether for a time in early autumn, or at least continues decidedly scarce through that quarter of the year and presumably through the first two months of winter.

The volumes of Limacina have averaged about as large in one subdivision of the area as in another, for all cruises combined (average, north, 29 c.c.; south, 37 c.c.; inshore, 48 c.c. offshore, 39 c.c.). And moderately large catches have been so widespread (Fig. 18) at the season of maximum abundance (May) as to suggest that one part of the area is as likely to support a considerable population as any other. Successive cruises have, however, shown that it is characteristic for the richest centers of Limacina to be confined to small areas, and for these to shift position and extent much more rapidly from month to month than is usual with most of the other dominant members of the planktonic community.

This was illustrated in 1930 by the fact that a rich center existing near Martha's Vineyard early in April, expanded southwestward, along the mid-belt of the shelf, as far as the offing of Delaware Bay, during the next two weeks, a second rich zone having meantime developed, offshore and to the south of Chesapeake Bay, to coalesce with the more northerly center by May, followed by a contraction eastward of the resultant rich area through June (Fig. 18). Two rich centers again developed in 1931, between February and May, a larger offshore, a smaller inshore, the former to be dissipated by June, while the latter (though not encountered that month) may actually have persisted until July, when a rich catch was made at a neighboring locality. And the seasonal succession proved still more complex in 1932, when the four separate centers that were encountered during the first week of May had given place in the second and third weeks to three centers (Fig. 18), which then dispersed by the last of the month, to be replaced early in June by a fourth center, which in its turn had entirely dispersed two weeks later.

It would require a much more extensive series of observations to fit alterations as complicated and as seemingly sporadic as these into a regularly seasonal schedule, if indeed, any such applies in this case.

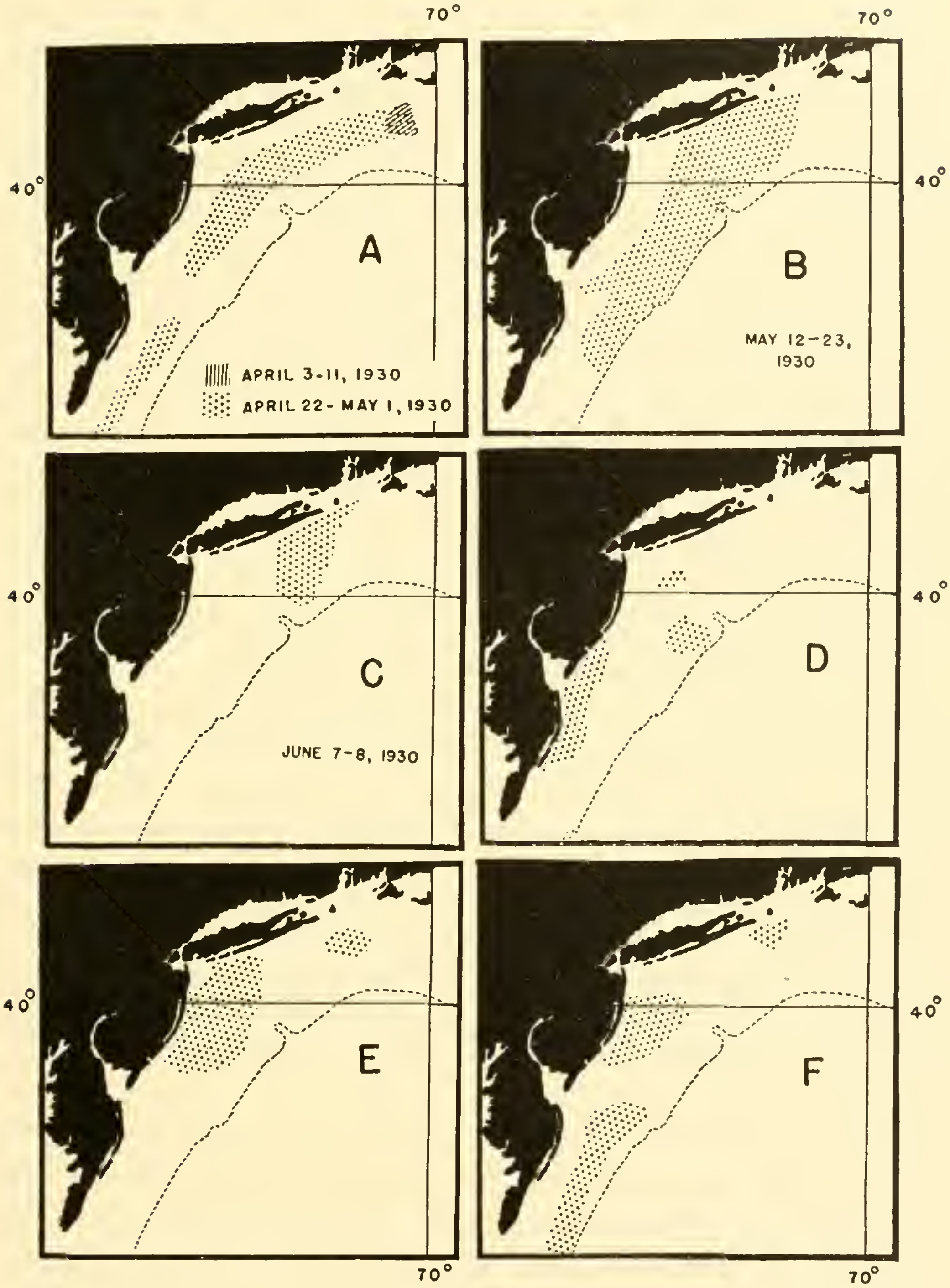


Fig. 18. Areas where the volume of *Limacina retroversa* averaged greater than 100 cc., per standard haul, in different months: A, April 3–11, 1930 and April 22–May 1, 1930; B, May 12–23, 1930; C, June 7–18, 1930; D, May 2–6, 1932; E, May 9–16, 1932: F, May 19–23, 1932.

Vertical distribution. Among the stations where tows were made at two levels, the shoal catch of Limacina was twice the larger of the pair slightly more often (55 cases) than the reverse (47 cases), though more frequently (97 cases), the two did not differ significantly, one from the other. The volumes also averaged slightly larger (average, 53.5 c.c., 200 cases), for hauls centering shoaler than 10 meters than for those centering deeper than 20 meters (average, 37.8 c.c., 201 cases).

Perhaps more significant is the fact that five of the seven catches greater than 400 c.c, that were made at pertinent stations, were from the shoaler, only two from the deeper haul, suggesting that centers for Limacina are more subject to transport by temporary wind-drifts than in the cases of species for which the centers of abundance lie deeper.

Relation to temperature. The data do not warrant any general comparison between average catch and the temperature of the water. It appears, however, that values higher than about 18° are not favorable for Limacina, for while the catch of the shoal hauls averaged about 27 c.c. in June and July as a whole, it averaged only about 5 c.c. (including one catch of 81 c.c.), at the group of stations where the upper 10 meters was warmer than 18°.

Annual variations. Average volumes for the period, February-June, were 5–6 times as great in the most productive years of the series (average, about 100 c.c. in 1930, and about 71 c.c. in 1932), as in the poorest (14 c.c., 1931). And it is not unlikely that a longer term might not have shown still wider variation, there being no warrant for assuming that any one of the four years illustrated an extreme state in either direction. *Limacina retroversa* is, in short, an extremely variable species, so far as prevailing abundance is concerned, not only from season to season, and from place to place, but also from year to year. And a similar variability is recorded for its frequency of occurrence, for while it was recorded at 83% of the stations in one of the years (1932), it was found at 51%, only, in another—1929.

Source of the local stock. Redfield's (1939) recent demonstration that the stock of Limacina in the Gulf of Maine draws—at least largely—on immigration from Nova Scotian shelf waters, and that the quantitative distribution within the Gulf is determined by the drifts undergone by the entering shoals and their offspring, opens the question to what degree this may also apply to the waters west of Cape Cod. Two lines of evidence are available, first, the presence or absence of very young stages, the implication of which is obvious, and second, the time intervals that intervened between the development of different centers of abundance, relative to their geographic locations, and to their distances apart.

The year 1930 is the member of the series in which a Gulf of Maine source might most plausibly be argued for an increase that took place between February and early April in the abundance of Limacina in the most easterly sector of our area, since the temperatures gave evidence of a coincident drift of cold water from the east, past Cape Cod (Bigelow, 1933, p. 30). But we cannot credit to this source the extension of the rich belt southward along the mid-zone of the shelf, past the offing of Chesapeake Bay, a distance of about 360 miles, (Fig. 18A), that took place between the first and third weeks of the month, unless we admit the prevalence, meantime, of a corresponding drift at the rate of at least 10 miles per day, which is forbidden, not only by navigational experience, but by the progress of vernal warming at the time (Bigelow, 1933, p. 30). And the development of rich centers, in the years, 1929, 1931, and 1932, centered chiefly in the mid-sector of our area, with little evidence of prevailing drift, whether north or south. It thus appears that if any mass immigration did take place into our area from the eastward in either year, this must have happened prior either to April (1929, 1930), or at least prior to May (1931, 1932), i.e., at a season when the stock of Limacina in the southwestern part of the Gulf of Maine and on George's Bank is low.

The evidence of the frequency of young stages among the population in April, 1930, also argues for a local source—or at least for sources not far distant, for rich centers that developed during that month, for such of the catches as were greater than 100 c.c. contained 57–86%, by number, of juveniles less than 0.6 mm. in diameter; they even contained 2–26% of specimens smaller than 0.3 mm., although the meshes of the nets used were large enough (about 0.5 mm.) to have allowed these to pass through. And rough examination has shown that considerable percentages of young specimens are also included in the rich catches for other years, which have not yet been examined in detail.

We have, in short, as good a reason for regarding Limacina as regularly and primarily endemic southward past Delaware Bay, and perhaps southward past Chesapeake Bay, as for so regarding any other member of the planktonic community.

Invasions of water past Cape Cod, would of course, add to the local population, if at a season when Limacina is abundant in the neighboring parts of the Gulf of Maine area—as would indeed, happen for any other member of the boreal assemblage. But there is no need to invoke such invasions to explain the continued presence of this pteropod within our area.

Other Molluscs

During July-August, 1913, the warm water pteropods, *Corolla calceola*, *Criseis acicula*, *C. conica*, and *C. virgula*, and the heteropod, *Firoloida desmarestia*, were taken at scattered localities on the shelf, inshore as well as offshore, from the Atlantic City profile southward: Corolla, in fact, in some abundance at one station, as described elsewhere (Bigelow, 1915, p. 302, Fig. 72). And warm water species of Limacina were again recognized at three stations, along this same sector, in the summer of 1916 (Bigelow, 1922, p. 155, Fig. 51). But our only record of this group during the period 1929–1932, was for odd specimens of tropical pteropods at one station off Bodie Island in February 1930, at one off Currituck in April of that same year, and at two on the New York profile in February 1932. These data show that it is an unusual event for members of this category to invade the shelf from offshore in numbers sufficient to be picked up in the tow nets. And the fact that they were most strongly represented in on the shelf in the summer of 1913 and again in 1916, but apparently not at all at that season in 1929, or in October 1931 (years in which the southern sector was surveyed in those months), is evidence that their temporary presence within our limits (resulting from transport by indrafts of water from the slope) is independent of precise conditions of temperature at the particular place and time where they may be encountered.

DECAPODS

Crab and hermit crab larvae

Crab or hermit crab larvae (not yet identified) were recorded at 1/3–1/5 of the stations for February, in each of the years of record, mostly over the outer half of the shelf, but indifferently from north to south, with a maximum catch of less than 1 c.c. They were slightly more general in April, when they were recorded at most of the stations in the southern sector in 1929, and scattered all along from south to north in 1930, in which year a catch of 82 c.c. near Delaware Bay on the 24th, showed that important contributions from this source, are to be expected locally, close inshore at this season (Fig. 19). And by May, crab larvae may be present in such abundance next the land as to yield catches as large as 200 c.c., as happened in 1932, though in other years (1931), their numbers may be insignificant in that month, even at inshore localities.

The catches made in successive cruises in May 1932 illustrate the wide fluctuations that may take place in their abundance within short intervals of time, for

Fig. 19. Locality records, all cruises combined: A, crab and hermit-crab larvae, volumes larger than 10 cc.; B, Crago, contour marking offshore boundary; C, euphausiid larvae, volumes larger than 25 cc; D, *Lucifer typus*, palinurid larvae and stomatopod larvae.

they practically disappeared from the whole area between the first and middle of the month, but soon reappeared in the southern sector in such abundance that catches up to 144–200 c.c. were made there during the third and fourth weeks, another center of abundance (maximum, 90 c.c.) having meantime developed near the northeastern boundary of the area. Wide variation has also been recorded from year to year in the order of change, from May through June, in the case of this heterogeneous category. The one extreme is illustrated by 1931, when they were recorded at 4 stations only in May, but had become general throughout the area by mid-June, the other extreme by 1929, when 100% frequency in May gave place to only about 50% frequency in June, while the other two years showed intermediate states, namely, a peopling of the coastal belt eastward from New York between mid-May and the first of June in 1929, contrasted with a decrease in frequency in the northern sector in 1932 from 100% of the stations in May, to only 37% in June. Until the several constituent species are studied in detail, it will be premature to postulate the order that exists in these fluctuations, beyond the two outstanding facts, (a) that crab larvae, on the whole, appeared in about twice as great frequency in June (67% of the stations), as in May (34% of the stations) for the term of years as a whole, and (b) that most of the June catches that were larger than 4 c.c., were made within 35 miles of the coast line.

The frequency of occurrence of crab larvae changed but little from June to July in 1929 or 1930. But in 1931, they had disappeared entirely by July from the northern sector, where they had been taken at 84% of the stations in the preceding month. The following tabulation also shows that they considerably decreased in volume from June to July in each of the years (1929, 1930) when they occurred in more than minimal amount in either of these months. The catches have also averaged so small in the offshore belt even at the peak season (average, 6 c.c., June 1931) as to show that the contribution made to the plankton above, by crabs living in depths greater than about 50 meters is usually negligible. And while experience in 1913 had already shown that larvae of the blue crab (Callinectes) may swarm, close in to the land near Chesapeake Bay in July (Bigelow, 1915, p. 271), we have no evidence that the product of this particular species ever adds appreciably to the plankton, for more than a few miles out from the land, though its breeding range extends northward at least to Woods Hole. No crab larvae were detected during October 1931 in the offshore belt, though they may have been present, in unknown number at the time, in the inshore belt, which was not visited during that cruise, nor have we any information for the months November-January.

The volume of crab larvae averaged about 10 times as large, for the area as a whole, in the most productive year (1931, 10 c.c.), as in the least productive (1930, 1 c.c.), in June—on the whole the peak month— while a maximum catch of 226 c.c. in 1932, contrasts with 68 c.c. in 1930.

Average volumes of crab and hermit crab larvae

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	<1	<1	<1	<1	<1	<1
	1931	0	<1	0	<1	<1	<1
	1932	<1	<1	<1	<1	<1	<1
April	1929	<1	<1	<1	<1	<1	7
	1930	3	<1	<1	4	2	82
May	1929	6	<1	2	6	4	31
	1930	5	1	4	3	3	36
	1931	1	0	1	0	<1	18
	1932	13	3	2	19	8	226
June	1929	7	1	7	3	5	87
	1930	3	<1	<1	7	1	68
	1931	12	6	11	8	10	70
	1932	4	1	3	2	2	38
July	1929	2	<1	<1	1	1	10
	1930	<1	0	<1	—	<1	<1
	1931				—		
October	1931	—					

Crago sp.

The records for Crago, in late stages of development—picked up no doubt when the nets were working closest to bottom—are sufficiently general (Fig. 19B) to show that a considerable population of this familiar benthonic genus of shrimp inhabits the inshore belt, as a whole, from the one boundary of our area to the other. But one only of the records was more than 40 miles out from the coast, the great majority lying within 30 miles of the latter. Thus, it appears that the offshore boundary to the regular occurrence of Crago lies not far from the 50-meter contour, depth rather than distance from land being in all probability the determining factor.

The capture of Crago at 35% of the inshore stations in February, and 27% in April, but only 10% in May, 6% in June, and 5% in July,[1] suggests that it rises (or is swept upward) from the sea floor in significant numbers, most commonly

[1] No hauls were made inshore in October.

in winter, when turbulent movements of the water are the most active, and that it does so less and less commonly, with the advance of spring and summer.

As a rule, odd specimens only were taken. Once, however, a volume of 35 c.c. of juveniles (13% of the total catch) was recorded (off New York, June 26, 1930), showing that on occasion the young stages, at any rate, of this genus may occur in the mid-depths in such abundance as to be an important item in the general planktonic community. And the fact that adults were so often picked up in our nets, suggests that—being of considerable size—they may be an important source of food for fish foraging near the bottom well out on the shelf, as has long been known to be true in shallow water near shore.

Palinurid larvae

The northern boundary to the normal range of the adult spiny lobster (*Panulirus argus*) along the American coast, lies some 120 miles south of the southern limits of our area. But it has long been known that the curious leaf-like "Phyllosome" larvae, probably of this parentage, often stray far to the northward with the general drift of the so-called Gulf Stream, as do many other tropical animals. Consequently, it would not be astonishing should odd specimens be carried here and there across the continental edge, in summer, when the surface waters are at their warmest. Actually, however, we have record of only one such incursion, namely, in July 1929, when the larvae were found in amounts varying from 1 c.c. to 9 c.c. at 6 out of the 9 stations that were occupied south of Delaware Bay (Fig. 19D), but when they seem entirely to have been confined to the southernmost sector.

Lucifer typus

The only decapod, apart from crab larvae, Crago, and palinurid larvae that has been detected in the catches, is *Lucifer typus*, a visitor from offshore. Lucifer was taken at two stations in February (1930, 1932), at one station in April (1930), three stations in June (1932), and five stations in July (1929), always in the southern sector as accords with its warm water origin (Fig. 19D). One catch of 23 c.c. was recorded in July 1929, one of 8 c.c. in that same month, and another of 8 c.c. in April, the other records being based on odd individuals only. There is nothing in this record to suggest that Lucifer is ever of volumetric importance within our area, even in the southernmost sector.

STOMATOPODS

Occasional stomatopod larvae were recorded in February (1 station), May (1 station), June (3 stations), and July (7 stations) at the localities shown on

Fig. 19D; also near the outer edge of the shelf, on the Winterquarter profile, in July, 1913 (Bigelow, 1915, p. 271).

EUPHAUSIIDS

Meganyctiphanes norvegica

Meganyctiphanes norvegica is an offshore and northern species in our area (Table, p. 292) as was to be expected. In February and April, its area of occur-

Fig. 20. Locality records, all cruises combined: A, *Nematoscelis megalops;* B, *Meganyctiphanes norvegica,* February-June; C, *Meganyctiphanes norvegica,* July and October; D, *Thysanoessa inermis.*

rence southward from the offing of Atlantic City has in fact been definitely confined to the outer part of the shelf (Fig. 20), while it was found only once inshore in May of either year. And though some slight dispersal, toward the land, seems to have taken place, in June in 1931 and 1932 it was wholly lacking inshore or in the south in June and July 1929, though present then at about 50% of the stations offshore, in the north.

In the northern sector offshore, it has averaged about as frequent in one month as in another, from February to June over the term of years. Its status there varies widely, however, in midsummer, from year to year, the one extreme being illustrated by 1929, 1930, and 1932, when it was about as frequent in July as in June, the other by 1913 and 1916, when it was not found at all in July-August inside the 200-meter contour. Neither is any correlation apparent between its presence or absence at this season, and the prevailing temperature, for one of the summers when it failed (1916), was notably cold in this part of the sea, the other (1913), warm. And the danger of confusing annual variations with seasonal makes us cautious in drawing from the tabulation of monthly averages the obvious inference that Meganyctiphanes tends to spread southward along the offshore belt, and inshore, in May and June, to vanish thence with the advance of summer.

Percent of stations at which Meganyctiphanes was taken, all years combined

Month	Offshore North	Offshore South	Inshore North	Inshore South
February	33%	0%	0%	0%
April	25	0	0	0
May	27	44	7	0
June	40	60	13	22
July	55	0	7	0
October	25	20	—	—

The records of capture of Meganyctiphanes in October of 1931 (Table, p. 293) suggest that in a year when it is widespread (at least in the northern sector) in summer, a scattering population may be expected to persist all along the offshore belt through the autumn.[1] But it appears that in years when it is absent in late summer, reestablishment is not to be expected during the subsequent autumn, and perhaps not until the following spring, for in 1916—a year of that type—it was not found at all in November whether inshore or offshore. It is unfortunate, in this connection, that no information is available as to the status

[1] No inshore data for that cruise.

of this euphausiid during the autumn of 1929, a year when it was widespread offshore in July.

The following tabulation suggests that it is characteristic (if not invariable) for Meganyctiphanes to increase somewhat in average abundance, and still more in maximum abundance, from a minimum in February and April, to a maximum in late spring or early summer, though perhaps never to an extent sufficient to make it of more than a very minor item in the general community of our area. In some years this vernal augmentation may culminate, as a more or less definite peak in June (1929, 1931), with a subsequent impoverishment by July. And it is possible that 1913 and 1916 represent the extreme in this direction, i.e., entire disappearance in summer, but our lack of information, earlier in the season, for either of these years leaves this an open question. In other years, e.g., 1930, Meganyctiphanes, while averaging somewhat less abundant in June than in May, may average about as abundant in July as in June, at least in the northern sector, or again, there may be no significant alteration in this respect between May and June (e.g., 1932).

In any case, the small volumes recorded for October 1931, combined with the fact that Meganyctiphanes was not taken at all in November 1916, suggest that this euphausiid may be expected to decrease in abundance through the autumn, or even to disappear entirely from our waters by that time, if it has not already done so earlier in the season.

Average and maximum volumes of Meganyctiphanes,
all cruises combined

	Offshore North		Offshore South		Inshore North		Inshore South	
Month	Average	Maximum	Average	Maximum	Average	Maximum	Average	Maximum
February	<1	<1	0	0	0	0	0	0
April	<1	<1	0	0	0	0	0	0
May	<1	18	1	39	<1	<1	<1	<1
June	5	89	1	16	<1	18	1	43
July	1	10	0	0	<1	5	0	0
October	1	1	1	1	—	—	—	—

Nematoscelis megalops

Records of the occurrence of *Nematoscelis megalops* on the continental shelf are interesting chiefly because this euphausiid may safely be regarded as an indicator of water from the continental slope. The fact that 48 of the 59 stations where it has been taken within our limits on one cruise or another have been more than 30 miles out from the land, and most of them near the continental edge (Fig. 20A), accords with its oceanic origin. And it occurred about as frequently offshore in the one sector as in the other (18% of the stations north, 25% south, all cruises combined).

Nematoscelis was taken at 20% of the stations on the outer half of the continental shelf in February, 15% in April, 15% in May, 23% in June, 6% in July, and 25% in October, suggesting some tendency toward temporary withdrawal in midsummer, corresponding to which it was not found at all inside the 200-meter contour in July-August of 1913 or of 1916, though it was recorded over the continental slope in both these summers. And seemingly it is more likely to stray inshore in June, than either earlier or later in the season, for the distribution of inshore records (1929–1932) was February, 0; April, 0; May, 1; June, 4; July, 1.

In the great majority of cases the catches of Nematoscelis in on the continental shelf have been smaller than 1 c.c., the only notable exceptions being the following:

February, 1930, average, offshore, 5–6 c.c., maximum, 34 c.c.,

April, 1929, average, offshore, 1–2 c.c., maximum, 23 c.c.,

May, 1932, 1 station, 60 c.c.

June, 1929, average offshore, 1 c.c., maximum, 13 c.c.,

June, 1932, average offshore, 2 c.c., maximum, 28 c.c.

Catches larger than 10 c.c. were made at two offshore stations in February, none in April, two in May, five in June, and none in July and October, a distribution suggesting that when scattered centers of moderate abundance do develop for this species, this is more apt to happen in summer or early autumn than in winter, spring, or late autumn. And the largest volumes of all (34 c.c., February 11, 1930; 60 c.c., May 9, 1932) were encountered in the southernmost sector off Bodie Island, and off Chesapeake Bay.

Nematoscelis—like most other planktonic species—varies considerably in its status in our waters from year to year, catches of 10 c.c. or larger having been made at two offshore stations in 1929, one in 1930, none in 1931, and six in 1932.

Thysanoessa inermis

Frequency. Discussion of the status of *Th. inermis* is hampered by the fact that in many cases, the catches of euphausiids were so damaged that it was not possible to carry identifications of the members of Thysanoessa farther than to their genus. The following estimate of the local abundance of *Th. inermis* must therefore be regarded as minimal—actually its importance was no doubt greater. Even allowing for this, it is, however, clear that adult *Th. inermis* occurs much less regularly in our area (detected at only 13% of the stations) than in the Gulf of Maine, where it has been recorded at about 50% of the stations where euphausiids were identified, summer and winter alike (Bigelow, 1926, p. 136). Nevertheless, the localities of record are so widespread (Fig. 20D) that *Th. inermis* is evidently to be expected anywhere within our area, at one time or another, south even past the offing of Chesapeake Bay.

Averages for different months indicate considerably greater frequency for July (33% of the stations) and October (25%) than for February (9%), April (4%), May (8%), or June (10%). But we must remind the reader that this applies only to the adults;—inclusion of the juveniles (which have not yet been identified) might result in quite a different seasonal picture. *Th. inermis* has also averaged more frequent in the north (15% of the stations) than in the south (5%), as was to be expected. In fact, it was recorded only twice south of Chesapeake Bay. And it also proved more frequent offshore (13% of the stations) than within 30 miles of the land (9% of the stations).

Abundance. The catches of adult *Th. inermis* have invariably been insignificant compared with those of the volumetrically more important species, the maximum being only 20 c.c. (Station, Shinnecock II, June 12, 1931), with 1.5 c.c. as the largest average for any one cruise (July 1930), while the species was not detected at all in the catches on two of the cruises (February 1932 and June 1929). This prevailing scarcity within our limits of adults of this species is an interesting contrast to the important rôle in the planktonic community that it often plays in higher latitudes, in both sides of the Atlantic.

Th. inermis was about 20 times as frequent in the richest year (1931, 40% of the stations), as in the poorest (1929, 2%). But the volumes have invariably been too small to warrant any statement as to annual variations in abundance.

Thysanoessa gregaria

Occasional adult specimens of *Th. gregaria* were taken in February 1932 at stations scattered from the northern boundary of the area to the southern (Fig. 21A). Other than this the recent record of the species in our area is confined to one station off New York in May, 1929, and a second off Block Island in February, 1931), both near the 200-meter line. These localities show a distinctly southern distribution, as was to be expected. And the numbers have, in every case been so small (invariably less than 1 c.c.) that it would evidently be exceptional for *Th.*

gregaria to form any appreciable proportion of the plankton, at least during the vernal half year.

Fig. 21. Locality records, all cruises combined: A, *Thysanoessa gregaria* and *Th. longicaudata;* B, Euphausia, Stylocheiron and Thysanopoda; C, Erythrops; D, *Neomysis americana.*

Thysanoessa longicaudata

The few records for this cold water species—3 for February and 3 for June of 1930, and one for February, 1932—have all been to the northward of Latitude 38° (Fig. 21A). The largest catch (Station, Cape May V, June 11, 1930) was at the rate of 7 c.c., all other records being based on odd individuals only.

Euphausiid larvae

Specific identification of the euphausiid larvae has not been attempted, but these have formed a sufficient proportion of the catches in some months (Table, p. 229) to justify some notes as to their frequency of occurrence and local abundance.

None were taken in February, though cruises were made in that month in three different years, hence we may conclude that there is no reproduction in significant amount by any of the local species of this group, in late winter. But the frequent occurrence, in April, May, June, and July, of juveniles large enough to be caught in our nets shows that one euphausiid or another may be breeding within our limits from early spring until midsummer. The monthly succession does not suggest any definitely seasonal gradient in the frequency of occurrence for larval euphausiids between April and July, other than the irregularities (regional and secular) that are to be expected in the distribution of a mixed plankton population, but they were found at one station only in October.

On different occasions, these larvae have been most generally distributed inshore, offshore, in the north, and in the south. But they have averaged considerably more frequent offshore than inshore in each month, April-July, for the several years combined, also more frequent in the north than in the south, in April, May, June, and October, for all years combined, suggesting that production in the spring and autumn is chiefly by boreal species, probably *Th. inermis* and Meganyctiphanes in combination. In July, however, of the one year when the midsummer survey covered the entire area, they were most frequent in the south.

Percentage of stations at which euphausiid larvae were taken

Year	April	May	June	July
1929	31%	40%	30%	56%
1930	53	7	15	12
1931	—	40	27	5
1932	—	54	62	—

Percentages of stations with euphausiid larvae, in the different subdivisions, all years combined

Month	Inshore	Offshore	North	South
April	24%	64%	54%	35%
May	30	62	54	25
June	33	43	42	22
July	30	30	30	66

In the years 1930 and 1931, the catches of euphausiid larvae averaged less than 1 c.c. for the area as a whole on 11 out of the 12 cruises, and only 5 c.c. (with a maximum of 60 c.c.) on the twelfth (April 22-May 1, 1930), stocks so small that they did not contribute significantly to the general volume of plankton for that pair of years. They were, however, considerably more abundant both absolutely and relatively in the other two years of the series, with average and maximum catches of 3 c.c. and 47 c.c. in April, 8 c.c. and 169 c.c. in May, 2 c.c. and 27 c.c. in June, and 6 c.c. and 118 c.c. in July, in 1929; also 8–10 c.c. and 121 c.c. in May and June, 1930. These values combined with the absence of euphausiid larvae in February and their great scarcity in the one October of record is evidence that in their years of abundance, production takes place chiefly from May into July.

The volumes of euphausiid larvae have also averaged 14 times as great offshore (average, 14 c.c.) as inshore (average, 1 c.c.), and somewhat greater in the north (8 c.c.) than in the south (about 5 c.c.), in the 8 surveys[1] (combined) for which the average was greater than 1 c.c., in either subdivision: evidence that the production of euphausiids in our area is centered chiefly along the outer belt of the shelf. And a similar segregation appears in the distribution of catches richer than 25 c.c. (Fig. 19C).

Other euphausiids

Odd specimens of Euphausia, Stylocheiron, and Thysanopoda (strays from offshore) were taken along the outer half of the shelf at the localities shown on Fig. 21B, but never in as large an amount as 1 c.c.

MYSIDS

A considerable proportion of the hauls yielded a scattering of adults of two species of mysids, *Neomysis americana* and *Erythrops erythrophthalma*. The captures of the former (Fig. 21D)—occasional specimens only—show that it is rather closely confined to the inshore belt, as was to be expected, since it is common in seaweed and swimming free in the water alongshore. And the fact that it was recorded both in the extreme south and in the extreme north of our area accords with its known distribution, coastwise, for it is plentiful near Woods Hole, on the one hand (Sumner, Osborne, and Cole, 1913), and in Chesapeake Bay, on the other (Cowles, 1930). The fact that the monthly percentage of stations in the inshore belt, where Neomysis was taken, varied only between 5% and 6% from February to July, shows it as continuing about equally frequent from late winter

[1] April, May, June, July, 1929; April, June, 1930; May, June, 1932.

through summer. In Chesapeake Bay, however, Cowles found it most plentiful in December and January. And this may be equally the case along the open coast, where we have no information for early or mid-winter.

In the case of Erythrops, the stations of record are generally distributed over the inner and mid-belts of the shelf; all but two, however, of the 41, are in the northern sector, with evident concentration toward the northeast (Fig. 21C). In fact, the discovery of this northern species, at all, to the west of Cape Cod, considerably extends its known range in that direction, for it had not previously been recorded south of Massachusetts Bay, on the North American coast, though long known to be widespread along the coasts of Europe, southward to the Irish Sea (Zimmer, 1909). And the fact that it was much more frequent in the northern sector in February and April (32% and 20% of the stations, respectively) than in May (8%), June (6%), July (8%), or in October when it was not taken at all, is evidence that its presence within our limits depends chiefly, if not wholly on immigration. The largest catch of Erythrops was 4 c.c., near Shinnecock on June 8, 1930.

AMPHIPODS

Euthemisto compressa

Until comparatively recently, it was generally accepted that the two named representatives of Euthemisto, that have long been known to abound off the northeastern coasts of the United States, *compressa* Goes, and *bispinosa* Boeck, were well defined species. Stephensen (1924, p. 103) has, however, shown from examination of extensive series from different parts of the Atlantic and Mediterranean that while typical specimens of the two are easily separable, intermediates occur so often that he has definitely classed them as "formae" of the one species *compressa*.

Frequency. The genus Euthemisto (treated here as a unit) rivals *Calanus finmarchicus* in frequency of occurrence, for it was taken at every station on eight of the cruises, and at 38% of the stations on all cruises combined, though it may be only irregularly represented on occasion, as in May and June 1929 (38% and 27% of the stations respectively). No preponderance is indicated either north or south, but slightly greater frequency is probably characteristic for it offshore (92%) than inshore (77%), which accords with what is known of its occurrence in the Gulf of Maine (Bigelow, 1926) and with previous records for the genus in the region now under consideration (Bigelow, 1915; 1922).

Relative monthly percentages perhaps warrant the generalization that Euthemisto tends in most years to be slightly less frequent in early or mid-summer, than in late winter or spring, it being especially suggestive that an alteration of this sort took place in 1930, for Euthemisto was universal in that year up to June. And sharper fluctuations may occur in other years, as illustrated by 1929, when the frequency decreased progressively by more than ½ from April through June, but then rose again by July to a level higher than had existed in April.

Abundance. With Euthemisto so nearly universal, throughout the area in most years, it is interesting to find the catches averaging only about 30 c.c., at most, in any month (May 1930), while the average for the whole area (all cruises combined) was only about 11 c.c. for the years 1930–1932, and 2.5 c.c. for 1929. Among 509 recorded catches of Euthemisto, only 26 were larger than 40 c.c., with a maximum of 320 c.c. at a station on the inner part of the shelf off Atlantic City, June 27, 1930.

The seasonal gradient in abundance has varied too widely from year to year for generalization as to the normal cycle, except that the catches averaged very small in February and in April, in each year. In two of the years (1931, 1932), the catches of Euthemisto continued to average small, right through the season in spite of an occasional rich catch, e.g., 63 c.c. at Station 21415, May 25, 1932. Considerable augmentation was, however, recorded in the other two years, culminating in June or July, as appears from the following tabulation:

Average volumes of Euthemisto

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	2	1	1	1	2	9
	1931	3	3	1	5	3	17
	1932	6	8	7	6	7	40
April	1929	<1	<1	<1	<1	<1	2
	1930	7	5	6	8	7	50
May	1929	<1	<1	<1	<1	<1	5
	1930	23	33	24	23	27	106
	1931	<1	<1	<1	<1	<1	<1
	1932	<1	<1	<1	<1	<1	63
June	1929	6	1	1	1	3	84
	1930	36	9	22	41	25	320
	1930	2	<1	<1	3	1	48
	1932	<1	6	<1	7	3	47
July	1929	4	2	2	5	3	19
	1930	37	3	27	—	27	94
	1931	1	4	1	—	1	27
October	1931	—	1	<1	3	1	15

Regional volumes also show that Euthemisto may average most abundant either inshore or offshore, or be about as abundant in the one belt as in the other, at any given time. But the inshore belt has most frequently been the more productive of the two on occasions when any significant inshore-offshore gradient has

Fig. 22. Locality records, all cruises combined: A, large volumes of *Euthemisto compressa;* B, Phronima; C, *Acartia longiremis,* inshore and offshore; D, *Anomalocera pattersoni* and Labidocera.

existed, resulting in a general average about twice as great there as offshore (Table, p. 300). And the few catches larger than 100 c.c., as well as the majority of those larger than 40 c.c. have all been within 45 miles of land (Fig. 22A), which contrasts sharply with conditions eastward from Cape Cod (Bigelow, 1926, p. 157, Fig. 55).

Euthemisto has averaged about equally abundant south as north, February-May, but considerably more so south than north, in June, on the three occasions when any significant gradient existed in this respect (Table, p. 300). But we have some evidence that the center of population tends to shift northward, as summer advances, in the fact that relatively large catches were recorded only in the most easterly sector of the area in July-August of 1913, and northward from the Cape May profile in the latter month of 1916 (Bigelow, 1915; 1922). A shift in this direction would, indeed, be the natural expectation for a boreal species, with the seasonal warming of the waters.

Conditions in October 1931 when Euthemisto averaged 3 c.c. in the southern sector, but less than 1 c.c. in the northern—if characteristic—suggest that the center of population again shifts southward, early in the autumn. And this is corroborated by the fact that rich catches were made near Delaware Bay and off Chesapeake Bay in November 1916 (Bigelow, 1922).

Annual variations. Little annual difference in the average volumes of Euthemisto has been recorded for February, April, or May. But in June and July, the catches averaged about 27 times as great in the richest year (1930, average, 27 c.c.) as in the poorest (1931, average, 1 c.c.), evidence that while the status of this species at the end of the winter and late spring is comparatively constant from year to year, very wide differences in this respect may develop in summer, even within a short series of years.

Other amphipods

Other than Euthemisto, and specimens of one gammarid or another picked up when the tows were made close to the bottom, the only amphipods detected in the catches were Phronima and Hyperia. The former has been recorded rather frequently offshore in the north, rather less so offshore in the south, and once close inshore off New York (Fig. 22B). The fact that Phronima was recorded at 2–5% of the stations from February to June, but at 15% in July and 13% in October suggests that this visitor from offshore is to be expected in on the shelf more often in midsummer and autumn than earlier in the year. The maximum catch (13 c.c.) was also made in July, all other records being based on occasional specimens only.

Hyperia was recorded at two stations—one in April 1930 off Currituck at the continental edge, the other at a similar locality off Atlantic City in June 1931.

COPEPODS

Acartia

In the Gulf of Maine, where *A. longiremis* is endemic and widespread, though never very abundant, it appears to be confined to the shoaler waters (including the offshore banks as well as the coastal zone) during the cold half of the year, to disperse out over the deep basin in spring, summer, or autumn, when its numbers increase (Bigelow, 1926, p. 180). And its distributional status is essentially the same to the west and south of Cape Cod, for while it is abundant in Chesapeake Bay throughout the year—most so, in fact, in March—(Wilson, 1932a, p. 20), we have only two records of it out on the shelf in February and one in April, whereas in May, June, and July, it was found about as frequently offshore (7% of the stations) as inshore (9%), for the several years combined (Fig. 22C), and at 20% of the offshore stations during the only October of record.

The records of occurrence do not suggest any regularly latitudinal gradient during the season of its offshore dispersal, between the offings of Martha's Vineyard and of Delaware Bay. But it was taken at one station, only, south of the Winterquarter profile, a failure in the extreme south that is difficult to explain in the face of its constant and abundant occurrence in Chesapeake Bay at the same times of year.

Within Chesapeake Bay and probably in other similar situations along our mid-Atlantic coast, *A. longiremis* ranks second only in abundance to *A. clausii* among the copepod fauna (Wilson, 1932a). Out over the continental shelf, however, our maximum catch was at the rate of but 16 c.c., while 11 only out of the 60 odd catches were as voluminous as 5 c.c. However, the fact that about 1/3 of the catches were 1 c.c. or larger, shows that a sufficient population of it exists (and widespread) in the shelf waters for local concentrations to be expected (though not actually encountered as yet) should a happy combination of circumstances favor its reproduction.

A. clausii is described by Wilson (1932a) as the chief copepod constituent of the plankton in Chesapeake Bay. We have but one record of it, however, out on the shelf, evidence that it is far more strictly neritic within our limits than in the Gulf of Maine, where it is widespread, inshore and offshore alike, and may constitute even up to 30–50% of the copepods by number locally, in the coastwise belt, at the season when it is most plentiful (Bigelow, 1926, Fig. 59).

A. tonsa—probably an indicator of coast water—swarmed at three stations near the mouth of Delaware Bay, in August 1916; otherwise, we have no record of it within our limits, nor did Wilson (1932a) report it from Chesapeake Bay, though it is a dominant species inshore, and in brackish situations near Woods Hole in summer (Fish, 1925; Sharpe, 1910; Sumner, Osborne, and Cole, 1913).

Anomalocera pattersoni

The "blue copepod," widespread, though never very abundant, in the Gulf of Maine (Bigelow, 1926, Fig. 63) had already been reported in summer at various localities along the continental shelf to the offing of Chesapeake Bay, inshore and offshore alike (Bigelow, 1915, Fig. 69). And the records for the period 1929–1932 corroborate this distributional picture, being generally distributed across the shelf, from the northern boundary of our area to the southern (Fig. 22D). It seems, however, that Anomalocera is considerably less frequent—though so widespread—to the west and south of Cape Cod than it is over George's Bank and in the Gulf of Maine, for it was detected at about 4% only of the stations for the series as a whole. And being so conspicuous an object, even after its beautiful blue color has faded in the preservative, it is not likely that any of its adults were overlooked.

It is questionable, with so few data, whether the monthly distribution of catches (2% of the stations for February, 7% for April, 4–5% for May and June, and 12% for July) indicates any regularly seasonal cycle between late winter and midsummer. But failure to take it at all during the one October cruise may perhaps reflect autumnal impoverishment.

We have no reason to suppose that Anomalocera is ever of volumetric importance in the waters under study, except on rare occasions, for while one catch was at the rate of 32 c.c. (near Cape May, June 1930), most of the other records for it were based on occasional specimens only.

Calanus finmarchicus

Frequency. In February, when (by present indications) Calanus is close to its lowest ebb for the year, it occurred generally throughout the area southward to Latitude 36°, both in 1930 and in 1931; southward, in fact, beyond Cape Hatteras in the latter year. But it was recorded at 38% only, of the stations inshore, in the southern sector, in the abnormally warm February of 1932, though it was universal then in the north, and almost equally so along the offshore belt in the south (90% of the stations).

If the data for April, of 1929 and of 1930, be representative of the normal mid-spring state, it appears (as might be expected) that Calanus tends by that month to populate any restricted areas where it may have been absent at the end of the winter. And it has either proved universal (100% of the stations), throughout the area as a whole from April or May through June, as was the case in 1930 and 1931, or has at most been lacking at scattered stations, here and there, as in 1929 and 1932:

Percentage of stations with Calanus, for the area as a whole

Month	1929	1930	1931	1932
February	—	77%	100%	56%
April	100%	95	—	—
May	100	100	100	95
June	91	100	100	97
July	91	100	100	—

Calanus has proved equally universal every year in July, in the sector eastward from the offing of New York. But wide differences in this respect are evidently to be expected from year to year in the southern sector, at that season, for while it was universal there also, in the summers of 1916[1] and of 1929, record of it south of New York in July 1913 was confined to a few scattered stations. Clarke and Zinn (1937) found it regularly through August and September near Martha's Vineyard. And it continues universal over our area as a whole through the autumn (at least in the years when it is widespread and abundant in summer) for it was recorded at 12 out of 13 stations along the offshore belt, north and south, in October 1931, and at every station in November 1916. Conditions in February (p. 304) suggest that at least a sparse population of Calanus persists throughout the area as a whole, over the winter in most years, as is certainly the case near Martha's Vineyard in the northeast (Clarke and Zinn, 1937). But our records do not show how early, in autumn, Calanus may repopulate the southern sector, after a summer when it is scarce or absent there, nor at what season it becomes scarce there, in a year (e.g., 1932) when winter cooling does not proceed to the usual extreme.

Abundance. Clarke and Zinn (1937) report Calanus as at its minimum, near Martha's Vineyard, during the autumn and winter, and this applies over our area as a whole, with an average volume of only about 14 c.c. for February 1930, 1931, and 1932 combined (Table, p. 309).

The most interesting event in the seasonal cycle of this copepod is that it

[1] Reexamination of samples, from the July-August cruise of 1916 has revealed the presence of at least a few Calanus at every station.

greatly increases in abundance at some time during the spring. Unfortunately, data for March are confined to the immediate vicinity of Martha's Vineyard (Clarke and Zinn, 1937), where Calanus was still as scarce in that month as in February. But the catches (for the area as a whole) averaged 18 times as great in April as in the preceding February in the one year (1930), when surveys were made in both these months, and 29 times, 9 times, and 10 times as great in May as in February of 1930, of 1931, and of 1932, respectively (Table, p. 309). Average volumes for successive months suggest that following this vernal augmentation, Calanus in the north may either decrease after April, as in 1929, or may continue at a roughly constant level of abundance through May, June, and July, as in 1930 and 1931[1] After an unusually tardy spring—as in 1916—Calanus may, in fact, continue in great abundance through August (Bigelow, 1922), even in the southern sector. But in other years, illustrated by 1929, Calanus markedly decreases in the south, through late spring and early summer; or in a warm summer—by the evidence of 1913—it may practically disappear thence by July. We should, however, caution the reader that description of the seasonal trend in terms as general as the foregoing applies only if regional and short term irregularities be smoothed out by the process of averaging, and that some such succession of peaks and valleys, as appears in Clarke and Zinn's (1937, Fig. 4) graph of seasonal abundance near Martha's Vineyard, would more correctly picture the conditions to be expected at any given station.

Data for early autumn are confined to the vicinity of Martha's Vineyard, where Clarke and Zinn (1937) record a sharp decline in the abundance of Calanus from July through August, with only trifling numbers in September, or later in the autumn. And this probably applies over our area generally, judging from the facts that average and maximum values had fallen, by October, about back to those existing in the preceding February, in the one year (1931), when surveys were made in both these months, and that Calanus also greatly decreased in abundance between July-August and November in 1916 (Bigelow, 1922). But the data fail to show whether it is characteristic for this autumnal impoverishment to follow after the spring or summer as abruptly, in other parts of our area, as it does in the extreme northeast, as illustrated by Clarke and Zinn's station, nor is any information available for December or January, elsewhere within our limits.

No rich centers for this species yet exist in February, nor do the average

[1] July data for 1930 and 1931 were limited to the northern sector.

volumes (Table, p. 309) suggest any definite gradient, either north-south, or inshore-offshore, as generally characteristic at this time of year, at least down to Latitude, about 36° N., south of which Calanus was negligible quantitatively in the one year of record (1931). In normal years, the vernal augmentation of Calanus is, however, accompanied by a localization of the chief centers of abundance within the sector bounded by the Montauk and Cape May profiles —such, at least, was the case in 1929, and again in 1930 (Fig. 23). And while the data for April do not indicate any more likelihood of greatest abundance in any one locality than in another within these boundaries, the center of abundance yearly becomes still more definitely concentrated by May within the area outlined in Fig. 23A. This alteration involves, on the one hand, a contraction seaward of the inshore margin of the productive area in the south, and on the other hand, its expansion eastward, at least as far as the Martha's Vineyard profile.

In normal summers (e.g., 1929, 1930, 1931), the situation in this respect, is much the same in June, and in July as it is in May. But after a cold and tardy spring (e.g., 1916), rich concentrations of Calanus may also persist along the outer belt of the shelf as far south as the offing of Chesapeake Bay, until well into August. Hence, (presumably) in a year of this type, vernal augmentation on a large scale, is not as definitely centered in the northern sector, as usual. Even in 1916, however, the largest catches of all[1] were to the northward of the Cape May profile, while catches of more than 800 c.c. for May, June, and July of all years combined (Fig. 23), have been so definitely concentrated, offshore, in the sector north and east of the Atlantic City profile, that this may well be named the "Calanus" belt. Here, the average volume for these months has been 252 c.c. (65 c.c., in 1932; 339 c.c. in 1929–1931), the maximum 1556 c.c., the minimum 0 c.c.

In the easternmost sector, east of Longitude about 73° W., the area of abundance may or may not reach shoreward within 5–10 miles of the coast, in late spring or summer. But the facts that our largest catch at any one of the three June-July stations near Block Island was only 583 c.c., with 10–33 c.c. at the other two, and that the maximum reported near Martha's Vineyard by Clarke and Zinn (1937) corresponds to less than 90 c.c. when reduced to our present standard, makes it unlikely that dense aggregations of Calanus ever occur close in to this part of the shore line, even at the season of peak abundance. And this

[1] Bigelow, 1922, 3000 c.c. or more per haul.

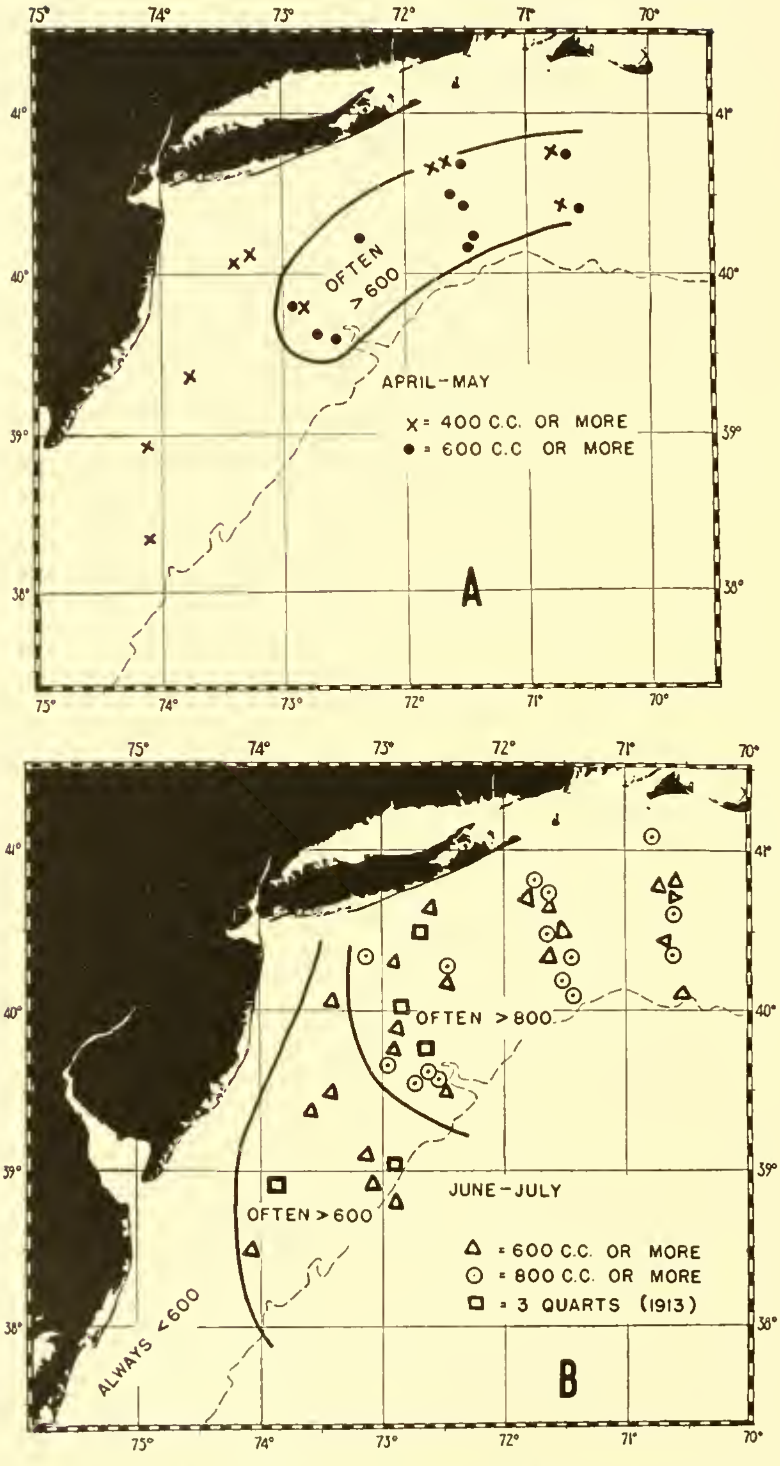


Fig. 23. Locality records for large volumes of *Calanus finmarchicus*, all cruises combined: A, April and May; B, June and July.

inshore belt of summer scarcity, some 20 miles wide off New York, expands seaward toward the south in normal years until it includes the entire breadth of the shelf off Winterquarter, as outlined in Fig. 23B. Neither have large volumes ever been recorded farther seaward than the 200-meter contour.

Data as to chief centers of abundance are lacking for September. But the situations existing in October 1931 and in November 1916 (Bigelow, 1922), make it unlikely that any areas, describable as "rich" by spring or autumn standards, characteristically exist anywhere westward or southward from the offing of Martha's Vineyard in normal years, at any time from late summer, through autumn or winter.

Average volumes of *Calanus finmarchicus*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum	Minimum
February	1930	9	5	11	3	7	24	0
	1931	29	30	6	32	29	117	<1
	1932	7	1	7	4	5	43	0
April	1929	115	256	228	128	173	1532	<1
	1930	129	119	172	71	121	852	0
May	1929	51	152	136	35	91	435	<1
	1930	163	260	259	138	206	1063	<1
	1931	117	429	309	105	251	1514	<1
	1932	22	106	60	33	50	407	0
June	1929	44	135	109	29	81	411	0
	1930	176	228	240	40	197	694	<1
	1931	301	578	497	237	406	950	<1
	1932	19	79	42	48	42	228	0
July	1929	81	68	99	18	75	377	0
	1930	281	236	254	—	254	856	<1
	1931	402	589	473	—	473	1274	<1
October	1931	—	17	18	15	17	62	0

Average volumes of *C. finmarchicus*, all years combined

Month	North	South	Inshore	Offshore
February	8	13	15	12
April	196	99	109	189
May	191	78	88	234
June	222	93	134	255
July	255	18[1]	298	275
October[2]	18	15	—	17

[1] 1929 only. [2] 1931 only.

Breeding periods. It seems reasonably established, from the brevity of the annual period of abundance, that there is only one major breeding period for Calanus in the waters southward from the New York profile. Clarke and Zinn's (1937) analysis of relative percentages of different stages pointed, however, to two shorter-lived generations during the spring, followed by a longer lived one in summer in the northeastern sector of our area. The offshore catches throw no light on this point, for the younger stages were not adequately sampled.

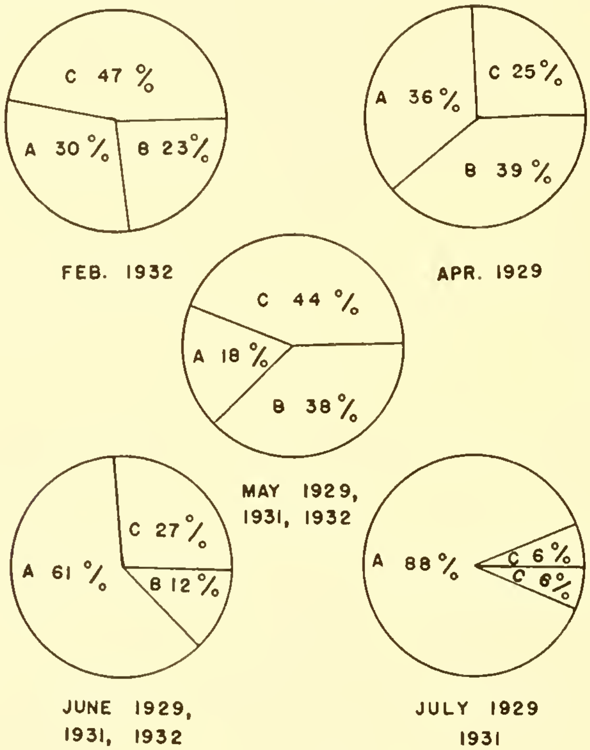


Fig. 24. *Calanus finmarchicus*: percentage of cases, in different months, where the deep catch was twice as large was the shoal (A); the shoal catch twice as large as the deep (B); and neither catch twice as large as the other (C).

But whether separate generations can be distinguished or not, the volumetric succession from month to month is sufficient evidence that effective reproduction is confined to spring and early summer, north as well as south.

Vertical distribution. In February (1932), April (1929), and May (1929, 1931, 1932) combined, the shoal catch was about as large as the deep (ratio, less than 1 to 2) at about one-fourth to one-half the stations where hauls were made at two or more levels, and significantly the larger as often as the reverse among the remaining cases (Fig. 24). The deeper catch was, however, at least twice the more voluminous in about 61% of the cases in June, and in about 88% in July, with only about 6% of the cases failing to show definite stratification of the one order or the other in the latter month (Fig. 24). The volumes of Calanus for all pertinent stations combined also averaged about 2–6 times as great at 20–40 meters as at 10–0 meters in February, April, and May, more than 25 times as large in June and about 400 times as large in July, as follows:

Average volumes of *C. finmarchicus* at deeper levels relative to those at 10–0 meters

Month	Year	20–40 Meters	No. of Cases	More than 40 Meters	No. of Cases
February	1932	2.6	11	1.3	7
April	1929	5.8	8[1]	2.3	12
May	1929 1931 1932	4.4	92	0.8	18
June	1929 1931 1932	23.5	80	8.2	14
July	1929 1931	399.2	28	105.8	13

[1] Omitting one case, where the deep catch was 135 times as great as the shoal.

And the vertical distribution of rich (> 300 c.c.) catches has shown a corresponding transition from June to July:

Frequency of large volumes (> 300 c.c.) at deeper levels relative to the upper 10 meters

	20–40 M.	<40 M.
February, 1932	—	—
April, 1929	1.8 to 1	0.8 to 1
May 1929, 1931, 1932	1.8 to 1	1.4 to 1
June 1929, 1931, 1932	6.2 to 1	4.3 to 1
July 1929, 1931	29.0 to 1	12.5 to 1

These depth relationships may be summarized as follows: In late winter and through the spring, the richest population of Calanus is close to the surface about as often as in mid-depths, but the stock averages somewhat more voluminous in the 20–40 meter stratum, than in the superficial 10 meters of water, even at this season. Rather an abrupt transition then takes place between May and June, to the summer state, in which Calanus is definitely concentrated at depths of 20 meters or more, and this vertical gradient is greatly accentuated from June to July. But it is not until the latter month that the stock living deeper than about 40 meters shows any great increase in abundance relative to that near the surface.

Diurnal migration. Successive hauls, day and night, were made at one station only, near Fire Island on May 17, 1929. And it is questionable how these should be interpreted, as regards Calanus—for while a disappearance of Calanus

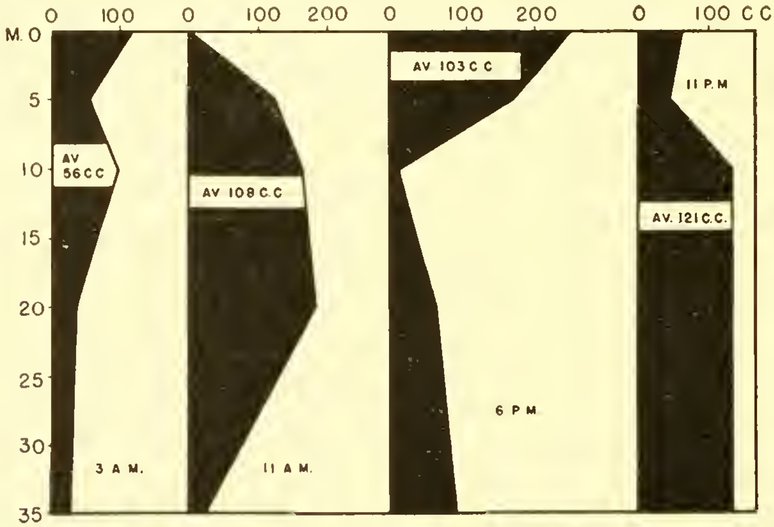


Fig. 25. Vertical distribution of Calanus, near Fire Island, May 17, 1929, at 3:00 a.m., 11:00 a.m., 6:00 p.m. and 11:00 p.m.

from the immediate surface, during the interval between 3 A.M. and 11 A.M., followed by reappearance in abundance there between 11 A.M. and 6 P.M. is compatible with diurnal migration, obviously this can not explain the subsequent decrease in the ratio of surface catch to deep catch between 6 P.M. and 11 P.M., nor the progressive increase in the average abundance of this copepod for the water column as a whole that took place during the period over which the observations were extended (Fig. 25). We are, therefore, forced to turn to a comparison of deep catches with shoal, from station to station, for information as to the extent to which diurnal migration affects the mass distribution of Calanus. Such a comparison shows that the deeper catch was significantly the larger of the pair about 1.3 times as often by day as by night as tabulated below, but that the shoaler was the larger about 1.4 times as often by night as by day, for the months February-June, as a whole. And while a contrast of the reverse order prevailed in July, the number of night hauls for that month was so small (12) that it may not be significant.

Percentage of cases in which the shoal catch was twice as great as the deep (A), the deep catch twice as great as the shoal (B), and neither one twice as great as the other (C), by day and by night.

	Day				Night			
	A	B	C	Cases	A	B	C	Cases
February, 1932	17%	17%	67%	6%	20%	30%	50%	10%
April, 1929	18	45	36	11	25	17	58	12
Average — February-April	17	31	52	17	23	24	54	22
May, 1929, 1931, 1932	26	37	37	38	38	21	40	47
June 1929, 1931, 1932	8	70	23	40	10	61	29	49
July 1929, 1931	10	80	10	20	8	92	0	12

The volumetric ratio of deep catch to shoal, similarly, averaged about 5 times as great by day as by night for February, April, and May combined, about 1.5 times as great by day as by night for June, and about 2.2 times as great by day as by night for July, details for individual cruises being as follows:

Volumetric ratio, deep catch to shoal

	8 A.M.–4 P.M.		8 P.M.–4 A.M.	
	Ratio, all Stas.	Cases	Ratio, all Stas.	Cases
February, 1932	3.3 to 1	6	10.0 to 1	10
April, 1929	30.4 to 1	11	1.0 to 1	13
May, 1929	14.5 to 1	11	0.9 to 1	13
May, 1931	20.7 to 1	9	0.6 to 1	7
May, 1932	4.5 to 1	17	2.0 to 1	27
June, 1929	2.4 to 1	14	7.0 to 1	16
June, 1931	35.7 to 1	12	8.8 to 1	11
June, 1932	35.0 to 1	14	34.0 to 1	22
July, 1929	159.0 to 1	16	75.7 to 1	7
July, 1931	311.9 to 1	4	136.2 to 1	5

If we omit from the calculation the one station for each cruise where the ratio of deep volume to shoal was largest, thus minimizing the effects of occasional cases of very strong stratification, we find this ratio averaging 2–4 times as great by day as by night, and with no outstanding alteration in this respect between spring and summer, as follows:

Volumetric ratio, deep catch to shoal

	8 A.M.–4 P.M.		8 P.M.–4 A.M.	
	Ratio	Cases	Ratio	Cases
February 1932, April 1929, May 1929, 1932, 1932	3.8 to 1	50	0.9 to 1	65
June 1929, 1931, 1932	11.7 to 1	37	6.0 to 1	46
July 1929, 1931	124.1 to 1	18	35.5 to 1	10

A prevailing tendency toward diurnal migration on the part of adult Calanus, upward toward (or even to) the surface during the hours of darkness, and downward again by day, and on a scale sufficient to cause widespread alterations of similar order in the vertical distribution of the stock seems the only plausible explanation for the relationship just brought out. And it is especially interesting to find the evidence of this hardly less clear for July, when the temperature of the upper 10 meters has risen above the optimum for Calanus, than it is for June or for May, when the entire water column is of a temperature suitable for this copepod.

It is equally clear, however, that the effects on the distribution of Calanus of this tendency toward vertical migration varies widely from time to time and from place to place, for it has frequently happened that the shoal catch has been the greater even by day, and still more often that neither haul was much more productive than the other, irrespective of the time of day. But our data are not sufficiently detailed to show whether irregularities of these sorts result from differences in the degree to which different individuals respond to the effective stimulus (light), or from mass movements of the water, with its contained plankton.

Distribution in relation to temperature. In the summer of 1916, the most abundant stock of Calanus was living at depths and in the belt where temperature was lower than about 7° (Bigelow, 1922). And the catches larger than about 400 c.c., on our recent cruises have all been made at times and localities where the bottom stratum was at least as cold as about 8°, i.e., where a reservoir of cool water was not more than about 50 meters distant, even though the Calanus may have been close to the surface, and in much higher temperatures, at the time of capture. The boundaries of the "Calanus zone" for June and July (Fig. 23B) also correspond closely to those of the pool of cold bottom water characteristic of the mid- and outer part of the shelf, to the eastward of the Barnegat profile, at

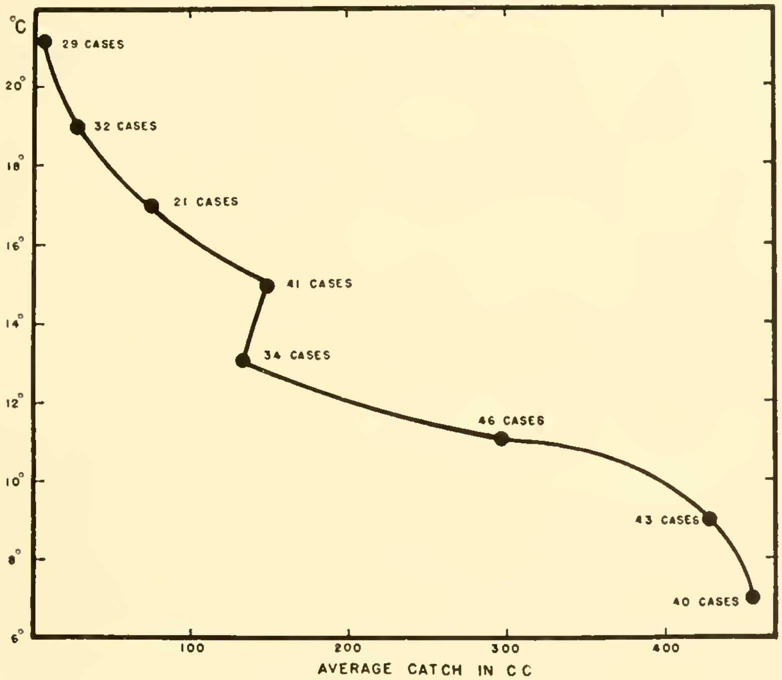


Fig. 26. Average catch of Calanus in water of different temperatures, irrespective of depth.

that season. Clarke and Zinn (1937) found, it is true, that Calanus was most numerous near Martha's Vineyard during July and August, when the bottom water averaged about 13°, but their maximum catches were at the rate of less than 90 c.c., when reduced to our standards, contrasted with the many catches larger than 1000 c.c. that were made closer to cold water on the "Albatross" cruises. And the relationship between average catch and temperature, for the several cruises on which hauls were made at two or more levels (Fig. 26), suggests that the lowest temperatures persisting on the shelf in summer (usually 6–10°) support, on the average, considerably the densest population of Calanus, and that the temperature range between 12° and 16° also may be classed as at least moderately favorable, with no apparent gradient within these limits. But Calanus is much less abundant at higher temperatures, largely deserting the surface stratum whenever and wherever the latter warms above 18°, and practically disappearing thence (probably by sinking), whenever the temperature rises above 19–20°. In fact, 24 out of a total of 43 hauls centering in water of 19° or warmer, proved absolutely barren of Calanus, while each of 10 others yielded not more than 1 c.c., of the sizes large enough to be sampled by our nets. And while exceptions occur to this as to every other "rule" regarding the distribution of plankton,[1] we seem justified in concluding that the warming of the water column from above is the chief (if not the only) factor responsible for the progressive intensification of the vertical volumetric gradient for this copepod from May through June to July. Light, we may note in passing, seems ruled out as the control in this case, by the fact that stratification of Calanus is much more pronounced in July than in May, though the intensity of illumination is about the same in the one month as in the other.

Annual fluctuations. The tabulation of average volumes (p. 309) makes it clear that the stock of Calanus varies widely in strength from year to year, not only near the southern margin of its range (where this might be expected), but equally in the more northern sector where the species usually has its center of abundance. The average catch was in fact about 4 times as great in the most productive year (1931) as in the poorest (1932) for February, 5 times as great for May, 9 times as great for June, and at least 6 times as great for July. And while the comparatively small volumes prevailing in 1932 perhaps approximate the lowest level to which Calanus is likely to fall in our area, it may not be unusual for it to exist in considerably greater volume than in 1931, for such seems to have been the case in the summer of 1916, when swarms were encountered (Bigelow, 1922, p. 143).

The record also suggests that when Calanus is relatively abundant at the end of winter (e.g., 1931), it is likely to maintain preeminence in this respect through the spring and summer, but that a year that is poor in Calanus in February may either continue poor through spring and early summer, as happened in 1932, or may experience an active vernal multiplication of this copepod as in 1930.

Comparison of the average catch, with temperature, for different years, leads to the rather astonishing conclusion that the rate of vernal augmentation is affected only indirectly by the thermal factor, if at all, for the year (1932) when

[1] The following productive catches were made in hauls centering in the upper 10 meters in water warmer than 18°: 150 c.c., 20.2°, Shinnecock II, July 1931; 166 c.c., 18.9°, Martha's Vineyard I, July 1929; 163 c.c., 18.2°, Cape May IV, June 1932; and 113 c.c., 18.1°, New York IV, June 1932.

production was poorest was not abnormally warm at the end of the spring or in early summer, though it had been so in February. It is a question for the future, whether a very warm winter in this part of the sea ordinarily presages a poor production of Calanus during the ensuing spring.

Calanus hyperboreus

Calanus hyperboreus[1] was taken at one station, only, in February, and was either absent altogether in April (1930) or was so scarce then that it was not detected. But it has appeared in one part of the area or another in May in each year of record with sufficient regularity to suggest that this is an annual event.

In 1930, for example, a year when a considerable indraft of cold water took place into the most eastern sector sometime in February or early March (Bigelow, 1933, p. 30), *C. hyperboreus* was generally distributed over the entire area by the middle of May right down to the offing of Chesapeake Bay (Fig. 27), locally in some abundance (up to 40–50 c.c.). It was similarly widespread east of the New York profile in that month of 1931, though chiefly confined to the outer part of the shelf farther south, which corresponds to the fact that little cold water had drifted past Nantucket in that year. And the first half of May again saw it at several stations in the eastern and mid-sectors, in 1932, and even off Chesapeake Bay where one haul yielded 23 c.c., seemingly following the indraft from the east that had taken place earlier (Bigelow, 1933, p. 30), though its presence was so short-lived that it was not found at all in the third week of the month.

In some years repeated invasions may also occur, as in 1932, when *hyperboreus* reappeared in small numbers, at the end of May, along a tongue extending from the outer part of the shelf off Martha's Vineyard and New York, westward to the offing of Atlantic City (Fig. 27), following a second invasion of cold water that had passed the offing of New York, two weeks or so before (Bigelow, 1933, p. 30). But in other years (e.g., 1930 and 1931), there may be only one invasion,—sometime perhaps none at all. In any case, we have no evidence that such events normally happen later than the end of May, for our records for *hyperboreus* in summer and autumn are confined to one station in July 1931, two in June 1932, and one in August 1916, off Martha's Vineyard, off Montauk, off New York, and off Delaware Bay respectively.

The evidence is thus conclusive that *C. hyperboreus* is not an endemic inhabitant of our area, but that it may be expected to appear here and there in late spring, after indrafts of water from the east, which accords with previous knowl-

[1] No regular record was kept of the presence or absence of this species in 1929.

edge that it is widespread throughout the Gulf of Maine at that season, at least in some years, as well as on George's Bank (Bigelow, 1926, Fig. 68, 69, Fish and Johnson, 1937). It also seems certain—from the brevity of the periods during which *C. hyperboreus* has been present in our waters—that the effects of each wave of immigration endure only for the lives of the individual concerned, i.e., that this species does not reproduce successfully anywhere west of Nantucket.

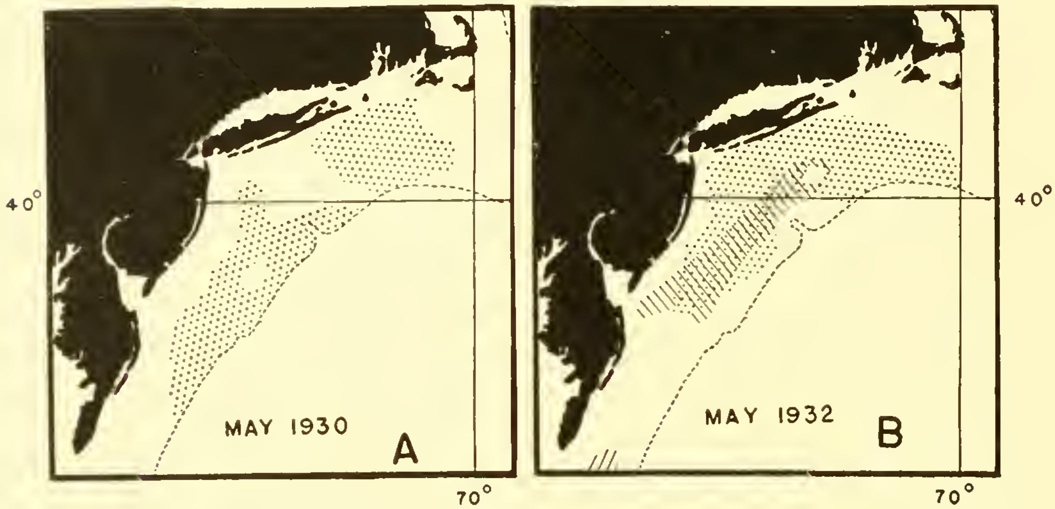


Fig. 27. Areas of occurrence of *Calanus hyperboreus:* A, May 12–23, 1930; B, May 2–6 (dotted), and May 9–16 (hatched), 1932.

C. hyperboreus is both so large and so easily recognized that it is perhaps the most reliable indicator-species for water from this source in our area. It is, however, negligible from the volumetric standpoint, except for brief periods, and of minor importance even then, witness a maximum catch of only 62 c.c. and an average of 25 c.c. within its area of occurrence in the month (May 1930) when it was taken most frequently and in greatest abundance.

Candacia armata

Previous records of this widely distributed copepod within our area were confined to the extreme south, where it was found in some abundance near the outer edge of the continental shelf and over the continental slope in the summers of 1913 and 1920, as well as in Chesapeake Bay on one occasion (Bigelow, 1915; Wilson, 1932a). But it was also to be expected in the north, having been found in the Gulf of Maine, as well as off the seaward slope of the latter (Bigelow, 1926, p. 219; Fish and Johnson, 1937, Fig. 25). And the records for 1929–1932 (Fig. 28) show that it does in fact occur about as generally as does *Euchirella rostrata*, throughout the offshore belt of our area (40% of the stations) and not rarely inshore as well (13% of the stations). It has also proved about as frequent rela-

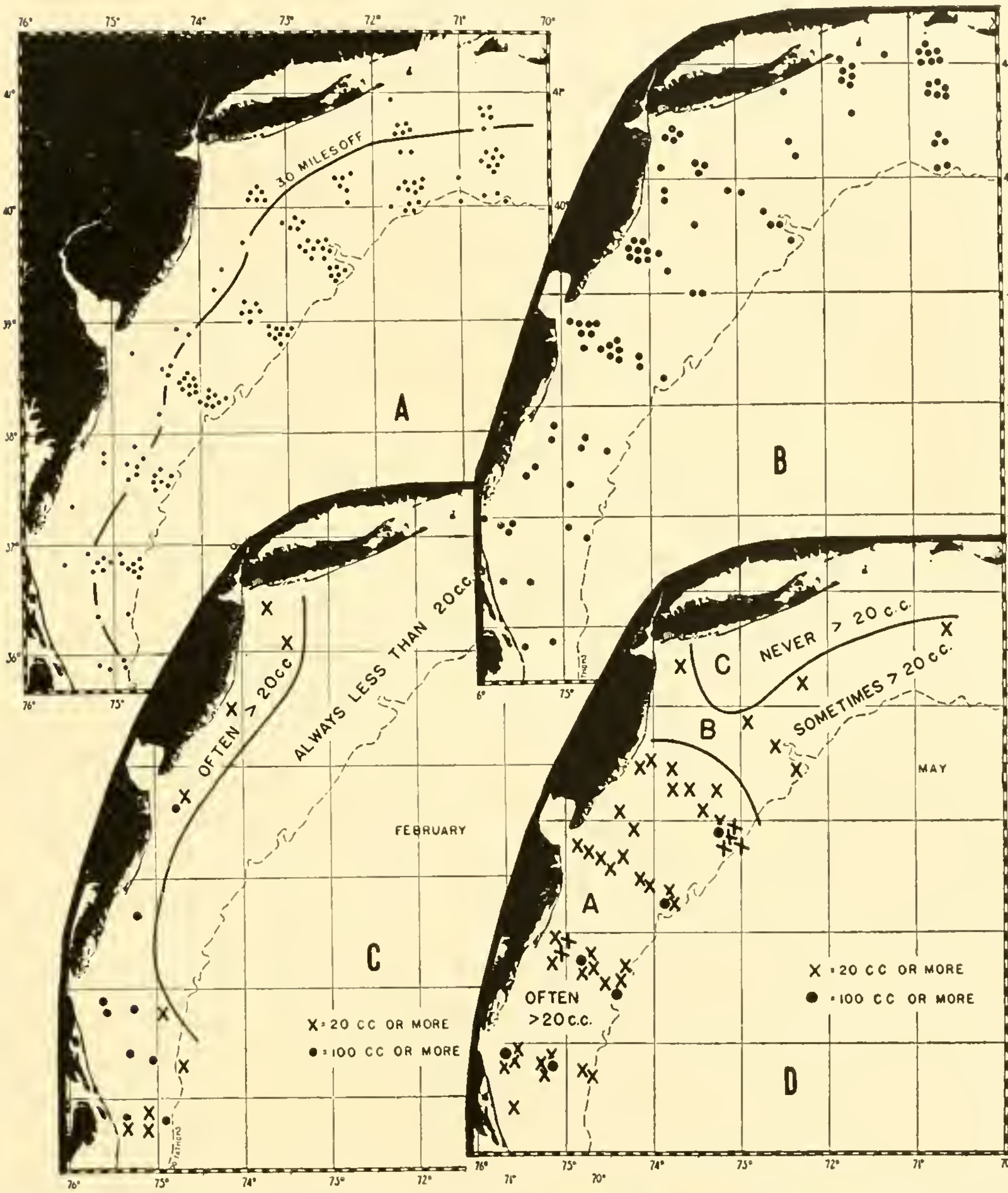


Fig. 28. Locality records, all cruises combined: A, *Candacia armata*, offshore and inshore; B, *Centropages hamatus;* C, *Centropages typicus*, large volumes, in February; D, *C. typicus*, large volumes in May.

tively, north (27% of the stations) as south (21%). The monthly percentage of stations at which Candacia was taken in the offshore belt (16–17%, February-April; 40–54%, May-July; 60%, October), show it as entering our boundaries much more often from late spring through the summer, than in late winter or early spring, and perhaps somewhat more often still, in the autumn, while the maximum catch of 113 c.c. was also made in October. But we have no evidence that this seasonal invasion extends to the inshore belt, where on the contrary, it proved about as frequent in February and April (19%, 10% of the stations) as in May, June, or July (14%, 13%, 10%), a regional difference associated no doubt with prevailing drifts.

In 132 out of the 154 cases, the catches were of stray specimens. A catch of 113 c.c. was, however, made midway of the shelf off Cape May on October 23, 1931, evidence that Candacia may occasionally occur in abundance over restricted areas in autumn, suggesting local centers of reproduction. But we have no evidence that this ever happens earlier in the season, for five only of the other catches were larger than 10 c.c., with 16 c.c. as the maximum for this group.

Centropages hamatus

This copepod, generally considered as of more definitely boreal habit than its relative, *C. typicus*, and common in the Gulf of Maine, had previously been reported as far south as the offing of Chesapeake Bay as well as within the latter (Wilson, 1932a). The records for the years, 1929–1932, show, in fact, that its range actually extends southward past the offing of Chesapeake Bay nearly to Cape Hatteras (Fig. 28), in early spring. But while Wilson (1932a) reports it off Chesapeake Bay in August, we have no records of it south of Delaware Bay as late as July either of 1929 or of 1913, suggesting that it tends to disappear from the southernmost sector by midsummer in normally warm years.

It is also interesting to find that the records of occurrence of *C. hamatus*—though most frequent inshore—extend across the whole breadth of the continental shelf, from the northern end of our area to the southern, in one month or another (Fig. 28B), whereas in the Gulf of Maine, this copepod is chiefly confined to the close vicinity of the coast (Bigelow, 1926, Fig. 70). The monthly distribution of catches (12–13% of the stations for February and April, 16% for May, 19% for June, and 10% for July), indicates a general tendency for this species to increase somewhat in frequency from late winter to June, and then to decrease somewhat later in the summer. And the data for the one October of record point to a still farther decline in the autumn, for it was not recorded at all on that cruise, nor in November 1916.

On rare occasions, a rich stock of *C. hamatus* may develop locally in the northern sector, suggesting active reproduction, cases in point being 189 c.c., near Martha's Vineyard, June 1930; 59 c.c. at that same locality on May 19, 1932; and 35 c.c., close in to Chesapeake Bay, in April, 1929. Other than these, however, the largest catches were 10–16 c.c. (5 cases), the average for the whole series being about 4 c.c. at the stations where *C. hamatus* occurred, and less than 1 c.c., if the stations where it failed be included in the calculation. Neither did *C. hamatus* form as much as 1% in any subdivision of the area during any cruise.

Centropages typicus

Frequency. *Centropages typicus* is but little less omnipresent than *Calanus finmarchicus* (p. 304) throughout the whole area, from north to south, and out to the 200-meter contour,—recorded, in fact, at about 90% of the stations, for all months and years combined—, and it is possible that young stages of the species may have been actually present, even at the few localities where the catches failed to show its presence.

Percent of stations with *Centropages typicus*

Year	February	April	May	June	July	October
1913	—	—	—	—	63%	—
1929	—	100%	95%	—	91	—
1930	86%	100	93	61%	94	—
1931	86	—	80	65	71	100%
1932	76	—	98	100	—	—
Aver.	82	100	94	77	85	—

The percentages of the stations where *C. typicus* was recorded suggest some increase as characteristic from February to April, succeeded in some years by some decline in summer, but then by recovery by October. In some years (e.g., 1932), however, this copepod may be as universal in June as in April.

Abundance. In the northern sector, the average stock of *C. typicus* is at its lowest ebb at the end of winter, and continues relatively low through spring and early summer, when an average of less than 15 c.c. is to be expected in normal years, but increases some 4–30 fold (to 90–100 c.c.) by July. Clarke and Zinn's (1937) records further show that *C. typicus* may continue numerous through August, in the easternmost sector of our area, with abundant production of young, and—by the evidence of the single year, 1931—it may be expected to remain at about the same high level until mid-autumn.

The seasonal cycle is much less regular in the south, where the average volume remained at a comparatively constant level from early spring through midsummer in one year (1929), but where more or less impoverishment took place in May or June in the other years, either for a brief period only, or of longer duration (see following Table). Monthly averages, however, for the several years combined of 83 c.c. for February, 31 c.c. for April, 21 c.c. for May, 25 c.c. for June, and 28 c.c. for July (this latter for 1929 only) suggest that volumes less than half as large are the normal expectation through spring and summer than at the end of the winter, but (by the evidence of 1931) with the peak of abundance to be expected in early autumn, when the average may rise above 100 c.c.

Average volumes of *Centropages typicus*

Month	Year	Inshore	Offshore	North	South	Area Surveyed	Maxi-mum	Mini-mum
February	1930	124	1	12	102	59	915	0
	1931	1	12	1	11	8	76	0
	1932	169	5	8	135	101	459	0
April	1929	24	21	18	27	23	87	<1
	1930	33	13	5	35	21	368	<1
May	1929	14	16	14	16	15	58	0
	1930	33	5	6	26	15	92	0
	1931	1	2	1	1	1	6	0
	1932	17	31	9	42	25	276	0
June	1929	15	12	6	27	14	107	0
	1930	7	1	3	2	3	35	0
	1931	11	7	9	12	10	120	0
	1932	31	22	13	57	32	276	<1
July	1929	59	31	35	28	46	256	0
	1930	208	12	92	—	92	1341	0
	1931	146	11	95	—	95	1070	0
October	1931	—	80	111	32	80	256	<1

In February, of the two years when Centropages occurred in more than minimal numbers in that month, the largest catches were made close to the mouth of Delaware Bay (1932), and from Chesapeake Bay southward (1930). But the locations of the centers of greatest abundance have varied widely, from year to year, during the other months (Fig. 28, 29), and also from year to year. In 1930, for example, the concentration of Centropages that was encountered off Delaware Bay in February had been largely obliterated by April. In May of 1929, the richest concentration (58 c.c.) lay mid-way out on the shelf, on the Martha's Vineyard profile, while in 1932, the more northerly of the two centers where Centropages had been most numerous in February, had broken down by May, whereas the more southerly (off Chesapeake Bay) had persisted, merely shifting some miles northward.

It seems, however, that the rich centers tend on the whole to become more generally distributed from February and April to May, out across the shelf in

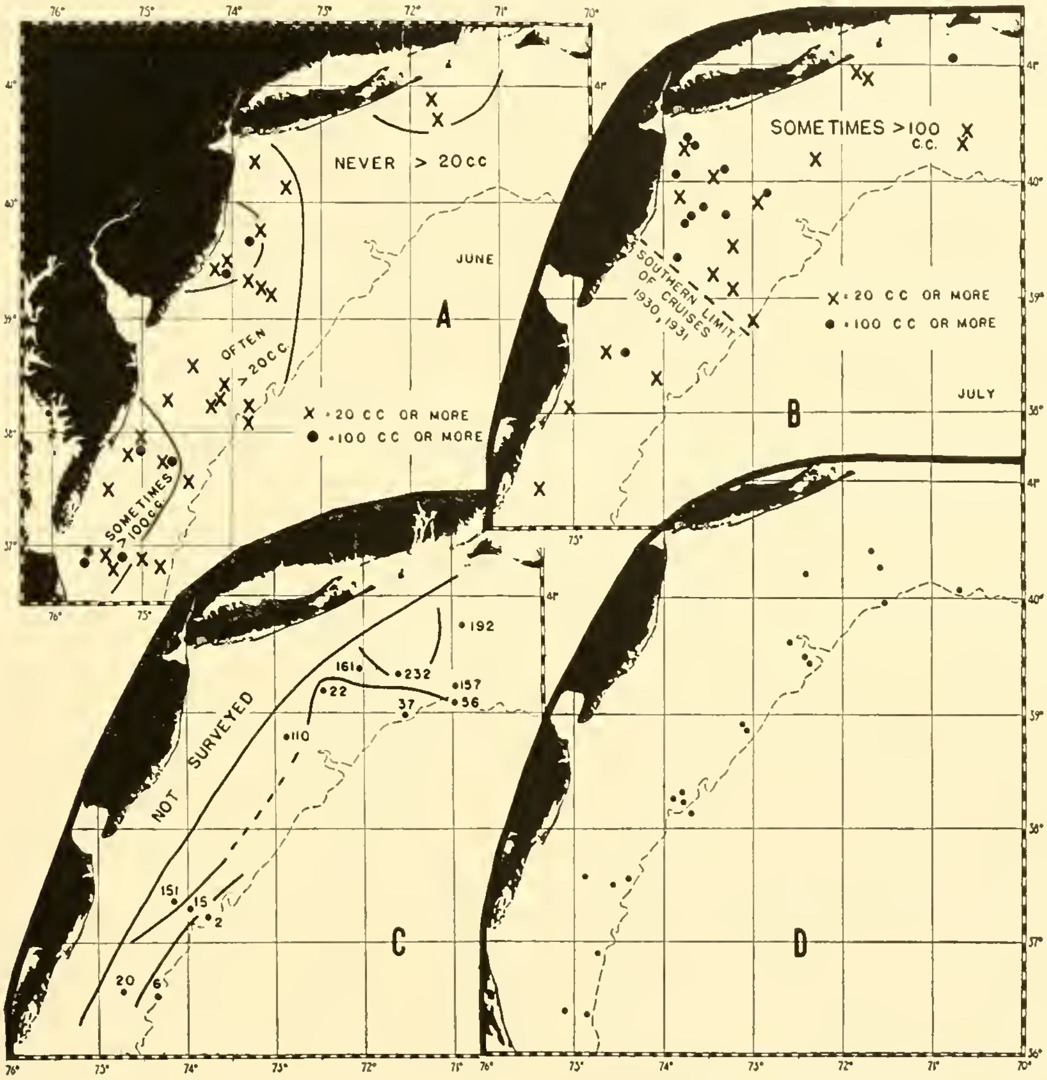


Fig. 29. Locality records, all cruises combined: A, *Centropages typicus*, large volumes for June; B, *C. typicus*, as above for July; C, volumes of *C. typicus*, per standard haul, October 19–28, 1931; D. locality records for *Centropages violaceus*, all cruises combined.

the sector southward from the offing of New York (to which they are so far confined). And although they may then contract again, in June, if the population be decreasing (cf. Fig. 28 and Fig. 29), centers of abundance may again appear offshore, from June through July, to the north as well as to the south, while the distribution for October 1931 shows the center of abundance (250 c.c.), as lying off Martha's Vineyard, instead of off New York and off New Jersey as had been the case in the preceding July.

The composite picture is thus of a progressive shift in the situation of the center of population from the Delaware Bay-Chesapeake Bay sector in February-April, progressively northward to the offing of New York in July, and finally by mid-autumn to the eastern boundary of our area. The result is that the volume of *Centropages typicus* may average about as large in the north, at the season of peak abundance there (July-October), as it is in the south in the months when largest there—February-April or June, according to the year. But Centropages has been so much more plentiful south than north in most of the individual months, other than July or October, that the average for the series as a whole is more than twice as large for the southern sector (42 c.c.) as for the northern (17 c.c.). *C. typicus* is therefore to be classed as primarily a southern species in our area. And while it occurs in considerable abundance as far north and east as the Gulf of Maine, it appears that Cape Sable, Nova Scotia, marks its approximate boundary in that direction (Bigelow, 1926, p. 223).

The inshore belt has also averaged from 1.5 to 7 times as productive of it as the offshore in each month, of the several years combined, maximum catches of 400–1000 c.c. or more, not being unusual there, at the season of maximum abundance.

Annual variations. The averages given in the column headed "Area surveyed" in the table on page 322, show that while Centropages may vary widely in abundance from year to year, at the end of the winter (when it has averaged 12–13 times as plentiful volumetrically in the richest year as in the poorest) and also through the spring, it would be a decidedly unusual event for a summer to be either extraordinarily rich or extraordinarily poor in this copepod.

Vertical distribution. In the one February of record, Centropages was distributed with approximate uniformity vertically, at more than half the stations (Fig. 30) and it was as often most plentiful deep as shoal at the others. But the center of abundance was much more often shoal, than deep in each other month, with more than half the stations showing one or the other type of vertical stratification. Similarly, the relative frequency of cases in which the catch was ten times as great from the one level as from the other, fails to suggest any definite vertical gradient in February or April, but enforces the conclusion that in May, June, and July, the zone of chief abundance for Centropages was much more often in the upper 10 meters or so, than at 20 meters or deeper.

On the other hand, the volumetric ratios of deep catch to shoal (listed below) suggest a seasonal reversal, for the deep averaged considerably the more voluminous of the pair on four cruises in February, April, and May, but the shoal the more voluminous on five cruises in May, June, and July.

Average ratio of volume at 10–0 meters to that at 20–40 meters: February, 1932, 1 to 2.5; April, 1929, 1 to 4.8; May, 1929, 1 to 2.3; May, 1931, 1 to 1.1;

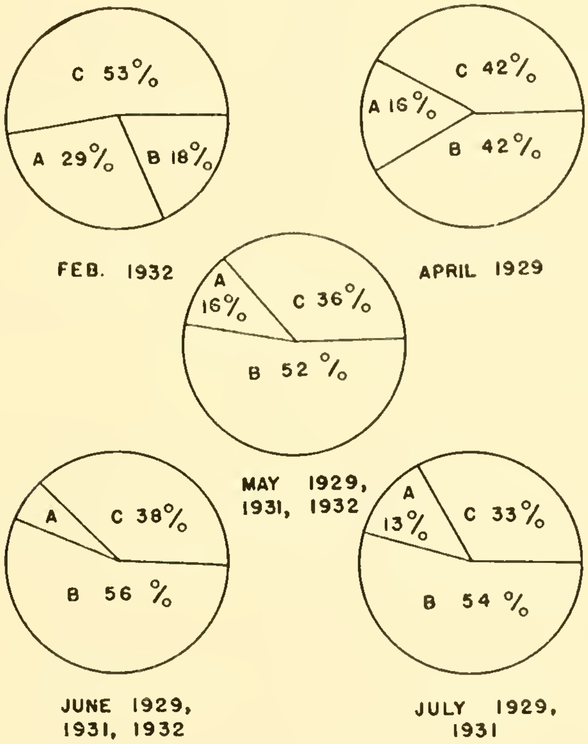


Fig. 30. *Centropages typicus:* percentage of cases, in different months, when the deep catch was twice as large as the shoal (A); in which the shoal catch twice as large as the deep (B); and in which neither catch was twice as large as the other (C).

May, 1932, 1 to 0.6; June, 1929, 1 to 0.6; June, 1931, 1 to 0.7; June, 1932, 1 to 0.6; July, 1929, 1 to 0.5; July, 1931, 1 to 1.0.

The danger of confusing regional and temporal gradients with vertical is so great, when the data are so few, that any attempt to harmonize such conflicting pictures, on the basis of present information, seems idle. The most we dare say is that the center of abundance for Centropages through spring and early summer lies much more often in the upper 10 meters than at any considerable depth, while its relative volumetric distribution through the water column is highly variable from time to time and from place to place.

The fact that a considerable proportion of the stock is living in the upper part of the vertical range of temperature from June on, shows that values higher than 18–20° are not unfavorable for Centropages, which added to its considerable abundance in February 1932 in temperatures of 9–13°, is evidence that the vertical gradient of temperature is not an important factor in determining the vertical distribution of this particular copepod.

Centropages violaceus

The records for this species have been confined (with three exceptions) to the outermost belt of the shelf, within 15–16 miles of the 200-meter contour (Fig. 29D). And the latitudinal distribution suggests that *C. violaceus* is as apt to stray in across the edge of the continent about as often in the one sector (north or south) as in the other. With so few data (20 localities), we can only say of its seasonal incidence that we have record of it within our limits in February, May, June, and October; based in every case, on scattered specimens.

Corycaeus sp.

Wilson (1932a, p. 42) has already reported four species of Corycaeus off Chesapeake Bay. And our records again yielded a scattering of these tiny copepods in the months of February, April, May, June, July, and October, not only in that same general region, but also northward along the edge of the continent to the offing of Delaware Bay (Fig. 31C).

Eucalanus sp.

Two species of this genus have been identified in the catches, *attenuatus* and *elongatus*, their chief interest, in the present connection being that they are sure indicators of a warm water source (see Wilson, 1932, for summaries of their known distribution). In the case of *attenuatus* the records are concentrated in the southernmost sector (Fig. 31A), where they extend close inshore, both off Chesapeake Bay and off Delaware Bay. To the northward, they are confined to the extreme outer edge of the shelf, though *E. attenuatus* again approaches the land in the Gulf of Maine with the peripheral drift of water from offshore (Bigelow, 1926, Fig. 71). The three records for *E. elongatus* were all well out on the shelf. And juveniles and damaged specimens, of the one species or the other were also detected at the additional stations marked on Figure 31A. All but one of the records for *attenatus* were for the month of April, as were two of the three

Fig. 31. Locality records, all cruises combined: A, *Eucalanus attenuatus*, *E. elongatus* and Eucalanus sp.; B, *Euchirella rostrata* and Euchirella sp. offshore and inshore; C, Corycaeus and Oncaea; D, Volumes of *Metridia lucens* greater than 100 c.c. (solid circles), boundary separating this area from that where the volume was usually less than 5 c.c.

records for *elongatus*, the others for May, whereas Eucalanus of doubtful identity were taken at all seasons.

It is interesting that while *E. attenuatus* occurs but so seldom in our waters and while the largest catch was only 32 c.c., 11 out of the 16 catches were of 1 c.c. or greater, averaging nearly 6 c.c., which suggests that a considerable population of it exists along the continental slope. But the records for *elongatus* were for strays only.

Euchirella rostrata

Previous records of this copepod, west and south of Cape Cod, were confined to the extreme outer edge of the shelf and continental slope (Bigelow, 1915; 1922). The data for 1929–1932 (Fig. 31B) show, however, that while this is distinctly an offshore species within our limits (recorded at 5% only of the inshore stations), it occurs much more generally in the offshore belt there (38% of the stations) than it does in the Gulf of Maine, where it appears to be sharply confined to the chief drift-tracks (Bigelow, 1926, Fig. 71; Fish and Johnson, 1937, Fig. 25). It has also averaged considerably more frequent in the northern sector (26% of the stations) than in the southern (12%) for all cruises combined. And the fact that it was recorded about as frequently, relatively, in one month as another from April to July (17–32% of the stations), but not at all in February, on the one hand, or in October on the other, equally identifies it as a spring and summer species in our waters.

Only two of the catches were larger than 1 c.c., with 6 c.c. as a maximum, all other records being of stray individuals only. Thus, we have no reason to suppose that it ever succeeds in breeding in significant amounts inside the continental edge, even at the warmest season, but rather that its status there is strictly that of a warm oceanic immigrant, which makes it a useful indicator-species.

Mecynocera clausi

It appears that *M. clausi*, like *Centropages violaceus* and *Pleuromamma gracilis*, strays in over the shelf about as frequently in the north as in the south. And the records show that it is as liable to drift farther in than do either of these, as is also the case in the Gulf of Maine, where it has been taken near land, on three occasions (Bigelow, 1926, p. 245). Even for it, however, the great majority of the captures were more than 30 miles from the coast (Fig. 33A). It also occurs, at times, in moderate numbers, for catches of 1–4 c.c. were recorded on 6 occasions, 11 c.c., once. The percentage of stations at which it was recorded

(30% for February, 0% for April, 6–14% for May-July, but 87% for October) may indicate a greater tendency for it to drift shoreward at the end of winter and in autumn than during the intervening period. We suspect, however, that these seasonal differences are evidence of irregular fluctuations, rather than of any definitely seasonal succession.

Metridia lucens

Frequency. The records for *M. lucens* show wide differences on individual cruises in the frequency and generality of its distribution, the one extreme being illustrated by April, 1929, when it occurred at only 27% of the stations, the other by February 1932, when it was at 88%. Neither does any definitely seasonal cycle appear in this respect for the area as a whole, monthly averages being: 65% for February; 53% for April; 59% for May; 57% for June; 55% for July; and 70% for October.

But Metridia was not only more frequent offshore than inshore in every month and year, as listed below, but was lacking altogether over larger or smaller areas next to the land on most of the cruises. The variations in the inshore boundary to its occurrence have been so considerable from cruise to cruise and from year to year that it is difficult to reduce them to any regular order. In three years, however, out of the four, the barren belt next the land was most extensive in February (1930, 1931) or April (1929, Fig. 32). But Metridia was found close in to the land at one locality or another by May in 1929 and 1931, while in 1930, it was at most of the inshore as well as the offshore stations by the last part of April (Fig. 32). In these same years, this shoreward encroachment was then followed by a retreat from the land, from May to June, most pronounced in 1929 and 1930, but suggested also in 1931. In the fourth year of the series (1932), Metridia was much more general inshore at the end of the winter than in the other years, but was absent from belts of fluctuating extent next the land through May and June.

Frequency ratio of *Metridia lucens* offshore relative to inshore

Month	1929	1930	1931	1932	Average
February	—	1 to 0.3	1 to 0.2	1 to 0.8	1 to 0.4
April	1 to 0	1 to 0.7	—	—	1 to 0.5
May	1 to 0.5	1 to 0.7	1 to 0.2	1 to 0.7	1 to 0.5
June	1 to 0.4	1 to 0.2	1 to 0.6	1 to 0.7	1 to 0.4
July	1 to 0.2	1 to 0.6	1 to 0.6	—	1 to 0.5
Average	1 to 0.3	1 to 0.5	1 to 0.5	1 to 0.7	

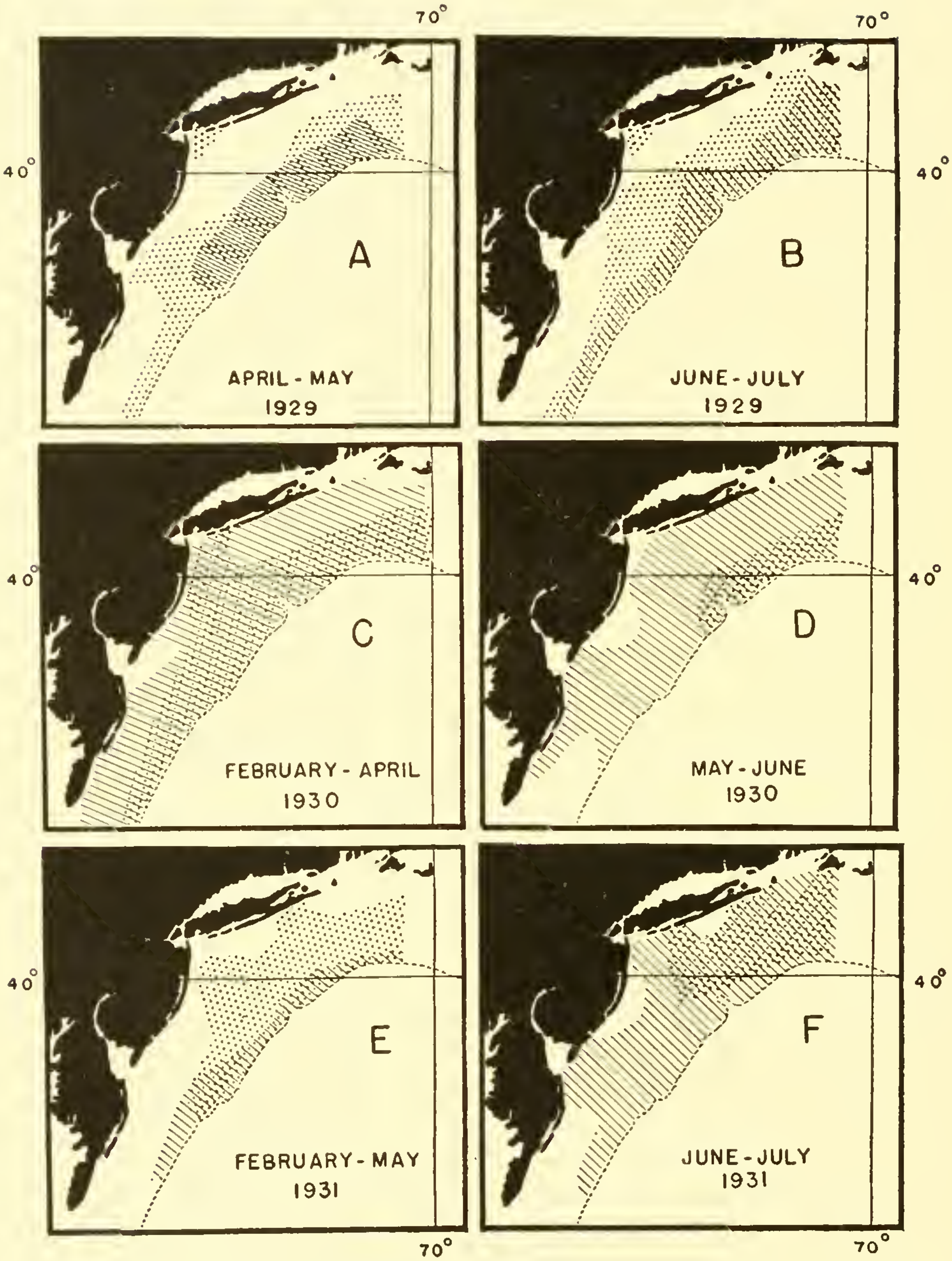


Fig. 32. Areas of occurrence of *Metridia lucens:* A, April 19–24 (hatched) and May 10–18 (dotted), 1929; B, May 28–June 5 (dotted) and July 11–August 1 (hatched), 1929; C, February 5–13 (dotted) and April 3–May 1 (hatched), 1930; D, May 12–23 (hatched) and June 7–18 (dotted), 1930; E, February 13–March 5 (hatched) and May 16–22 (dotted), 1931; F, June 12–19 (hatched) and July 10–16 (dotted), 1931.

These alternate states suggest that Metridia is to be expected near land only locally, if at all, at the end of a normally cold winter, but that it tends to spread close in to the coast line through considerable sectors at some time in the spring, to disappear again progressively, from parts of the inshore belt, during the summer. After a warm winter, Metridia may, however, be widespread inshore as early as February, and the tendency toward local disappearance from the coastwise belt may become effective as early as the middle of May. Minor or short-period oscillations in the inshore boundary to the occurrence of this copepod, no doubt reflect the appearances and disappearances of successive broods, or incursions from the offshore reservoir where the species is constantly present.

Metridia also averaged consistently more frequent in the north than in the south in spring and summer, in the following ratios:

Frequency ratio of *Metridia lucens*, north relative to south

Month	Year		Month	Year	
February	1930	1 to 1.0	June	1929	1 to 0.4
"	1931	1 to 2.7	"	1930	—
"	1932	1 to 0.8	"	1931	1 to 0.1
Average		1 to 1.5	"	1932	1 to 0.7
April	1929	1 to 0.2	Average		1 to 0.5
"	1930	1 to 0.9	July	1929	1 to 0.8
Average		1 to 0.5	"	1930	—
May	1929	1 to 0.7	"	1931	—
"	1930	1 to 0.7	October	1931	1 to 0.9
"	1931	1 to 0.1			
"	1932	1 to 0.9			
Average		1 to 0.6			

Its frequency indeed, averaged as high at this season (70–100%) as that of Calanus (p. 305) in the northern offshore sector. But the fact that it averaged rather more frequent in the south than in the north in February (3 years) suggests a seasonal reversal in this respect.

Abundance. Metridia averaged considerably more abundant (volumetrically) offshore than inshore, on 15 of the 16 surveys (Table, p. 332), as well as more frequent, the sole exception being in February 1932. And the offshore-inshore ratio of about 5 to 1 that results for the series as a whole is perhaps a reasonable expectation for the vernal six months combined, taking one year with another. The tabulation suggests, however, that there may be some tendency for this regional contrast to reach a maximum in April or May, in which months the ratios of volume offshore to inshore averaged, respectively, about 12 to 1 and about 8 to 1, contrasted with average ratios of about 5 or 6 to 1 in June and July, and about 1.2 to 1 in February.

Average volumes of *Metridia lucens*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maxi-mum	Mini-mum
February	1930	<1	6	5	2	6	42	0
	1931	<1	23	2	20	13	78	0
	1932	34	13	7	33	26	165	0
April	1929	0	19	13	3	8	106	0
	1930	16	78	71	26	47	272	0
May	1929	2	6	5	2	4	37	0
	1930	10	68	57	9	36	168	0
	1931	2	59	31	14	26	193	0
	1932	8	47	28	17	25	220	0
June	1929	11	27	11	9	11	210	0
	1930	<1	24	11	2	9	83	0
	1931	6	28	17	9	14	159	0
	1932	5	35	13	13	15	189	0
July	1929	<1	9	6	<1	3	71	0
	1930	<1	23	13	—	13	102	0
	1931	3	6	4	—	4	20	0
October	1931	—	17	26	4	17	104	0

It is not astonishing in view of the foregoing that nearly all the large catches (> 100 c.c.) of Metridia were made more than 35 miles out from land, and north of Latitude 38° (Fig. 31D), the only exception being that two large catches were made close inshore, off Currituck and Bodie Island in February 1932. Equally demonstrative of the offshore nature of Metridia is the contrasting fact that only 18 out of 204 stations, within 20 miles of land yielded volumes as large as 5 c.c., whatever the season of the year, most of these being northward from the offing of Delaware Bay. Indeed, no one of the 32 stations near Chesapeake Bay, or thence northward along the coast of Virginia yielded as much as 20 c.c., while Metridia failed altogether at twenty-five of them, marking this as the most barren region for this species. Unfortunately, no information is available in this respect for autumn, the one October cruise having been confined to the offshore belt. The volume of Metridia has also averaged greater—usually more than twice as great—in the north than in the south in every individual month, April to July, excepting in June 1932, when it averaged about the same in the one sector as in the other. But the fact that an even stronger contrast of the reverse sense obtained in

February, in two years out of the three, suggests a regularly seasonal reversal in this respect. Monthly changes in the volume of Metridia have been so irregular and so small inshore, that the ostensible succession there may not be seasonally significant. But the volume of this copepod has averaged 2–11 times as plentiful (by volume) in the offshore belt in April, May, or June, as in February, in at least three out of the four years, and maximum catches have shown a corresponding monthly contrast, suggesting that more or less vernal augmentation is characteristic for it in the zone of chief abundance.

Maximum volumes of *M. lucens*

Month	1929	1930	1931	1932
February	—	42	78	13
April	106	272	—	—
May	21	168	193	47
June	210	83	159	35
July	71	102	18	—

Present indications are that this offshore augmentation may culminate as early as April (e.g., 1930), or by June, at latest (e.g., 1929), and that it is then usually followed by some impoverishment. In some years (1931, for example), partial recovery then follows in the offshore belt by October. But our failure to find Metridia, at all, in the November catches of 1916 suggests that in other years, it may continue extremely scarce right through the autumn. And we lack quantitative data for December or for January.

Annual variations. The differences that have been recorded from year to year, in the inshore boundary to the regular occurrence of Metridia in different months are discussed above (p. 329). We should also point out that the volume of Metridia averaged rather more than three times as large for the area as a whole in the richest years (average, about 22 c.c. in 1930 and 1931, all cruises combined) as in the poorest (1929, average, about 6 c.c.).

Oithona sp.

The copepods of this genus are so small (about 0.75–1.5 mm. long when adult) that consequently even its adults may have passed through the nets. And because Oithona never formed as much as 1% of the catch in any subdivision, we have not attempted the time-consuming task of estimating the relative abundance of the two species, *similis* and *brevicornis*, that have long been known to occur in the area.

Oithona, of one species or other, was recorded in the catches at 92% of the stations in February, 59% in April, 51% in May, 36% in June, 53% in July, and 57% in October, proving that it is as regular, and probably as frequent an inhabitant of our area as it is of the Gulf of Maine and Bay of Fundy (Fish, 1936b), also about as frequent, north (49% of the stations) as south (54%), and offshore (48%) as inshore (53%). Oithona must, in fact, be extremely numerous at times, for on one occasion (off Bodie Island, in February 1932), no less than 30 c.c., of these tiny copepods were entangled in our coarse-meshed net. But most of the other catches were less than 1 c.c.—often odd specimens only. And the very strong probability that, in many cases, a good part of the local stock passed through the nets, prevents us from drawing any conclusions as to seasonal variations in abundance, from the monthly variations in frequency of occurrence. As a case in point, we may quote a frequency of 86% on the second June cruise of 1932, contrasting with 0% on the third cruise that same month, evidence, perhaps, of the presence of a strong stock of adults on the one occasion, but of their replacement by juveniles, by the time of the second.

Oithona, being so small, is not likely ever to form any considerable percentage of the volume of the total plankton present in our waters. But from experience elsewhere, and from its frequency of occurrence, it may well be a major item in the local diets of larval fishes.

Oncaea sp.

The grouping of the localities of capture of the scattering specimens of Oncaea (Fig. 31C) suggests that most of them, at least, belong to the widely distributed pelagic species, *O. venusta*, which Wilson (1932a) has already reported in some abundance over the outer edge of the shelf, off Chesapeake Bay, but not within the latter. Apparently, this is a warm-water stray within our limits. But it may be of greater faunistic importance there, on occasion, than might be suggested by the fact that our records are all based on stray individuals, for our nets did not adequately sample animals so small.

Pleuromamma

Two species of Pleuromamma were detected in the catches, *robusta* and *gracilis*, the only previous reports of which, inside the 200-meter contour, within the limits of the present survey, were near Martha's Vineyard (Wilson, 1932), though both of them enter the Gulf of Maine not infrequently, as strays from the continental slope (Bigelow, 1926; Fish and Johnson, 1937). *P. gracilis* was taken not uncommonly on the outer edge of the shelf (Fig. 33), but only five of the 40

Fig. 33. Locality records, all cruises combined: A, *Mecynocera clausi;* B, *Pleuromamma gracilis* and *P. robusta;* C, *Paraeuchaeta norvegica;* D, large volumes of Pseudocalanus.

records of it were more than 10 miles in from the 200-meter contour, nor have we any evidence that it ever strays shoreward farther than the mid-belt of the shelf.

P. robusta, on the other hand, was recorded about as often in the inshore belt (4 stations) as offshore (5 stations), once close in to land on the Montauk profile (Fig. 33B).

Since it seems certain that both these species enter our waters from offshore, this distributional contrast suggests that *gracilis* is the more sensitive of the two, to the conditions it encounters in over the shelf.

The monthly distribution of the captures suggests that *P. gracilis* crosses the offshore boundary of the shelf much more often in late winter and early spring, and again in mid-autumn than during the intervening season, for it was taken at 30–37% of the stations in the offshore belt in February, April, and October, but at 17% only in May, and 3% in June and July. Catches of 1 c.c. or more (15 in number) were correspondingly confined to the months of February, April, May, and October. And the fact that the maximum volume of *P. gracilis* was only 10 c.c. (off Montauk, May 21, 1931) is good evidence that it would be a most unusual event for this species ever to develop a rich center within our limits. In the case of *P. robusta*, the captures were confined to the months of February-June. But the number of captures was not large enough to warrant any conclusion as to seasonal gradient within this period. And the records are based in each case on stray specimens.

Paracalanus parvus

This copepod, like Pseudocalanus, is so small that our nets could be expected adequately to sample the adults alone. Even with this reservation, however, the record points to very wide fluctuations from month to month and year to year both in its frequency of occurrence, and in its abundance. In 1929, for example, it was not detected at all in April, May, or June, but was found at 100% of the stations inshore and 62% offshore in July, when it averaged 2 c.c. in volume over the area as a whole. But it seems to have vanished entirely from our area at some time during the subsequent autumn or winter, for it was not found at all in 1930, and at one station only, during the late winter, spring or summer of 1931. But it was at every station visited that October, averaging 62 c.c. in volume. And it may have persisted through the following winter for it was at 86% of the stations in the next February (1932), averaging 26 c.c., and about as frequent in one subdivision of the area as in another. However, it—or its adults, at any rate—had entirely vanished, by the following May and June.

In the absence of any knowledge as to the abundance of its young stages, it is an open question whether these fluctuations in its status are connected with the incidence of successive broods, or whether they are the visible evidence of extreme susceptibility, on the part of this particular species, to the favorability, or the reverse, of its external surroundings. In either case, it is clear that the production of a large crop of adults is a decidedly unusual event within our limits. But when this does occur, which may be either in late winter, in high summer, or in autumn, the resultant volumes may be so large as to make Paracalanus an

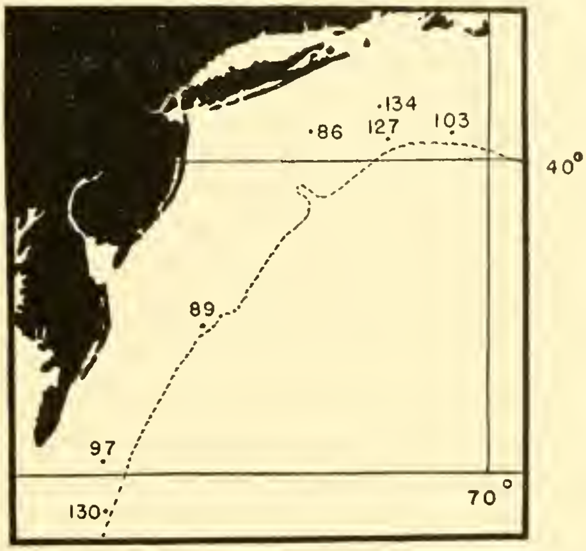


Fig. 34. Volumes, per standard haul, of Paracalanus, all cruises combined.

important item in the total community, for the time being; and perhaps as important in one subdivision as in another, for the concentration of rich catches offshore shown in Fig. 34 may reflect simply the failure to survey the inshore belt in the month (October 1931) when this copepod was the most abundant (p. 336). The largest catches for February were in the south, those for October in the north, the maximum so far recorded being 134 c.c. (Fig. 34).

Paraeuchaeta norvegica

This large copepod—a familiar inhabitant of mid-depths in boreal seas—is one of the most characteristic members of the plankton in the deep basin of the Gulf of Maine, where females with their blue egg clusters are familiar objects, and larvae are plentiful (Campbell, 1934, p. 4, 34). It also occurs with considerable frequency from the offing of Martha's Vineyard westward and southward (Fig. 33C) to that of Chesapeake Bay, outside the 100-meter contour, where Wilson (1932a) also reports it. But it so seldom drifts farther in on the shelf, that while taken at 23% of the stations offshore, it was at only 2% inshore within our limits. When this does happen it is about as apt to be off one part of the coast as off another; stray specimens, indeed, may come close in to the land, and consequently into very shoal water on rare occasions, as may any other oceanic waif.

The percentages of the stations at which *P. norvegica* was taken in the offshore belt in different months point to a rather regular increase in the frequency of its occurrence from February (23%) through April (32%) to May (49%), followed by a decrease in June (14%) and July (12%), leading—by present data—to a complete disappearance from this sector of the shelf in the autumn, for it was not found anywhere inside the 200-meter contour at this season either in 1916 or in 1931. And fluctuations of this sort are of special interest in the case of this particular species, because of its reliability as an indicator of continental slope water within our limits.

Paraeuchaeta has proved entirely negligible from the volumetric standpoint, throughout the entire series of observations, for the records have been of stray specimens only, irrespective of the time of year.

Pseudocalanus minutus

Frequency. Pseudocalanus was detected at about 82% of our stations, evidence that it is one of the most regularly distributed species over the area as a whole, and one of the most nearly universal there. But this copepod is so small (adults average only about 1–1.6 mm. in length) that most of the younger individuals and even a considerable percentage of adults may have passed through the nets. It is therefore possible that an increase in recorded frequency from an average of 79% of the stations in February, to 84% in April, and 92% in May, followed by a decrease to 74% in June and 60% in July, but by a subsequent increase to 73% in October may have been due to seasonal alterations in the relative abundance of the older stages (that were caught) and of the juveniles (that were not), rather than to corresponding fluctuations in the actual frequency of the species.

The average frequency was about the same inshore (80%) as offshore (77%); about the same also for the southern sector as a whole (75%) as for the northern (81%), right down to the offing of Chesapeake Bay, where Pseudocalanus was found at 77% of the stations. But the fact that it proved somewhat less frequent farther south, and was lacking at four out of the five stations near Cape Hatteras

(February 1931), suggests that the southern boundary of regular occurrence for it lies not many miles to the south of the Chesapeake Bay profile, as also for sundry other boreal animals.

Abundance. Pseudocalanus, though so nearly universal, was usually present in only small volumes, as emphasized above (Table, p. 229), in the discussion of the relative importance of different species. In fact, the catch was at the rate of not more than 1 c.c. at about ¼ (109) of the 410 stations where this copepod was recorded, while only eight of the catches were greater than 100 c.c., three greater than 200 c.c., with 560 c.c. as the maximum. But for the reason just stated, it is likely that this understates the actual abundance of this species (see also, Fish, 1936a).

The average catches for the area as a whole parallel the monthly frequencies (p. 338), in showing a slight increase from February (average, 10 c.c.) to April (14 c.c.) and May (15 c.c.) followed by a slight decrease through June (12 c.c.) to July (10 c.c.). And while the record for October is confined to a single year (1931), the low average for that cruise (5 c.c.), as contrasted with the preceding July (14 c.c.), probably represents the normal seasonal cycle, for that year was the most productive of the series for this particular copepod. Adults of Pseudocalanus thus appear to average most numerous over the area late in spring, much less so in autumn, though with some recovery through the winter. And while so few juveniles were taken that they do not figure to any significant degree in this summary, they are individually so small that their omission would not greatly affect the volumetric picture.

Average catches for February-June (1929–1932) combined, of 14 c.c. in the inshore belt, 9 c.c. offshore, 11 c.c. in the northern sector, and 9 c.c. in the southern do not differ, one from the other more widely than might be expected from the roughness of the method. Neither do the small catches made in July of 1929 or 1930 show any definite regional gradient, though the waters in the north averaged some 7 times as productive inshore (21 c.c.) as offshore in that month of 1931. And it is doubtful whether the contrast, between greater abundance in the south (10 c.c.) than in the north (3 c.c.) in the offshore belt in the following October, can be taken as characteristic for the time of year. In short, we have no definite evidence that any one part of the area averages significantly more productive of Pseudocalanus than another. But the distribution of the richer catches and especially of the few that were more productive than 100 c.c. (Fig. 33) suggests that it is rather more common for localized centers of abundance to develop within 30–35 miles of the land than farther out on the shelf.

Average volumes of Pseudocalanus for area surveyed

Month	1929	1930	1931	1932
February	—	10	7	13
April	4	24	—	—
May-June	2	1	31	25
July	1	1	14	—

Annual variations. The volume of Pseudocalanus averaged about twice as large, for the area as a whole in the richest year (1932, 13 c.c.) as in the poorest, at the end of winter, while May and June, combined, show an average some 25–30 times as great in two of the years as in the other two, a range much wider than any seasonal or regional contrast that can be deduced from our data. This marks this species as one of the most variable from year to year, of those that figure regularly in the catches.

It is also interesting that the relative ranking of a given year as to the abundance of this copepod may either continue low or high right through the spring and early summer as happened in 1929 and 1932, or it may be abruptly reversed as happened in 1930, when Pseudocalanus was relatively abundant in February and April, but very scarce from May to July.

Rhincalanus nasutus

Frequency. This offshore copepod has been taken widespread throughout the area at one time or another (Fig. 35A) except in the coastal belt between the New York and Martha's Vineyard profiles, where we have no record of it. But the localities of record have been chiefly concentrated in the offshore belt, as was indeed to be expected, some 61% of the catches on the shelf north of Latitude 36° N., having been made within 30 miles of the 200-meter contour. It is no doubt a corollary to the narrowness of the shelf to the southward, that Rhincalanus appears much more frequently near land, south of Delaware Bay, than to the northward.

Rhincalanus has averaged about equally frequent in February, April, and May, but progressively less so in June and July, and this seasonal decline in the regularity of occurrence takes place both earlier inshore, i.e., between February and April, and is more abrupt there than offshore, with no apparent difference in this respect between the northern and southern sectors, as follows:

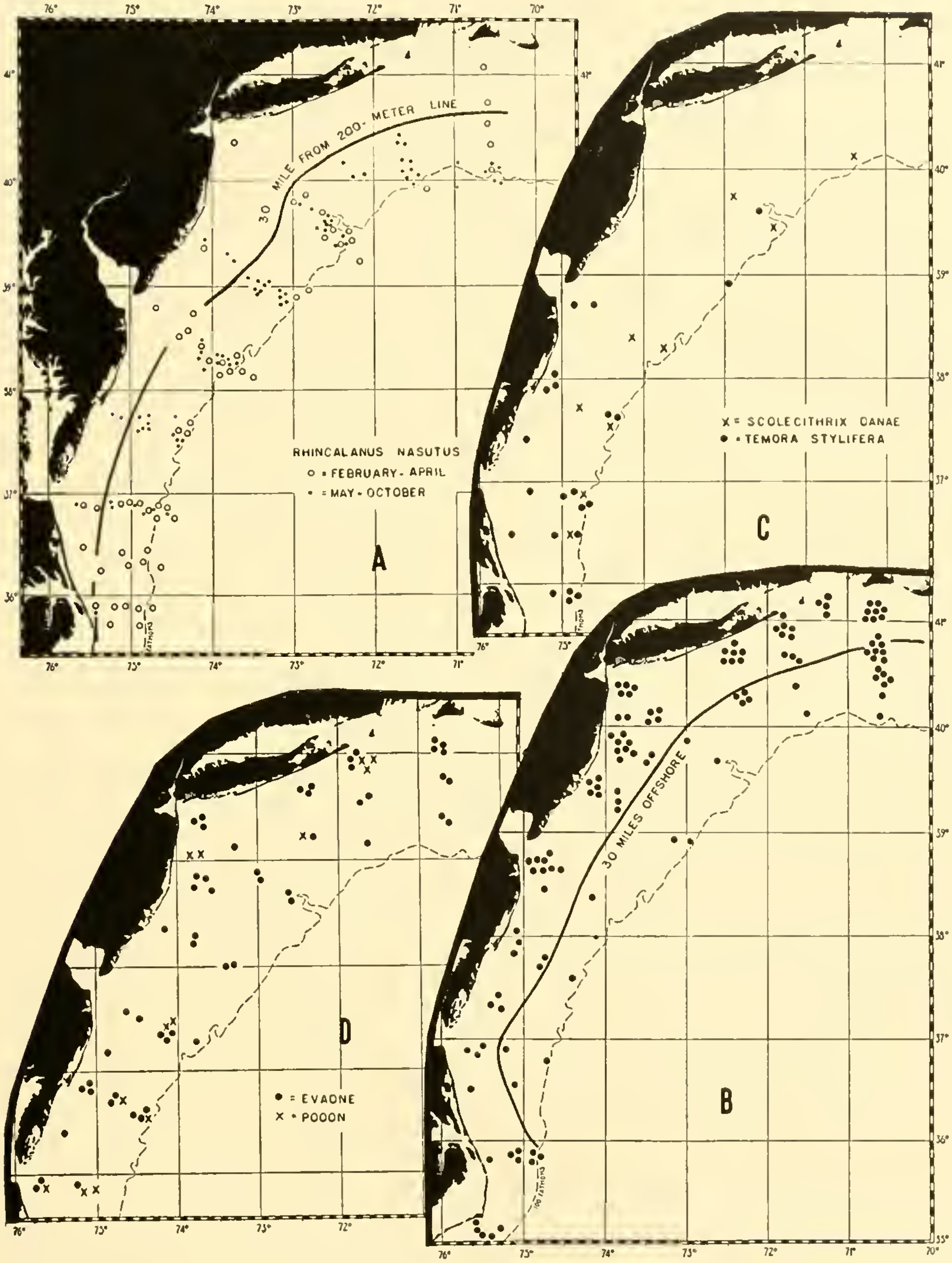


Fig. 35. Locality records, all cruises combined: A, *Rhincalanus nasutus;* B, *Temora longicornis* inshore and offshore; C, *Temora stylifera* and *Scolecithrix danae;* D, Evadne and Podon.

Percentage of stations with Rhincalanus

Month	Offshore	Inshore	North	South
February	57%	53%	49%	55%
April	52	4	22	32
May	51	15	25	41
June	37	5	11	31
July	18	0	—	—
October	66	—	—	—

The evidence from 1931 is that the frequency of Rhincalanus rises again during the early autumn in some years—at least in the offshore belt to which the data for that October were confined. But it was not detected at all within our limits in November in 1916, showing that conditions may vary widely in this respect from year to year. We have no information as to the status of Rhincalanus in any part of our area during the first two months of winter.

Abundance. The great majority of the records for Rhincalanus inside the 200-meter contour have been based on occasional individuals, and this large copepod is so easily recognized that the distributional picture is no doubt more nearly complete for it, than for other less conspicuous strays. In fact, Rhincalanus never averaged as much as 1% of the catch for any cruise, even in the offshore belt. A catch of 74 c.c. was made on one occasion, however, with an average of 40 c.c. at three stations near the 200-meter contour from the offing of Delaware Bay to that of Chesapeake Bay (May 2–6, 1932), evidence that it may occasionally be of considerable volumetric importance, within short sectors along the continental edge—doubtless over the slope as well. And when this does happen, Rhincalanus may be expected to form an important item in the diet of any local pelagic fishes, thanks to its large size. Catches of 5 c.c. or more have also been recorded more frequently in the southern sector (8 cases) than in the northern (2 cases).

It appears that Rhincalanus may be expected to invade the shelf in appreciable quantity more often in late spring, than either in winter, on the one hand, or in summer or autumn, on the other, 3 catches larger than 5 c.c. having been made inside the 200-meter line in April, and seven in May, but only one in July and none in October, November, or February.

The distributional picture, as outlined above, seems sufficient ground for concluding that Rhincalanus enters our area only as a stray from the waters of the continental slope. There is no evidence that it can maintain itself, anywhere over the continental shelf north of Cape Hatteras.

Scolecithrix danae

The only previous records of this oceanic copepod off the east coast of North America, with which we are acquainted, are for George's Bank and for the offings of Nantucket and Martha's Vineyard (Wilson, 1932, p. 82). The present records—nine in number and scattered along the offshore belt from the offing of Currituck to that of Montauk—show, however, that it is to be expected anywhere on the outer part of the shelf, within our limits (Fig. 35C). Four out of the nine records are for October, though one cruise (1931) only was made in that month during the four years. The two catches of more than minimal numbers (3 c.c. in each case) that were made inside the 200-meter contour were also in that October, cumulative evidence that this oceanic visitor crosses our boundaries most often in the autumn, but never in any great frequency or abundance.

Temora longicornis

In the winter—by the evidence of 1931—the range of this little brown copepod extends southward to Cape Hatteras (Fig. 35B). And it is possible that this is also true through the spring, for it was found on the Bodie Island profile on each April cruise and off Currituck on the one May cruise (1929) that extended so far south. In June, however, it was taken at but one out of eight stations on the Chesapeake Bay profile, while in July, it was recorded southward only as far as Winterquarter in 1929, as far as Fire Island in 1913, and as far as New York in 1916. While not conclusive, this evidence suggests that the southern boundary to its frequent occurrence tends to recede northward, during the summer, though to different degrees in different years, corresponding to which, it was recorded at 22% of the stations in the northern sector (all cruises combined), but at 14% only in the southern. In the one year (1916), however, when the inshore waters west and south from Cape Cod were visited in autumn, its recorded range extended to the offings of Delaware Bay and of Chesapeake Bay in November (Bigelow, 1922, p. 146).

T. longicornis occurs with some regularity right out to the edge of the continent. But it is much more frequent inshore (26% of the stations) than offshore (11%), which agrees with its status in the Gulf of Maine, where it has its center of distribution inside the 100-meter contour, including in that case the extensive shoal ground of George's Bank (Bigelow, 1926, Fig. 85). It may, in fact, occur as frequently close in to the land as farther out, witness the frequency of records at our innermost stations off Delaware Bay and thence north and east (Fig. 35B), likewise at Woods Hole (Fish, 1925). But available evidence suggests that it does not regularly penetrate estuarine situations along our coasts, unless the renewal of water, from outside, be active, for while it occurs abundantly in Passamaquoddy Bay, tributary to the Bay of Fundy (McMurrich, 1917; Bigelow, 1926; Fish and Johnson, 1937), Cowles (1930) and Wilson (1932a) report it in Chesapeake Bay only at stations near the mouth.

The percentages of the stations at which Temora was recorded north and south, in different months (1929–1932), tabulated below, show it as averaging the most frequent in both sectors in May, followed by impoverishment through the summer, much more extreme in the south—as just outlined—than in the north. The evidence of 1929 and 1930 combined, also is that Temora, in the north, suffers a marked impoverishment for a time in early spring, of which no evidence appears in the south, which can hardly be charged to invasions by eastern water, because Temora is relatively high in frequency in the Gulf of Maine at that same season.

Percentage of stations with *T. longicornis*

	February	April	May	June	July
North	17%	3%	38%	19%	20%
South	13	12	22	12	8[1]

[1] 1929 only.

During the cruises of 1929–1930, only 14 out of the 604 stations yielded catches of Temora as large as 1 c.c., only one as large as 10 c.c., with 13 c.c. as the maximum.

The most interesting feature of these records is that Temora should have invariably been insignificant in the general community, throughout our area, during every cruise, for swarms of it have been encountered close to Martha's Vineyard, July 26, 1916, over Nantucket Shoals, on July 9, 1913, and near Gloucester, on October 31, 1916, while Fish (1925, p. 143) describes the winter samples at Woods Hole as "literally filled with them" in some years. Nor does it seem likely that our nets can have consistently missed the richer aggregations of Temora, characteristic though it be of the latter to form "swarms of great density but of limited extent" (Farran, 1910, p. 72), when one considers that hauls were made at so many stations in different months and years.

We can only conclude that if Temora ever does occur in sufficient volume within our limits to be an important item there, this happens but rarely. And this prevailing scarcity, in the southern part of its range, raises the question of the origin of the local stock, for while we have encountered no centers of active reproduction, the distributional picture is not of a sort to suggest regular immigration, whether out from the coast line, or from the more abundant stocks that exist in winter in the Woods Hole region (Fish, 1925) and in late spring and early summer in the Gulf of Maine.

Temora stylifera

The only previous reports of this wide-ranging tropical copepod off the east coast of North America were near Cape Sable, Nova Scotia (Bigelow, 1926, p. 307), and at six "Albatross" stations in the general vicinity of Nantucket and Martha's Vineyard (Wilson, 1932). The records for 1929–1932 now show that it not rarely enters our area, and about equally frequent inshore and offshore (Fig. 35C). But it is so definitely a southern species there that only two out of the 22 captures of it were north of Delaware Bay—both in May—although a considerably greater number of stations were occupied in the northern sector than in the southern. The total number of records for this species was so small (22) that we doubt whether its capture at 50% of the southern stations in July and 19% in April, but at only 2–6% in February, May, or June, and not at all in October, represents any regularly seasonal cycle. The maximum catch, near Winter-quarter, July 1929 was at the rate of 26 c.c., with 6 c.c. and 9 c.c. at two stations off Chesapeake Bay in that same month, evidence that *T. stylifera* may be of faunistic importance locally in the south in midsummer. But the catches in other months were all minimal.

Other copepods

The regional distribution of records for other copepods, stray specimens of which were recorded here and there, is summarized in the following table:

Species	Inshore North	Offshore North	Inshore South	Offshore South
Aetidius armatus	0	0	0	3
Calanus minor	0	0	0	1
Undinula vulgaris	0	0	0	1
Calocalanus pavo	1	1	0	1
Centropages furcata	0	0	0	1
Euchaeta marina	0	0	0	1
Eurytemora sp.	1	0	1	0
Eurytemora herdmani	1	0	0	0
Pseudophaenna typica	0	0	0	1
Sapphirina sp.	0	2	0	1

CLADOCERANS

Podon and Evadne

The captures of Podon and Evadne do not adequately represent the volumetric status of these little cladocerans of neritic affinity, for they are so small that the greater part of the existent stocks may well have passed through the nets. Nevertheless the records for Evadne, between the offings of Martha's Vineyard, and of Chesapeake Bay, are generally distributed across the whole breadth of the continental shelf, while those for Podon also extend some 40 miles out from the coast (Fig. 35D). This distribution is in striking contrast to the situation as existing in the Gulf of Maine, where they have been seldom found more than 15–16 miles out from land (Bigelow, 1926; Fish and Johnson, 1937), suggesting that coastal water is much more generally dispersed offshore across the shelf west and south of Cape Cod than is the case to the east of the latter.

So far as frequency is concerned, the monthly averages suggest that the winter spores of Evadne do not hatch until well into the spring, but that the peak of abundance for it is reached very soon thereafter, to be followed by a decline in frequency through the summer, for the genus was not recorded at all in February and April, was at 21% of the stations in May, but at only 13% for June, and 7% for July, whereas in the Gulf of Maine the peak is not reached until late summer and early autumn (Bigelow, 1926, p. 307). The data for October 1931, when Evadne was detected at 3 out of 15 stations, would point to a secondary peak in autumn, if accepted at face value. But we hesitate to draw the apparently obvious conclusion, from so small a number of hauls, all from the outer half of the shelf.

The records for Podon are scattered through May, June, July, and October. But they are not sufficiently numerous to warrant deduction as to the seasonal cycle within this period.

The largest catches were at the rates of 6 c.c. and 9 c.c. for Evadne (both in May), of 1 c.c. for Podon, in October, all other records being based on small numbers of individuals.

Penilia

Penilia schmackeri Richard, was so abundant midway out on the shelf off Cape May on October 23, 1931 (121 c.c.) that it formed 21% of the total catch at one station there, though detected at only one other station off Winterquarter on that cruise, and not at all on any other. Indeed, the only previous record for it on the Atlantic coast of North America is at Beaufort, North Carolina, where according to Sudler (1899, p. 109), it suddenly appeared in swarms during June 1898, to disappear as suddenly. But the fact that it has been reported—always near land—in the Straits of Gibraltar and the Mediterranean, along the east coast of South America, off the west coast of Africa, off the Cape of Good Hope, off India, off Australia, off New Zealand, and off southern China (Gibitz, 1922; Ramner, 1933) shows that it is to be expected anywhere on the continental shelves in warm latitudes, and even in the temperate belt in the warm half of the year.

CHAETOGNATHS

Eukrohnia hamata

Eukrohnia hamata, an indicator of water from mid-depths along the continental slope (Bigelow, 1922, Fig. 50) within our limits, though a regular inhabitant of the deep water of the Gulf of Maine (Bigelow, 1926, p. 328), was recorded at 22 stations scattered along from the offing of Martha's Vineyard to that of Currituck, all but one of them, however, within some 20 miles of the continental edge (Fig. 36A). The seasonal distribution of these records (February, 0; April, 16; May, 4; June, 1; and July, 1) suggests that this species is much more apt to invade our area in early spring than at any other time of year.

In each case, the catch was of stray individuals only.

Sagitta elegans

Frequency. Sagitta elegans rivals *Calanus finmarchicus* in its frequency of occurrence throughout our area, but it is doubtful whether its range extends farther south than Latitude about 36°, for it was not taken near Cape Hatteras on the winter cruise of 1931, though present at every station to the northward on that occasion. It also corresponds to Calanus in being least frequent on the average in February (67% of the stations, all cruises combined). And while it may be widespread southward past the offing of Chesapeake Bay, at the end of winter, in some years (e.g., 1931), the offing of Delaware Bay may be the southern boundary to its range at that season in others, as was the case in 1932. And the fact that it is the southern margin of its range that most clearly shows these variations from winter to winter, accords with the general rule that it is in the north that it is most abundant, even at times when its distribution is universal to the southward, as well.

In the years when *S. elegans* is scarce or absent in the southern sector at the end of winter, its range expands southward as the season advances, as happened

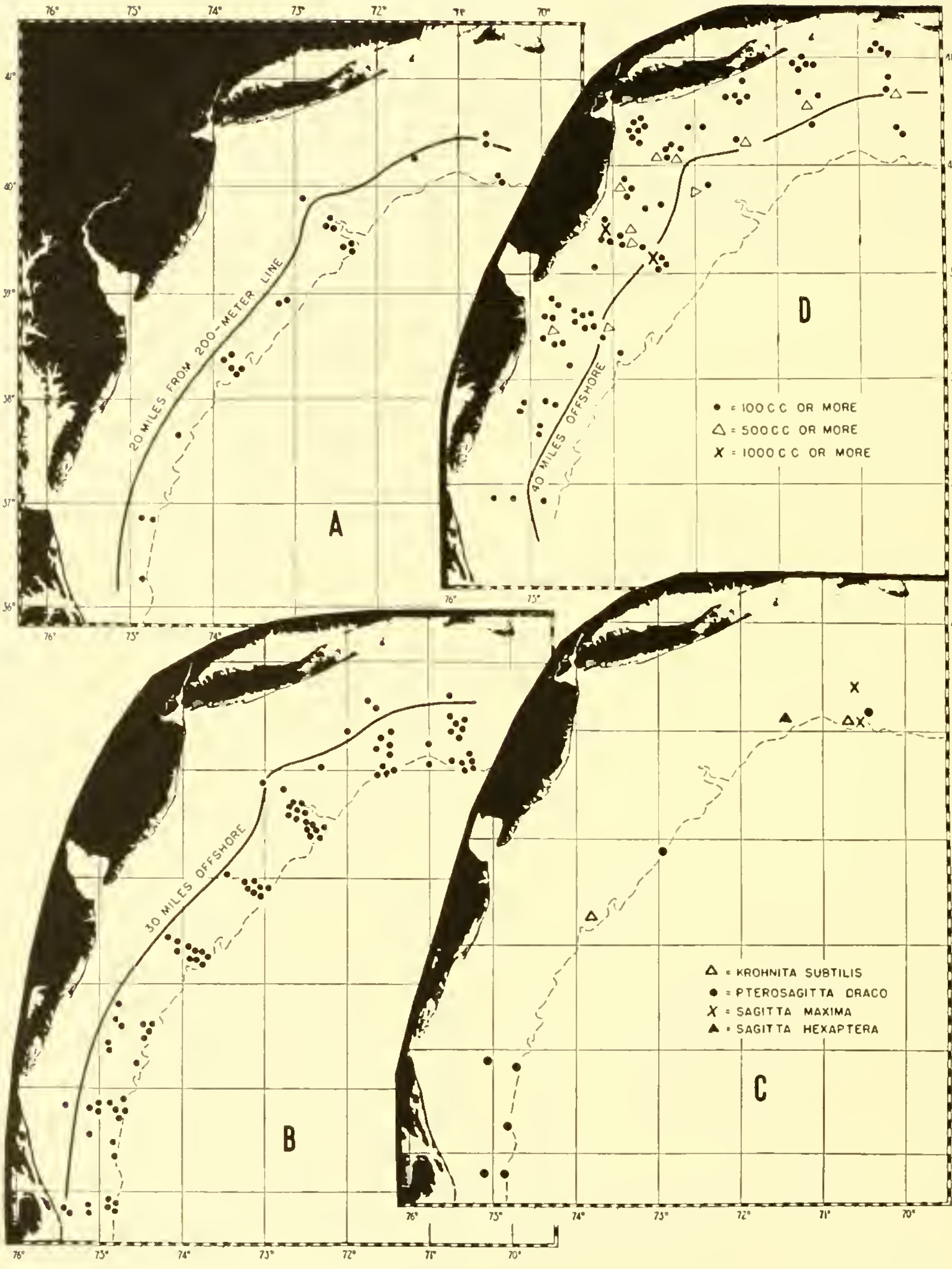


Fig. 36. Locality records, 1929–1932; A, *Eukrohnia hamata;* B, *Sagitta enflata;* C, *Krohnita subtilis, Pterosagitta draco, Sagitta maxima* and *S. hexaptera;* D, large volumes of *S. elegans.*

in 1929, when its boundary shifted about thirty miles in that direction between the third week of April and the third week of May; and again in 1932, when it was lacking south of Delaware Bay in February, but was taken at scattered stations to the offing of Chesapeake Bay, in May. And its presence at 74% of our stations, for April, and at 89% for May (all cruises combined) is perhaps a fair index to the normal expectation, taking one year with another. *S. elegans* was taken at every station on the continental shelf, in June, down to the offing of Chesapeake Bay in 1929, 1930, and 1931; at 97% of the stations in 1932—as close an approach to universal distribution as is ever likely to obtain for any planktonic animal, over any considerable extent of sea.

In the northern sector, it continues equally frequent into July in some years (1930, 100%; 1931, 95%), nearly as frequent in others (1929, 76%). But the facts that it had disappeared from the inshore stations off Chesapeake Bay between June and July of 1929, that it was lacking both there and near Delaware Bay in the latter month of 1916, that it was not found at all in the southern sector in July of 1913, and that it was lacking at three out of seven stations south from the New York profile in October 1931, show that it tends to become less regular in the southern part of its range from mid-summer to mid-autumn, or even to disappear over considerable areas there at this season. And this accords with Cowles' (1930) report of it as common inside Chesapeake Bay in winter and early spring, but very scarce or even absent there in summer.

In some years, as in 1916, *S. elegans* becomes universally distributed, once more, south to the offing of Chesapeake Bay by November, but its February status (p. 347), indicates that in other years its range may not expand southward again until spring.

The present data fail to show how far *S. elegans* may penetrate the estuaries, or other indentations of the coast. Cowles (1930), however, has already reported that it regularly enters Chesapeake Bay in considerable numbers, through the winter and spring with the drift of saline water near the bottom, and that while its numbers decrease going up the Bay, it may survive, in abundance, in salinities as low, even, as 13‰. Offshore, the boundary to its regular occurrence lies near the 200-meter contour, which accords with its neritic nature in boreal seas generally.

Abundance. In a year when *S. elegans* is relatively abundant in February (e.g., 1931), it may remain at about the same level through the spring and early summer, in the more productive inshore belt, increasing slightly meantime in the less productive offshore belt. But in years when it averages low in abundance in February or April (e.g., 1929, 1930, 1932), a decided augmentation may take place through the late spring, both inshore and offshore, to culminate either in June (1930, 1932), or in July (1929), though with wide irregularity from month to month, and with the richest centers often very small in extent. The fact that the volume of *S. elegans* averaged 30 times as great over the region as a whole, at the peak season, as in the preceding winter in 1932, and 46 times as great in the offshore belt in July as in April, in 1929, gives some measure of the magnitude of vernal augmentation in years of this type, while the rapidity with which the volume of *S. elegans* may increase at a given locality, with the advance of the season, may be illustrated by the following examples:

Station, Martha's Vineyard I, April 3, 1930, 99 c.c.; April 29, 1930, 418 c.c.
New York II, April 10, 1930, 20 c.c.; April 28, 1930, 203 c.c.
Cape May II, April 5, 1930, 1 c.c.; April 24, 1930, 166 c.c.
Martha's Vineyard I, May 19, 1932, 11 c.c.; May 28, 1932, 208 c.c.

At the seasonal peak, the volume of this chaetognath has averaged about 90 c.c. inshore and 40 c.c. offshore, for all years combined.

The evidence of 1931 suggests that an average decrease by about ½ in the average volume of *S. elegans*, is to be expected in the offshore belt, between mid-summer and mid-autumn (October). But nothing is known of its quantitative status then, or later in the season, in the inshore belt, except that it was reported in relatively high abundance, in the extreme northeastern sector, in January and February of 1936, by Clarke and Zinn (1937).

The only significant exceptions to the general rule that *S. elegans* has averaged somewhat more abundant volumetrically, in the inshore belt than the offshore, was in 1929, when the reverse was true during May, but with the more usual relationship reestablished in June. Evidently, then, this can be accepted as the normal state, interrupted only for brief periods, in some years, but not at all in others (Table, p. 351). For the series as a whole, the volume have averaged about three times as great inshore (57 c.c.) as offshore (22 c.c.), and large catches ($>$ 100 c.c.) have for the most part, been within 40 miles of land. But the strength of this inshore-offshore contrast has varied so widely from cruise to cruise that calculation of seasonal ratios would not be significant.

The order of north-south contrast has been much less regular, for while *S. elegans* averaged from 10–23 times as abundant in the north as in the south in one year (1929), it was most abundant in the south (though the spread was not so wide) in a second (1931), while a shift in the center of population from the northern sector to the southern took place in the other two years, between February and June in the one case (1930), but between the first and fourth weeks of May in the other (1932).

And the catches of 100 c.c. or more (whatever the month or year) have been distributed indifferently, north and south.

Average, maximum, and minimum volumes of *Sagitta elegans*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maxi-mum	Mini-mum
February	1930	17	2	19	1	9	87	0
	1931	121	16	29	73	58	431	0
	1932	<1	<1	<1	<1	<1	<1	0
April	1929	10	1	10	0	6	82	0
	1930	37	10	44	8	24	418	0
May	1929	22	35	46	2	25	229	0
	1930	60	37	39	58	49	230	0
	1931	132	19	54	158	84	406	0
	1932	28	12	16	9	18	203	0
June	1929	40	33	55	3	39	217	0
	1930	78	11	34	129	51	1296	0
	1931	136	88	61	225	118	448	<1
	1932	37	15	39	32	31	326	0
July	1929	105	46	81	73	78	520	0
	1930	44	16	27	—	27	129	0
	1931	45	23	37	—	37	242	0
October	1931	—	11	8	16	11	69	0

Annual differences. The fact that 1932 was somewhat the least productive year of the series for *S. elegans* (Table above), 1929 and 1931, on the whole, the most so, suggests that conditions are less favorable for this chaetognath in our area after a warm winter than after a cool. With *S. elegans* averaging nearly 4 times as abundant in some years (1929, 1931) as in another (1932), at the peak season, and more than 58 times as abundant at the end of winter, within a term of four years only, a longer observational series might reveal extremes still further apart.

Sources of the local stock. On the occasions when the boundary of occurrence for *S. elegans* shifts southward from April to June, as happened in the years 1929 and 1932 (p. 349), we may assume that dispersal from the populated waters farther north has been responsible, it being unlikely (in the case of so large an animal) that enough specimens were actually present in the south, early in the season (but passed through our nets) for the local increase to have been the result of their progeny. Cowles (1930), however, has already offered strong evidence that in others years, *elegans* may breed continuously from late winter through the spring as far south as the immediate offing of Chesapeake Bay, though perhaps never within the latter. And it seems sufficiently established that *S. elegans* is regularly endemic farther north, by the facts that the winter and early spring catches have contained a considerable proportion of very small individuals, and that the geographic locations of the richest catches have afforded no evidence of renewals from the waters to the east of our area.

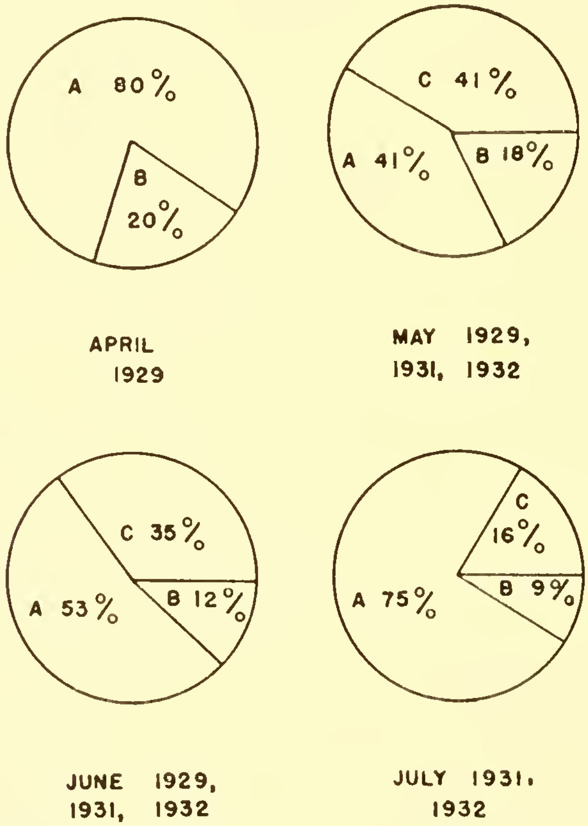


Fig. 37. *Sagitta elegans*: percentage of cases in which the deep catch was twice as great as the shoal (A), the shoal catch twice as great as the deep (B), and neither twice as great as the other (C).

Vertical distribution. The deeper catch of *S. elegans* was significantly the larger of the pair much more often than the reverse (Fig. 37) in every month when pertinent data were obtained, except for February (1932), when the numbers were not large enough to be significant in this respect. The extreme case was in April 1929, when *S. elegans* was twice as abundant deep as shoal at 80% of the stations, whereas May 1932 showed the closest approach to vertical uniformity with the deep catch significantly the larger at 35% of the stations, the shoal catch the larger at 21%, and with the one catch about as productive as the other at the remaining 44%.

The volumetric ratio of deep (20–40 meters) catch to shoal (less than 10 meters) has similarly averaged greater than 1 to 1 on every cruise (Table, below), tending to increase from the period April-June (average about 10 to 1) to July, when it averaged 131 to 1 for 1929 and 1931. Catches of 100 c.c. or greater were also made about twice as frequently, relatively, at 10–20 meters (16% of the cases) and at 20–40 meters (16%) as in hauls centering at depths smaller than 10 meters (7%). Thus, it seems sufficiently established that *S. elegans* has its center of abundance in the deeper strata of water below 10 meters. The combined data—if taken at face value—would, in fact, suggest that *S. elegans* averages somewhat the most abundant of all, at depths greater than 40 meters, at least in April, May, and June. But the situation was so variable in this respect from cruise to cruise that the ostensible richness of the deepest strata may perhaps have been caused by the chance that the net encountered rich concentrations of this species at one particular level, but missed them at another.

Average volumetric ratios of *S. elegans* at deeper levels relative to volumes at 10–0 meters

Month	Year	20–40 Meters	No. of Cases	More than 40 Meters	No. of Cases
April	1929	12.3 to 1	6	53.2 to 1	5
May	1929	10.9 to 1	8	48.0 to 1	12
	1931	5.6 to 1	16	1.2 to 1	6
	1932	4.7 to 1	57		
June	1929	10.1 to 1	12	31.3 to 1	11
	1931	32.3 to 1	24	1.2 to 1	3
	1932	6.2 to 1	44		
July	1929	168.6 to 1	10	10.2 to 1	8
	1931	83.0 to 1	14	24.9 to 1	4
Average, April, May, June		11.7 to 1		27.0 to 1	
Average, July		125.8 to 1		17.5 to 1	

The picture as regards diurnal migration is not as clear for *S. elegans*, as it is for *Calanus finmarchicus*, because of wide variability from station to station, in the volumetric ratio of the deeper catch to the shoaler, this having ranged between 540 to 1 and 0.1 to 1, by day, and between 348 to 1 and 0.01 to 1, by night, on one cruise or another. An average ratio, however, of about 37.3 to 1, by day, for April, May, and June[1] (all pertinent stations combined), but of only 5.7 to 1 by night, is evidence of a prevailing tendency for *S. elegans* to sink from the surface by day, to rise again by night, at this season of the year. But the great variability, just emphasized, shows that this tendency is frequently counterbalanced by other factors, probably by movements of the water. Catches made

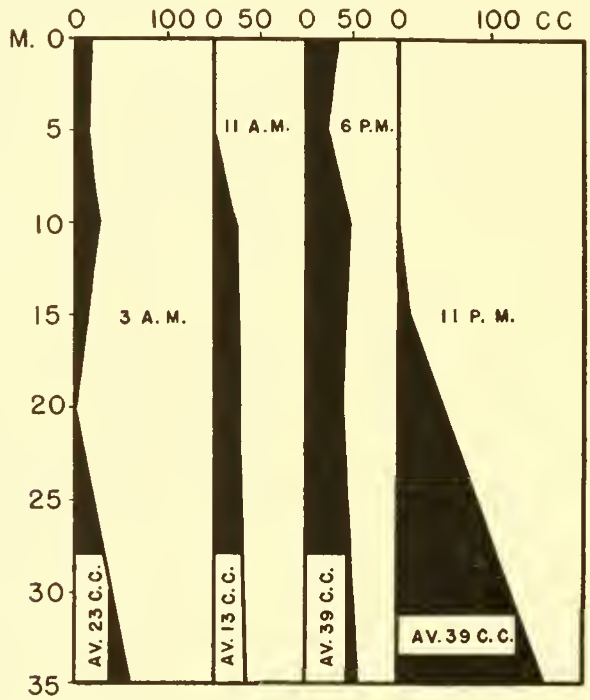


Fig. 38. Vertical distribution of *Sagitta elegans*, near Fire Island, May 17, 1929, at 3:00 a.m., 11:00 a.m., 6:00 p.m., and 11:00 p.m.

at 3 A.M., 11 A.M., 6 P.M., and 11 P.M., off Fire Island, May 17, 1929, do, in fact, provide as good an example of this for *S. elegans* (Fig. 38) as they do for Calanus (p. 312), for while diurnal migration may explain the impoverishment of the surface recorded between 3 A.M. and 11 A.M., an increase in the ratio of the deep catch to surface catch between 6 P.M. and midnight is not explicable on this basis, nor is the increase that took place between 11 A.M. and 6 P. M. in the total volume of plankton present in the water column as a whole. And the fact that the ratio of deep catch to shoal in July has averaged about the same

[1] *S. elegans* was so sparsely represented in February 1932, that this cruise is omitted from the calculation.

by day (65.4 to 1), as by night (61.9 to 1), is sufficient evidence that vertical migrations, of a diurnal sort, are almost entirely prohibited in mid-summer, probably by high temperature.

The vertical thermal gradient in our area is, for the most part so small from February through May that it offers no apparent explanation for the prevailing concentration of *S. elegans* at depths greater than 20 meters, at this season. But the average catches in hauls centering at different temperatures, irrespective of depth, show the following decrease with rising temperature for the several June and July cruises for 1929, 1931, and 1932, combined:

Average volumes of *S. elegans* at different temperatures

Temperature at mid-level of haul	6–8°	8.1–10°	10.1–12°	12.1–14°	14.1–16°	16.1–18°	18.1–20°	>20°
Average in c.c.	52	174	84	59	50	12	4	1
No. cases	37	31	43	39	37	21	30	30

On only four occasions, in fact, was the shoalest catch larger than the next deeper, at a station where the upper 10 meters were warmer than 16°, namely:

Station, New York IV, July 22, 1929, Surface, 21°, 12 c.c.;
58 meters, 8.1° less than 1 c.c.
New York III, June 7, 1932, 8 meters, 16.2°, 21 c.c.;
27 meters, 8.6°, less than 1 c.c.
Cape May III, June 16, 1932, 8 meters, 19°, 38 c.c.;
27 meters, 9.4°, 24 c.c.

This relationship between catch and temperature obviously suggests that the lower values are the more favorable for this species with 18–20° perhaps the upper limit for its continued existence. The warming of the surface thus appears to be the factor chiefly responsible for the rather abrupt rise between June and July, in the volumetric ratio of deep catches of *S. elegans* to shoal (p. 352), just as for Calanus, and likewise for the coincident break-down of effective diurnal migration.

We hesitate, however, to assert that 8–10° is the optimum for *S. elegans*, as the tabulation would suggest if accepted without reservation, for the chance that particular hauls hit or missed rich aggregations may have been partly responsible. And this is made the more likely by the following wide range of volumes from station to station at each temperature interval (irrespective of depth), in the years when hauls were made at two levels or more:

Temp.	6–8°	8.1–10°	10.1–12°	12.1–14°	14.1–16°	16.1–18°	18.1–20°	>20°
C. C.	<1–540	<1–1258	<1–1040	1–823	0–679	0–75	0–38	0–13

Sagitta enflata

This warm-oceanic chaetognath, already recorded not only along the continental slope, but coastwise south of Delaware Bay (Bigelow, 1915, Fig. 71; 1922, Fig. 50), and even as a stray in Chesapeake Bay (Cowles, 1930, p. 334), was found widespread from the one end of our area to the other, for about 30 miles in from the edge of the continent (Fig. 36B), which brings its area of most frequent occurrence close in to the land to the south of Chesapeake Bay. Northward, however, from Delaware Bay, the coastal belt has usually been bare of it, with the one notable exception that a large catch of juveniles was made close in to Martha's Vineyard in 1935. In this respect, the shelf west of Cape Cod contrasts strongly with the sector next to the east—George's Bank and the Gulf of Maine—where *S. enflata* has not yet been found inside the 200-meter contour.

The distribution of stations does not suggest any greater tendency for this species to enter our area more frequently in the one sector (north or south) than in the other. Its presence, however, at 6% of the stations in the offshore belt in February, at 24% in April, at 31% in May, at 22% in June, and at 15% in July, but at 80% in October, suggests that it invades the shelf least frequently in winter (as was to be expected) and most frequently in autumn, with some tendency toward a second (but minor) peak of frequency in the early spring.

The maximum catch was 66 c.c. off Winterquarter in October 1931, and four other catches of 3–7 c.c. were recorded in that same month. Other than this, the record of it in our waters is based on odd individuals only.

Sagitta serratodentata

Frequency. This warm-water chaetognath ranks among the half dozen most generally distributed members of the plankton in the offshore belt, north and south, where it was recorded at 92% of the total stations and at every station on 16 out of the 24 cruises. It was, in fact, at every station throughout the area, as a whole, for February 1930 and 1932. And it has averaged but little less frequent in the inshore belt in the south, than offshore. It has even been recorded occasionally in Chesapeake Bay (Cowles, 1930). But it has been much less frequent close to the land to the northward of Chesapeake Bay, and especially so to the eastward of New York (Fig. 39), where it failed altogether at 54 out of 77 stations.

In the face of this regional contrast, it is interesting and somewhat astonishing that segregation of the data by months fails to suggest any definitely seasonal gradient, in frequency of occurrence, for *S. serratodentata,* whether inshore, where the species is least frequent or offshore, where it is most so. At the most, some

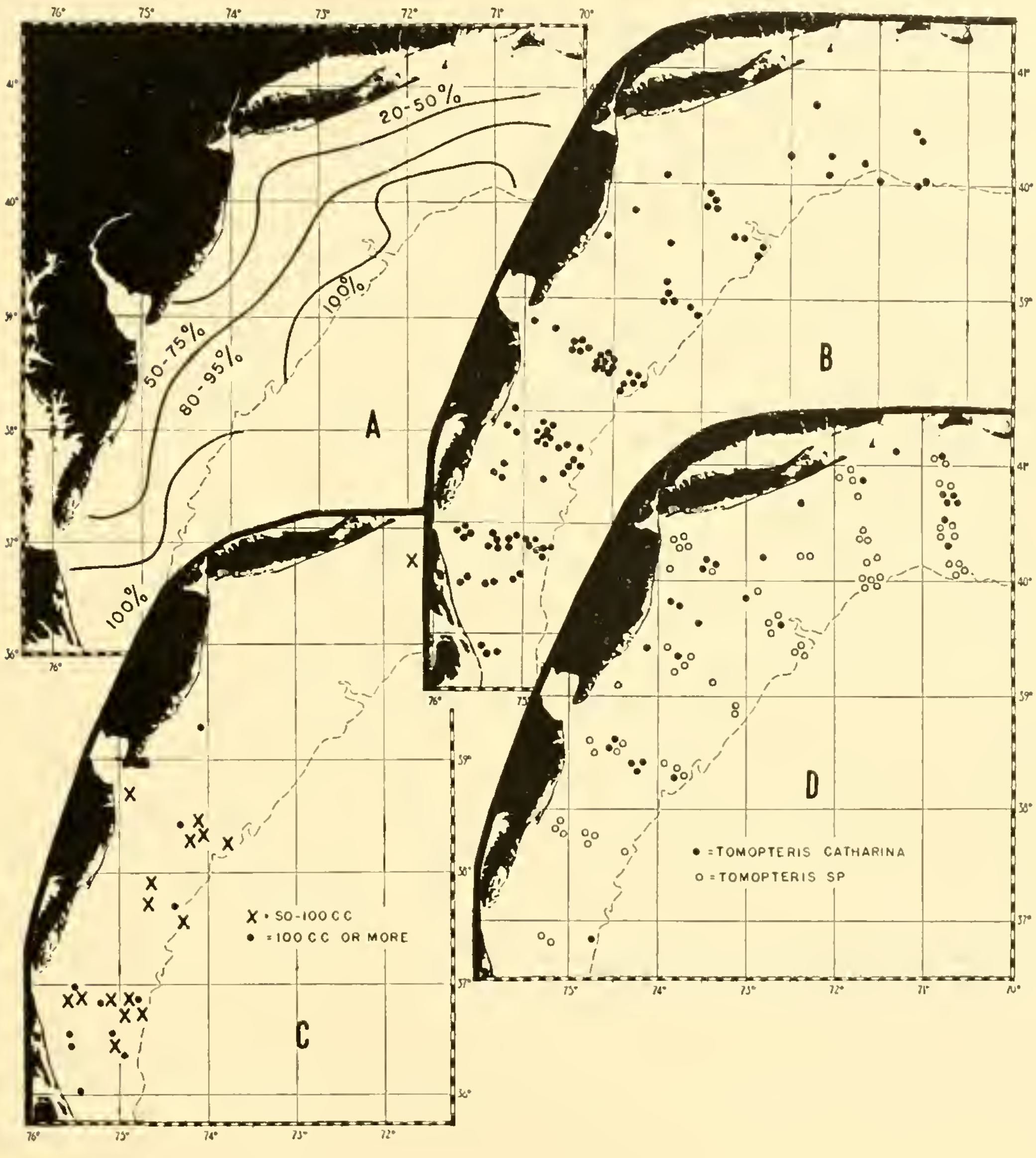


Fig. 39. A, relative frequency of occurrence of *Sagitta serratodentata* in different areas; B, locality records for volumes of *S. serratodentata* greater than 10 cc.; C, volumes of *S. serratodentata* greater than 50 cc.; D, locality records for *Tomopteris catherina* and for Tomopteris sp.?

decrease may be indicated from February-April to June-July for the inshore belt from New York eastward, but data here are perhaps not numerous enough to warrant definite conclusion.

Percentage of stations with *S. serratodentata*

Month	Year	Inshore	Offshore	North	South	Area surveyed
February	1930	100%	100%	100%	100%	100%
	1931	57	77	20	91	69
	1932	100	100	100	100	100
April	1929	69	84	46	100	76
	1930	86	100	87	97	93
May	1929	50	64	33	79	52
	1930	86	100	93	91	92
	1931	30	86	58	20	54
	1931	84	92	79	93	84
June	1929	30	64	25	75	43
	1930	36	100	65	50	62
	1931	47	100	62	77	67
	1931	58	93	61	100	72
July	1929	47	81	69	50	63
	1930	59	100	81	—	81
	1931	84	100	90	—	90
October	1931	—	100	100	100	100

Abundance. *S. serratodentata*, while ranking so high in our area in frequency of occurrence, ranks far below its relative, *S. elegans* (Table, p. 351) in volumetric abundance, for the highest average for it in any month was only 53 c.c., even in the subdivision that was richest in it at the time, with a general average, for all regions and months combined of only 12 c.c., contrasted with 225 c.c. and 39 c.c., respectively, for *S. elegans*; 589 c.c. and 144 c.c. for *Calanus finmarchicus*; and 208 c.c. and 37 c.c. for *Centropages typicus*. The maximum catch of *Sagitta serratodentata*—335 c.c.—likewise falls far below that for *S. elegans* (1296 c.c.), for Calanus (1532 c.c.), for Limacina (2666 c.c.), or for Centropages (1341 c.c.).

It is doubtful whether any definite inshore-offshore gradient, in average abundance could be deduced for *Sagitta serratodentata* from our data, for volumes have averaged about as large in the one belt as in the other, both in the south (average, 35 c.c., offshore; 25 c.c., inshore) and in the north (average, 6 c.c., inshore; 5 c.c., offshore), while one very large catch (335 c.c.), close to Atlantic City, on February 8, 1930, was responsible for the only case when any great preponderance was indicated for either sector—inshore, on this occasion. But *S. serratodentata* has on the whole averaged considerably more abundant in the southern sector than in the northern, not only for the series as a whole, but in most of the individual months as well, while in no months was there a strong contrast of the reverse order.

The contrast in this respect between the two sectors may, in fact, average as high as 13 to 1 for a given year as a whole (1931), or 35 to 1 for an individual cruise (February 1931), while the north-south ratio averaged 4 to 1 even in the year (1930) when it was smallest. And the southerly nature of this species is further illustrated by the fact that the rich catches (50 c.c. or more) have been very definitely concentrated from the offing of Delaware Bay southward (Fig. 39B, C). It appears, furthermore, that the northern boundary to common occurrence in abundance is a surprisingly sharp one, for while catches as great as 50 c.c. were made repeatedly on the Cape May profile this seldom happened north of the latter, though an occasional concentration (17–31 c.c.) of *serratodentata* may develop as far east as the Martha's Vineyard profile (e.g., July, 1929), or even in the Gulf of Maine, for that matter.

The volume of *S. serratodentata* in the southern sector, inshore and offshore, has averaged largest either in February or in April, and considerably smaller in May, but with little evidence of any further seasonal alteration through midsummer, while the only high average for the north was also recorded in February. On the other hand, the majority of occasions when *Sagitta serratodentata* has averaged nearly or quite as abundant in the north as in the south have fallen within the period mid-May to October, whereas most of the occasions when there was a notable preponderance of this species in the south have fallen as early as mid-May, or earlier. Averages, for all cruises combined, similarly show the north-south ratio as decreasing from 24 to 1 in February and 18–19 to 1 in April, to 11 to 1 in May, 7 to 1 in June, 1 to 1 in July (one cruise only), and 5 to 1 in October.

The coastal belt from Delaware Bay northward, thus appears more and more nearly to equal the more southerly and offshore waters in suitability as an environment through the late spring and early summer, as the water warms. But it is doubtful whether the small recorded contrast in this respect between July and October is seasonally significant, for the one set of observations was made in one year, the other in another. Neither is information on this point available for the late autumn or early winter.

The regularity of occurrence of this chaetognath, combined with the narrowness of its fluctuations from year to year (p. 360) points to local reproduction rather than to immigration as the chief source of the stock in our waters. And the fact that in 1932 the center of abundance continued in the same region off

Chesapeake Bay from February through the first three weeks in May is further evidence that the coincident decrease that took place in its volumetric abundance during that period was primarily the result of a predominance of death rate over production, not of a mass drift of population away from the locality where it had previously been relatively plentiful.

Average and maximum volumes of *S. serratodentata*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	53	10	36	25	30	335
	1931	55	2	1	35	23	170
	1932	19	15	2	24	18	70
April	1929	26	14	2	37	21	129
	1930	7	10	5	12	8	122
May	1929	4	10	<1	14	7	64
	1930	1	1	9	5	5	230
	1931	<1	1	<1	<1	<1	12
	1932	1	7	1	11	5	98
June	1929	2	4	1	3	3	35
	1930	<1	<1	<1	<1	<1	3
	1931	1	14	<1	15	6	133
	1932	1	7	3	13	6	70
July	1929	2	7	4	5	4	31
	1930	<1	6	3	—	3	31
	1931	7	1	5	—	5	64
October	1931	—	12	5	22	12	69

Annual Variations. The average volumes of *S. serratodentata*, for the area as a whole (including the poorer areas with the richer) and for all cruises for different months combined were 9.5 c.c. for 1929, 9.4 c.c. for 1930, 8.2 c.c. for 1931, and 9.9 c.c. for 1932, a varietal range much smaller than the probable error of observations as rough as ours. And the frequency for any year as a whole was only about 1.4 times as great at the maximum (85%, 1932) as at the minimum (58%, for 1929). Such evidence marks this species as varying much less widely in its status in our area from year to year than do most of the members of the dominant community that are volumetrically more abundant there.

Other chaetognaths

Other species of chaetognaths (*Sagitta hexaptera, Sagitta maxima, Krohnita subtilis, Pterosagitta draco*), recorded over the outer edge of the shelf, at the localities shown on Fig. 36C, D are no doubt to be classed as strays from offshore. In every case, the records are based on occasional individuals.

ANNELIDS

Tomopteris

Tomopteris catharina was taken at localities widely scattered, inshore and offshore alike, from the Martha's Vineyard profile to the Chesapeake profile. And inclusion of the additional locality records for tomopterids probably belonging to *catharina*, but not positively identifiable because of their poor condition (Fig. 39D), would show this species as generally distributed throughout our area between these limits, as it is also in the Gulf of Maine (Bigelow, 1926, Fig. 94), and about as frequent in one subdivision as in another. We have only one record, however, of Tomopteris of any species on the continental shelf, south of Chesapeake Bay, an additional reason for referring the doubtful specimens to *T. catharina*.

Although so general, *T. catharina* appears to be much less frequent, in the waters as a whole to the west of Cape Cod, than it is in the Gulf of Maine to the east, for while it was taken at 38–50% of the stations there, February-May, August, and December-January (Bigelow, 1926), its maximum frequency in our area in any month was only 27%, the average about 14% for all months combined. Monthly frequencies of 20% in February, 4% in April, 21–27% in May-June, and 7% in July and October, also mark it as more definitely seasonal in the southwestern part of its range (with peaks in late winter and in May-June) than it is in the more typically boreal regions to the east and north, where the only indication of any seasonal cycle, yet reported, is an apparent scarcity in late autumn and early winter.

It is interesting that a species so constantly present, and so generally distributed, should never, in all our experience have developed a population abundant enough to yield even one catch as large as 1 c.c., for in the case of so large an animal that would have meant only a few hundred individuals. And the case is similar in the Gulf of Maine, where the catches were "usually from one to half a dozen individuals per haul" (Bigelow, 1926, p. 335).

Other annelids

Annelid worms (not yet identified) were recorded at one station only (off Bodie Island, April 8, 1930). But on that occasion they were in such large volume (47 c.c. or about 24% of the total catch) as to show that they, rarely, may be an item of considerable local importance in the plankton though never (by present evidence) over any considerable area within our limits.

MEDUSAE

Aglantha digitale[1]

Regional. At the end of winter the records for Aglantha—scattered, widespread from the offing of Martha's Vineyard, southward to Cape Hatteras—have (with two exceptions) been within 40 miles of the coast. With the advance of the season, it tends to become more frequent inshore, having been recorded at 80–100% of the stations in that belt on each of the May cruises of 1930 and 1932.

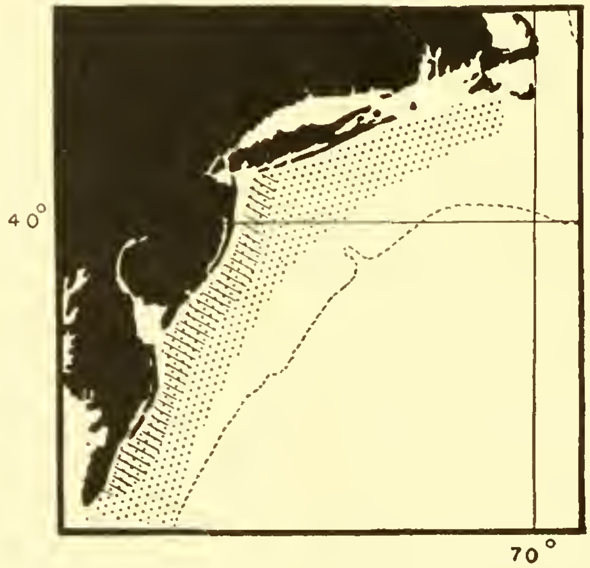


Fig. 40. Areas of occurrence of *Aglantha digitale* in February (dotted) and in April (hatched) 1930.

It appears also characteristic for it to disperse offshore during the last half of the spring, judging from its presence at 57–90% of the offshore stations on those same cruises, and at about the same percentage offshore (46%) as inshore (45%) in that month of 1931. That Aglantha is to be classed as an inshore form in our area (notwithstanding its holoplanktonic nature and wide distribution), also appears in the fact that catches greater than 10 c.c. have (with one exception) been confined to the inshore belt in February, April, and May, though with the offshore boundary for this level of abundance lying some 20 miles farther out to sea for June (Fig. 40, 41). It appears, however, to be about equally frequent north

[1] For a recent discussion of varietal relationships within this species, see Ranson (1936).

as south, and equally abundant, for the catches, for May, June, and July, combined have averaged about the same in the one sector as in the other (39 c.c., north; 43 c.c., south).

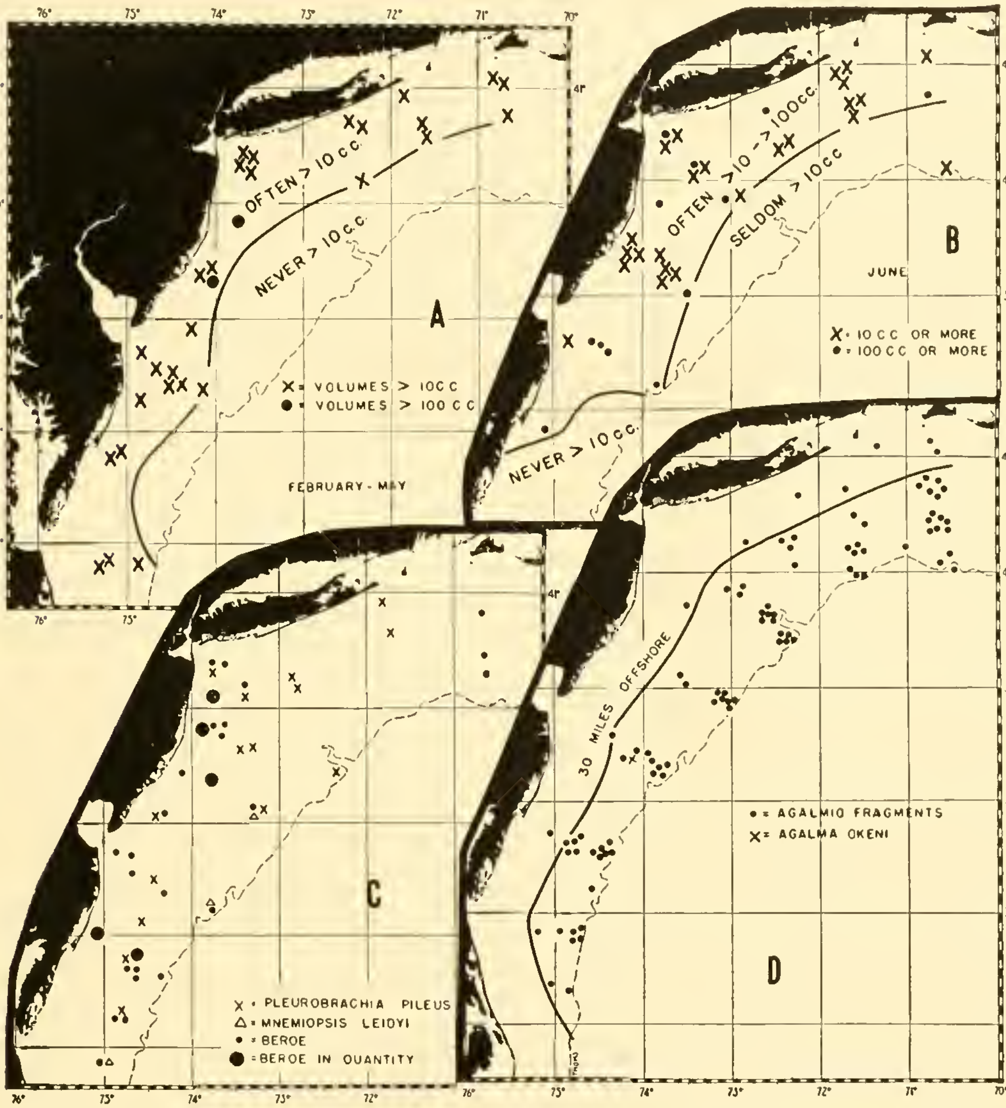


Fig. 41. A, *Aglantha digitale*, regional abundance, February–May, all cruises combined; B, Aglantha, regional abundance for June; C, locality records for Pleurobrachia and Mnemiopsis and for large and small catches of Beroe, 1929–1932; D, locality records for agalmid fragments and *Agalma okeni.*

Seasonal and annual variations. The fact that Aglantha may appear only sporadically in some years, as in 1929, when it was recognized at two stations only (both in July), but widespread and in considerable volume in others (e.g., 1932), shows that annual variation in its status is wide. More or less vernal augmentation seems, however, to be characteristic for it in its years of abundance. In 1930, for example, it increased in average volume from less than 1 c.c. in April to about 8 c.c. in May-June, while in 1932, the minimal population (average, less than 1 c.c.) existing in early May, was succeeded by average volumes of 56 c.c. inshore, 17 c.c. offshore, 37 c.c. in the north, and 33 c.c. in the south in the succeeding month. Unfortunately, we lack data later in the season, for that particular year. But the facts that Aglantha averaged less than 1 c.c., in any subdivision in July of 1930 and 1931, that it was found only twice west of Cape Cod in the summer of 1913 (Bigelow, 1915), and that the richest catch in October 1931 was less than 1 c.c., added to its apparent absence in 1916, whether in August or in November, marks it as definitely a spring and early summer species, as far as occurrence in significant numbers is concerned.

The very wide annual differences recorded within so short a series of observations, between years (1932), when Aglantha is in high frequency with a very considerable vernal augmentation, as described above, and those (1929), when it is represented within our boundaries by stray individuals only, are most reasonably explained on the assumption that while it may be generally and effectively endemic in some years, it may disappear altogether in others, with repopulation depending on immigration from the east and north.

Average and maximum volumes of *Aglantha digitale*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	2	0	1	1	1	10
	1931	<1	0	<1	<1	<1	<1
	1932	<1	<1	<1	<1	<1	<1
April	1929						
	1930	<1	<1	<1	<1	<1	10
May	1929						
	1930	7	1	3	6	4	32
	1931	<1	<1	<1	<1	<1	<1
	1932	17	8	9	12	11	180
June	1929						
	1930	7	1	5	1	4	62
	1931	<1	<1	<1	<1	<1	2
	1932	56	17	37	33	40	191
July	1929	<1	<1	<1	0	<1	<1
	1930	0	1	<1	—	<1	7
	1931	<1	<1	<1	—	<1	<1
October	1931	—	<1	<1	<1	<1	<1

Leptomedusae

A mixed population of small leptomedusae, belonging for the most part to the genus Obelia, call for notice here, since they formed about 1% of the catch in May and June 1932, as well as in July 1929, and 4% in May 1931 (Table, p. 229). In frequency of occurrence these have shown an unmistakable seasonal cycle, for while wholly lacking in February of either year, and at only 3% of the stations in April, they were at 34% in May, and at 18% in June, but at only 10% in July, while they were not taken at all on the one October cruise (1931)—at least in the offshore belt, to which the latter survey was confined.

These medusae have proved much more frequent inshore (24% of the stations, April-July) than offshore (3%), as was to be expected; also more frequent in the north (13%) than in the south (3%).

The average catches, for the months when they occurred in more than minimal numbers, show the same contrast between larger inshore and smaller offshore as do the average frequencies of occurrence; all thirteen of the catches larger than 50 c.c. were, in fact, made inshore. But it is doubtful whether any strong north-south contrast in their abundance, is characteristic, for while catches larger than 50 c.c. were made more often south (10) than north (3), the average volumes were not only somewhat larger south than north as tabulated below, but the largest average volume for either subdivision, in any individual month (May 1931, 32 c.c.) was also in the south.

Average and maximum volumes of Leptomedusae

Month	Inshore	Offshore	North	South	Area surveyed	Maxima
May	11	<1	5	11	6	188
June	3	1	3	2	2	120
July	6	<1	3	5[1]	4	185
Average	7	<1	4	6	4	

In the month of greatest abundance, the average volume of these small leptolines was more than 19 times as great for the area as a whole in the year when they were most abundant (1931, average, 19 c.c.), than in the year (1930) when they were least so; when in fact they were not detected at all though minimal numbers may have actually been present in the water.

[1] 1929 only.

Other medusae

Other medusae were negligible from the volumetric standpoint, none other than those mentioned above having formed as much as 1% of any individual catch: nor has time allowed complete identification of the scattered specimens of various species that were included in the catches. We refer the reader to earlier papers (Bigelow, 1915; 1922) for lists of the hydro- and scyphomedusae taken during the summers of 1913 and 1916. Captures of *Laodicea cruciata* off Chesapeake Bay and off Hog Island, in July 1929, added to the locality records for it in the summer of 1913 (Bigelow, 1915, Fig. 79) afford cumulative evidence that this species is widespread in summer well out on the shelf in the southern sector, though apparently it is closely confined to the vicinity of the shore line in the northern, for it was not represented there in any of our July collections, though plentiful at that season along the coasts of southern New England (Mayer, 1910, p. 203). The genus Liriope also proves to occur over the shelf in the southernmost sector in February, as well as in summer, when the inshore species (or race?) *scutigera* is common in and off the southern harbors and bays, while the genus Aequorea—already known to be widespread throughout the area in summer (Bigelow, 1915, p. 319, Fig. 79)—also occurs sparingly in May and June, as well, at least in the southern sector.

SIPHONOPHORES

Agalmidae

Recent towings have shown that one member of this group, *Stephanomia cara*, occasionally swarms in the Gulf of Maine. But we have no evidence that any agalmid is ever of volumetric importance in the planktonic community of the shelf waters west or south of Cape Cod, for while agalmid fragments were recorded at some 93 stations (Fig. 41D), they did not form as much as 1% of the total volume in any subdivision in any individual month. Agalmids appear to be about equally frequent north and south. But the distributional picture shows them to be much more frequent offshore than inshore, in our area, for about 76% of the stations of record, lay in the former belt contrasted with about 24% only in the latter. The seasonal distribution of the records (present at 11% of the stations in February, at 0% in April, at 13–23% in May and June, at 5% in July, and at 93% in October) suggests a decided peak of frequency in autumn, alternating with a period of great impoverishment in the early spring. Previous experience (Bigelow, 1915, Fig. 81) would suggest that in the northern sector, we were dealing with both *Stephanomia cara* and with *Agalma elegans*, and with the latter alone in the southern sector. But the specimens were all in condition so fragmentary (bare stems, or mere remnants of nectophores and bracts), as to prevent identification.

Muggiaea kochii

The records for this calycophore are confined to the south, one for June, and eight for July, all in the year 1929. In the latter month, the average catch of *M. kochii*, "south," was, indeed, 5 c.c., equivalent to about 2% of the total plankton for that sector at the time (Table, p. 229) with a maximum of 19 c.c. But the fact that it was not recorded at all within our limits, except in the summer of that one year, shows that such invasions occur less frequently off our coasts than they do in the English Channel, where Russell (1934) found it quite regularly, in summer, from 1925 to 1931. We have yet to learn whether *M. kochii* is a reliable indicator—other than of warm water in general—within our limits. It is worth comment, however, that the record (so far as it goes) suggests that *M. kochii* and *M. atlantica* are as mutually exclusive in our area as Russell (1934) has found them to be in English waters, for all our records for the former were in one year (1929), those for the latter in another (1930).

Other Siphonophores

The seasonal incidence of the only other siphonophores that were taken at more than two stations each, was as follows:

Abylopsis tetragona, February, 5 stations; May, 2 stations; July, 1 station; October, 1 station.
Bassia bassensis, February, 1 station; May, 2 stations; June, 3 stations.
Lensia conoidea, May, 6 stations; June, 4 stations; July, 3 stations; October, 2 stations.
Muggiaea atlantica, February, 3 stations; April, 5 stations; all in 1930.

Most of the localities of capture for each of these lie close to the 200-meter contour, and this applies equally to the few other members of the group that were recorded within our limits (Fig. 42). In most cases, the records of siphonophores other than agalmids and *Muggiaea kochii* have been based on odd specimens only.

The Portugese man-of-war (Physalia) drifts in to the coast, near Woods Hole, in considerable numbers in some years, in summer or early autumn after strong southerly winds. And we have heard reports of them at various localities in on the shelf to the southward. Velella and Porpita have also been recorded at Woods Hole and Newport, Rhode Island (Sumner, Osburn, and Cole, 1904,

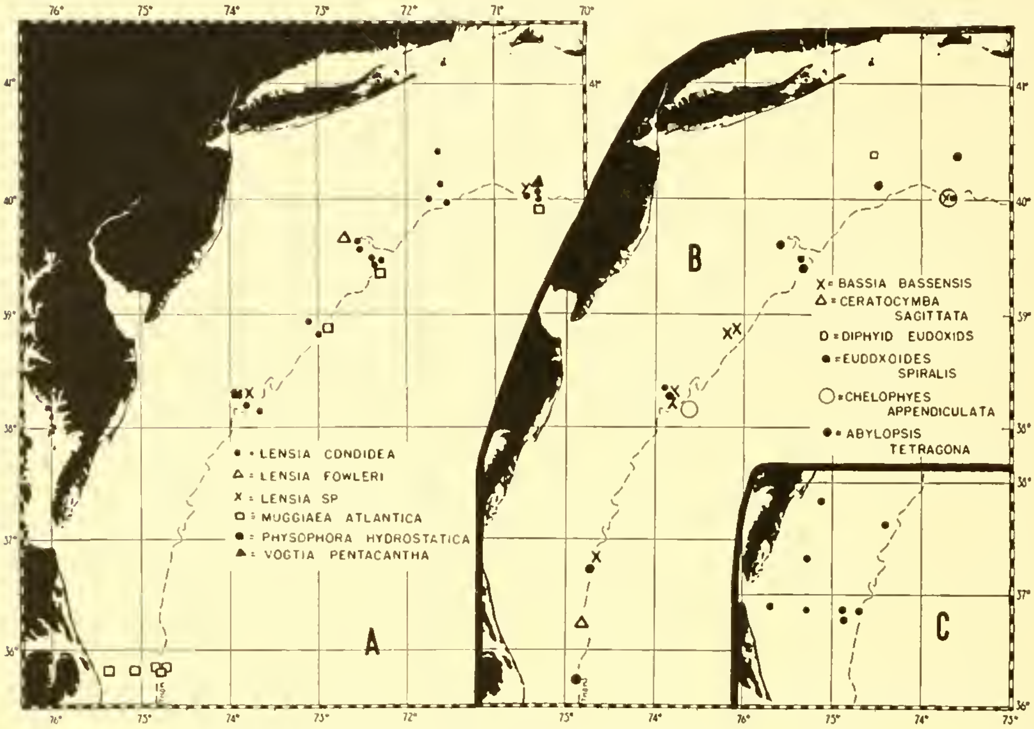


Fig. 42. Locality records, all cruises combined: A, *Lensia conoidia*, *L. fowleri*, *Muggiaea atlantica*, *Physophora hydrostatica*, and *Vogtia pentacantha;* B, *Bassia bassensis*, *Ceratocymba sagittata*, dyphiid eudoxids, *Eudoxoides spiralis*, *Chelophyes appendiculata*, *Abylopsis tetragona;* C, *Muggiaea kochii.*

p. 574). None of these genera have any real place, however, in the plankton of our area, except as waifs from tropical waters; neither were any of them represented in the present collections.

CTENOPHORES

Beroe sp.

Our records for Beroe are based chiefly on field notes in the station log books, and on fragments battered beyond specific recognition. Previous experience justifies us, however, in assuming that the two species, *cucumis* and *forskalii*, were both represented in the catches (Bigelow, 1915, p. 316; 1926, p. 372).

The earlier record of Beroe within our limits was confined chiefly to the offing of Chesapeake Bay, where *B. forskalii* was abundant in July in 1913 and

1916. Since that time, Beroe has been reported at a number of stations thence northward to New York and again in the offing of Martha's Vineyard, though once only in the intervening sector. The records include February, May, June, and July—there are none for April or for October—but large catches were noted in the log only in June (3 instances) and in July (1 instance). And they were likewise concentrated regionally, inshore, between the Atlantic City and Winter-quarter profiles (Fig. 41C).

The most we dare to hazard from the foregoing is that Beroe may occasionally multiply to great abundance in the inshore belt, between the offings of Chesapeake Bay and of Atlantic City, most frequently toward the south, perhaps due to the influence of the outflow from Chesapeake Bay, nor have we any evidence that Beroe is ever an important factor in the plankton of the north-eastern sector of our area, or of the offshore belt, south or north. Rich aggregations of Beroe seem, also, to be confined to the summer months, suggesting that *forskalii* is the species chiefly responsible.

Pleurobrachia pileus

During the summer of 1913, this familiar ctenophore was taken at all but two of the stations over the shelf, and in such abundance in the inshore belt between the New York and Cape May profiles that it practically monopolized the deeper water layers there. In 1916, however, the "Grampus" had it at but four stations within our limits at this same season, once only in any abundance (off Chesapeake Bay), and not at all in that November, while it was detected at only 16 of the 604 stations for the period 1929–1932 (Fig. 41C). Definite record of it within our limits has also been confined so far to May, June, and July-August, whatever the year.

As already remarked Pleurobrachia may have been "more widespread in small numbers than these captures suggest, such a fragile organism being easily destroyed in the mass of unsorted plankton" (Bigelow, 1922, p. 158). Nevertheless, the evidence seems sufficiently convincing that while this ctenophore is to be expected anywhere within our limits—offshore and inshore alike—and while it sometimes multiplies enormously, locally, near land, such events are unusual, and perhaps confined to summers of such years as 1913, when the surface waters warm to a temperature somewhat higher than usual. For a further discussion of the local status of this ctenophore, see Bigelow, 1915, p. 321.

Other Ctenophores

In the summer of 1913, the large lobate ctenophore, *Mnemiopsis leidyi*, was not only distributed generally over the inshore belt southward from Barnegat, but swarmed in the surface waters near the coast between that point and Cape May to the practical exclusion of everything else, as described elsewhere (Bigelow, 1915, p. 323). It was again encountered in abundance locally, in that same general region in August 1916, though its observed range was then restricted to the vicinity and offing of Delaware Bay (Bigelow, 1922, p. 158). And the fact that it has been reported near Woods Hole in every month in the year (Sumner, Cole, and Osborne, 1904, p. 579) points to its constant presence in greater or lesser number and at one stage of development or another, along the inshore belt in general.

Unfortunately, the catches for 1929–1932, add nothing to the foregoing, for if they did originally contain any representation of Mnemiopsis, the latter had been battered beyond recognition before the collections were examined, either in the nets, or among the other more resistant animals after capture. And while "Mnemiopsis" is occasionally named in the station log book, the specimens in question may actually have been some other lobate genus.

The positive record for Mnemiopsis is, however, sufficient to show that it is likely to play a very important role in the general planktonic community over considerable areas in the inshore belt at least near the surface, in any year when summer temperatures are relatively high, and locally even in years when temperatures are relatively low. But we have no definite record, as yet, of such a happening to the eastward of New York, except close in to the coast, as at Woods Hole, where Mnemiopsis swarms in some summers. Neither have we any reason to suppose that the adult Mnemiopsis ever occurs beyond the Martha's Vineyard profile, unless as a stray destined to perish in the colder waters of George's Bank, of Nantucket Shoals, or of the Gulf of Maine, to which a drift in that direction would carry it, but where it has never been recorded. If, however, low temperature be actually the barrier to its dispersal in that direction, we must assume that the young stages of this ctenophore are much more resistent to low temperature than is the adult, else this species could not survive the winter chilling to which the waters of the continental shelf are yearly subjected, southward to Chesapeake Bay. Mnemiopsis appears also to be definitely neritic in habit, for while it has been recorded well out on the shelf (Bigelow, 1915, Fig. 80), the largest catches of it were made near shore. During the summer of 1913, when Mnemiopsis was more abundant than at any other time during our observational series, it was taken only close to the surface, which accords with its frequent abundance, right in to the tide line around Woods Hole. Consequently, "the swarms of Mnemiopsis and of Pleurobrachia were mutually exclusive" (Bigelow, 1915, p. 324).

The evidence at hand that adult Mnemiopsis is not abundant—if it occurs at all—in waters colder than about 20°, or more than a few miles out from the coast inclines us to believe that lobate ctenophores of large size, six liters of which were reported in the log book (under the name "Mnemiopsis"), as taken near the outer edge of the shelf off Cape May on May 15, 1929, and as clogging the nets midway out, off Chesapeake Bay, two days later, actually referred to the northern species, *Bolinopsis infundibulum*, which has long been known to abound from Arctic Seas southward to the Gulf of Maine (Bigelow, 1926, p. 372) on our side of the Atlantic.

PROTOZOANS

Our nets were too coarse of mesh for sampling any but the largest protozoa. But the catches made off Bodie Island and off Currituck in May 1929 yielded a few Noctiluca, which had already been found in great abundance at the mouth of Chesapeake Bay in November 1916 (Bigelow, 1922, p. 163); cumulative evidence that it is of widespread occurrence in the southernmost sector, in late spring and autumn. This agrees with its status in Chesapeake Bay, where it is most plentiful at this season, and least so in January and March (Cowles, 1930, p. 328).

BIBLIOGRAPHY

Apstein, C.

1906. Plankton in Nord- und Ostsee auf den deutschen Terminfahrten. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. IX, pp. 1–25, 14 figs., 10 tables.

Beebe, William

1929. Deep Sea Fish of the Hudson Gorge. Zoologica. Sci. Contr. N. Y. Zool. Soc., Vol. XII, No. 1, 19 pp., 1 textfig.

Bigelow, H. B.

1914. Oceanography and Plankton of Massachusetts Bay and Adjacent Waters, November, 1912-May, 1913. Bull. Mus. Comp. Zool., Vol. LVIII, No. 10, pp. 385–419, 7 textfigs., 1 pl.

1915. Exploration of the Coast Water between Nova Scotia and Chesapeake Bay, July and August, 1913, by the U. S. Fisheries Schooner Grampus. Oceanography and Plankton. Bull. Mus. Comp. Zool., Vol. LIX, No. 4, pp. 151–359, 82 textfigs., 2 pls.

1922. Exploration of the Coastal Water off the Northeastern United States in 1916 by the U. S. Fisheries Schooner *Grampus*. Bull. Mus. Comp. Zool., Vol. LXV, No. 5, pp. 87–188, 53 textfigs.

1926. Plankton of the Offshore Waters of the Gulf of Maine. Bull. U. S. Bureau of Fisheries, Vol. XL, 1924 (1926), Part 2, pp. 1–509, 134 figs.

1933. Studies of the Waters on the Continental Shelf, Cape Cod to Chesapeake Bay. I. The Cycle of Temperature. Papers in Physical Oceanogr. and Meteorol., Vol. II, No. 4, 135 pp., 66 textfigs.

Bigelow, Henry B., and Schroeder, William C.

1939. Notes on the Fauna above Mud Bottom in Deep Water in the Gulf of Maine. Biol. Bull., Vol. LXXI, No. 3, p. 303-324, 8 textfigs.

Bigelow, Henry B., and Sears, Mary

1935. Studies of the Waters on the Continental Shelf, Cape Cod to Chesapeake Bay. II. Salinity. Papers in Physical Oceanogr. and Meteorol., Vol. IV, No. 1, 94 pp., 55 textfigs.

1937. Siphonophorae. Rep. Dan. Ocean. Exp. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. II, Biology, H. 2, 144 pp., 83 textfigs.

Bigelow, Henry B., and Welsh, William W.

1925. Fishes of the Gulf of Maine. Bull. U. S. Bureau of Fisheries, Vol. XL, 1924 (1925), Part I, 567 pp., 278 figs.

Boschma, H.

1936. Biological data. Snellius-Exped. in the Eastern Part of the Netherlands East-Indies 1929–1930, Vol. VI, 29 pp., 11 textfigs., 1 chart.

Büse, Theodor

1915. Quantitative Untersuchungen von Planktonfängen des Feuerschiffes "Fehmarnbelt" vom April 1910 bis Marz, 1911. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XVII, pp. 229–280, 3 textfigs., 7 tables.

BRANDT, K.

1898. Beiträge zur Kenntniss der chemischen Zusammensetzung der Planktons. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. 3, pp. 43–90, Tables A-G.

CAMPBELL, M. H.

1934. The Life History and Post Embryonic Development of the Copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. Jour. Biol. Board Canada, Vol. 1, No. 1, pp. 1–65, 18 textfigs.

CLARKE, GEORGE L., and ZINN, DONALD

1937. Seasonal Production of Zoöplankton off Woods Hole with Special Reference to Calanus finmarchicus. Biol. Bull., Vol. LXXIII, No. 3, pp. 464–487, 7 textfigs.

CONSEIL PERMANENT INTERNATIONAL POUR L'EXPLORATION DE LA MER

1904. Bulletin des Résultats acquis pendant les courses périodiques. Année 1903–1904, 230 pp.

1905. Bulletin des Résultats acquis pendant les courses périodiques. Année 1904–1905, 195 pp.

1907. Bulletin Trimestriel des Résultats acquis pendant les Croisières périodiques et dans les Périodes intermédiares. Année 1906–1907, No. 1, Juillet-Septembre 1906, Part D, 38 pp.

COWLES, R. P.

1930. A Biological Study of the Offshore Waters of Chesapeake Bay. Bull. U. S Bureau of Fisheries, Vol. XLVI, 1930, pp. 277–381, 16 textfigs.

DAMAS, D.

1905. Notes biologiques sur les Copépodes de la Mer Norvégienne. Publ. Circ., No. 22, Cons. Perm. Int. Expl. de la Mer, 23 pp., Pl. 1.

DELFF, CHRISTIAN

1912. Beiträge zur Kenntniss der chemischen Zusammensetzung wirbelloser Meerestiere. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel., Vol. XIV, pp. 51–81.

FARRAN, G. P.

1910. Copepoda (Part). Resumé sur le Plankton des Mers. Bull trimestr., Cons. Perm. Int. Expl. de la Mer, Part 1, 1910 pp. 60–80, Pls. VIII-X.

FISH, CHARLES J.

1925. Seasonal Distribution of the Plankton of the Woods Hole Region. Bull. U. S. Bureau of Fisheries, Vol. XLI, 1925, pp. 91–179, 81 textfigs.

1936. The Biology of Calanus finmarchicus in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXX, No. 1, pp. 118–141, 11 textfigs.

1936a. The Biology of Pseudocalanus minutus in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXX, No. 2, pp. 193–216, 9 textfigs.

1936b. The Biology of Oithona similis in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXXI, No. 1, pp. 168–187, 9 textfigs.

FISH, CHARLES J., and JOHNSON, MARTIN W.

1937. The Biology of the Zooplankton Population in the Bay of Fundy and Gulf of Maine with Special Reference to Production and Distribution. Jour. Biol. Board Canada, Vol. 3, Ser. 3, pp. 189–322, 45 textfigs., 29 tables.

Fowler, H. W.
1912. The Crustacea of New Jersey. Report, New Jersey State Museum, 1911 (1912), pp. 29–650, Pls. 1–150.

Fraser, C. McL.
1915. Pelagic Hydroids, in Bigelow, 1915, pp. 306–315, textfigs. 73–78.

Furrestin, Jean
1938. Influence de la salinite sur la répartition du genre Sagitta dans l'Atlantique nord-est. Revue des Travaux de l'office des pêches maritimes, Vol. XI, No. 3, pp. 425-437, 6 textfigs.

Gibitz, Anton
1922. Verbreitung und Abstammung mariner Cladoceren. Verhandl. zool.-botan. Gesellschaft Wien. Jahrgang 1921, Vol. LXXI, pp. 85–105, 6 charts.

Hargitt, Charles W.
1905. The Medusae of the Woods Hole Region. Bull. U. S. Bureau of Fisheries, Vol. XXIV, 1904 (1905), pp. 21–79, pls. I-VII, textfigs.

Hensen, Victor
1890. Einige Ergebnisse der Plankton-Expedition der Humboldt-Stiftung. Math. Naturwiss. Mittheil. Sitzungsbericht. König Preuss. Akad. Wiss. Berlin. Jahrgang 1890, pp. 167–177 (243–253).
1895. Methodik der Untersuchungen bei der Plankton Expedition. Ergebn. Plankton-Exped. des Humboldt-Stiftung, Vol. 1, B, 200 pp., 14 textfigs., 11 tables, 1 chart.

Hjort, Johan and Ruud, Johan T.
1938. Deep Sea Prawn Fisheries and Their Problems. Hvalrådets Skrifter, Norske Videnskaps-Akad. Oslo, No. 17, Pt. 1, pp. 1–144, 21 textfigs.

Holmes, S. J.
1905. The Amphipoda of Southern New England. Bull. U. S. Bureau of Fisheries, Vol. XXIV, 1904 (1905), pp. 459–529, pls. I-XIII, textfigs.

Huntsman, A. G.
1919. Biology of Atlantic Waters of Canada. Some Quantitative and Qualitative Plankton Studies of the Eastern Canadian Plankton. 2. On the Quantity of Plankton obtained at one hundred and seventy-nine stations during the Canadian Fisheries Expedition, 1915. Canadian Fish. Exped. 1914–1915, Depart. Naval Sci., pp. 407–420.
1919a. Biology of Atlantic Waters of Canada. Some Quantitative and Qualitative Studies of the Eastern Canadian Plankton. 3. A Special Study of the Canadian Chaetognaths, their Distribution, etc., in the Waters of the Eastern Coast. Canadian Fish. Exped. 1914–1915, Depart Naval Sci., pp. 421–485, 12 textfigs.

Jespersen, P.
1923. On the quantity of Macroplankton in the Mediterranean and the Atlantic. Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. III, No. 7, Misc. Papers, Pt. 3, pp. 1–17, 8 textfigs.
1924. On the quantity of Macroplankton in the Mediterranean and the Atlantic. Internat. Rev. Gesamt. Hydrobiol. Hydrogr., Vol. XII, pp. 102–115.

1935. Quantitative Investigations on the Distribution of Macroplankton in Different Oceanic Regions. Dana Report, No. 7, 44 pp., 28 textfigs.

Johnstone, James
1908. Conditions of Life in the Sea. 332 pp., 29 figs. Cambridge, England.

Kemp, Stanley
1938. Oceanography and the Fluctuations in the Abundance of Marine Animals. Brit. Assoc. Advance. Sci. 1938 Meet., Sect. D., Zool., pp. 85–101.
1938a. Oceanography and the Fluctuations in the Abundance of Marine Animals. Nature, Vol. 142, No. 3600, pp. 777–779.

Kraefft, Fritz
1910. Über das Plankton in Ost- und Nordsee und den Verbindungsgebieten, mit besonderer Berücksichtigung der Copepoden. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XI, pp. 29–108, 9 textfigs., 3 tables.

Lohman, H.
1901. Die Appendicularien. Nordisches Plankton, Zool. Teil, Vol. II, 3, pp. 11–21, 12 textfigs.
1911. Die Appendicularien. Nachtrag. Nordisches Plankton, Zool. Teil, Vol. II, 3, pp. 23–29, 3 textfigs.

Lücke, Fr.
1912. Quantitative Untersuchungen an dem Plankton bei dem Feuerschiff "Borkumriff" in Jahre 1910. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XIV, pp. 101–128, 3 textfigs., 2 tables.

Mayer, A. G.
1910. Medusae of the World. Hydromedusae. Carnegie Inst. Washington, Publ. No. 109, Vol. 1, 230 pp., 119 textfigs., 29 pls.
1912. Ctenophores of the Atlantic Coast of North America. Carnegie Inst. Washington, Publ. No. 162, 58 pp., 17 pls., 12 textfigs.

Mielck, W.
1911. Quantitative Untersuchungen an dem Plankton der deutschen Nordsee-Terminfahrten im Februar und Mai 1906. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XIII, pp. 313–357.

Mielck, W., and Künne, C.
1935. Fischbrut- und Plankton-Untersuchungen auf dem Reichsforschungsdamfer "Poseidon" in der Ostsee, Mai-Juni 1931. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Helgoland, N. F., Vol. XIX, 120 pp., 12 textfigs., 8 text-tables, 39 tables.

Orr, A. P.
1934. On the Biology of *Calanus finmarchicus*. Pt. IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIX, pp. 613–632, 5 textfigs.

Ostenfeld, C. H., and Jespersen, P.
1924. Standard Net for Plankton Collections. Publ. Circ., No. 84, Cons. Perm. Int. Expl. de la Mer, 16 pp., 11 textfigs.

Parr, A. E.
1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. Bull. Bingham Oceanogr. Collection, Vol. 4, pp. 1–90, 28 textfigs.

Ramner, Walter
1933. Die Cladoceren der "Meteor" Expedition. Wiss. Ergebn. Deutsch. Atlantisch. Exped. ...... "Meteor" 1925-1927, Vol. XII, Lief. 2, pp. 111-121, textfigs. 51–52.

Ranson, Gilbert
1936. Méduses provenant des campagnes du Prince Albert I de Monaco. Res. camp. sci. Monaco, Vol. XCII, 248 pp., 2 pls.

Rathbun, Richard
1889. Notice of the small surface organisms taken in the tow-nets, and of the contents of mackerel stomachs. Bull. U. S. Fish Comm., Vol. VII, 1887 (1889), pp. 259–267.

Redfield, Alfred C.
1939. The history of a population of Limacina retroversa during its drift across the Gulf of Maine. Biol. Bull., Vol. LXXVI, No. 1, pp. 26-47, 10 textfigs.

Rosenfeld, Georg
1904. Studien über das Fett der Meeresorganismen. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Helgoland, N. F., Vol. V, pp. 57–83.

Russell, F. S.
1925. The Vertical Distribution of Marine Macroplankton. An Observation on Diurnal Changes. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIII, pp. 769–809, 6 textfigs.
1927. The Vertical Distribution of Marine Macroplankton. V. The Distribution of Animals Caught in the Ring-trawl in the Daytime in the Plymouth Area. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIV, pp. 557–608, 11 textfigs., 4 tables.
1934. On the Occurrence of the Siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochii* (Will) in the English Channel. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIX, pp. 555–558.
1935. On the Value of Certain Plankton Animals as Indicators of Water Movements in the English Channel and North Sea. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XX, pp. 309–332, 7 textfigs.

Rudé, G. T.
1938. New methods of marine survey. Proc. Am. Phil. Soc., Vol. 79, pp. 9–25, 11 textfigs.

Savage, R. E.
1931. The Relation between the Feeding of the Herring off the East Coast of England and the Plankton of the Surrounding Waters. Fishery Invest., Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XII, No. 3, 88 pp., 32 tables, 10 pls., 23 textfigs.
1937. The Food of North Sea Herring 1930–1934. Fishery Invest. Min. Agr. Fish. (Great Brit.), Ser. II, Vol. XV, No. 5, 57 pp., 16 textfigs., 29 tables.

SCHMIDT, JOHANNES
1912. Introduction. Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. 1, Pt. 1, pp. 1–75, 12 textfigs.

SHARPE, RICHARD W.
1911. Notes on the marine Copepoda and Cladocera of Woods Hole and adjacent regions, including a synopsis of the genera Harpacticoida. Proc. U. S. Nat. Mus., Vol. 38, 1911, pp. 405–436, 20 textfigs.

STEPHENSEN, K.
1924. Hyperiidea-Amphipoda (Part 2, Paraphronimidae, Hyperiidae, Dairellidae, Phronimidae, Anchylomeridae). Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. II, Biol., D. 4, pp. 71–149, 20 textfigs., 15 charts.

STEUER, ADOLF
1910. Planktonkunde. 723 pp., 365 textfigs., 1 pl. Leipzig and Berlin.

STØRMER, LEIF
1929. Copepods from the "Michael Sars" Expedition, 1924. Rapp. et Proc.-Verb., Cons. Perm. Int. Expl. de la Mer, Vol. LVI, 57 pp., 13 textfigs.

SUDLER, MERVIN T.
1899. The Development of Penilia schmackeri Richard. Proc. Boston Soc. Nat. Hist., Vol. XXIX, pp. 109–131, 3 pls.

SUMNER, FRANCIS B., OSBURN, RAYMOND C., and COLE, LEON J.
1913. A biological survey of the waters of Woods Hole and vicinity. Pt. II, Sect. III. A catalogue of the marine fauna of Woods Hole and vicinity. Bull. U. S. Bureau of Fisheries, Vol. XXXI, Pt. II, pp. 547–794.

THIEL, MAX EGON
1938. Die Chaetognathen-Bevölkerung des Südatlantischen Ozeans. Wiss. Ergebn. Deutsch. Atlantisch. Exped. .... "Meteor" 1925–1927, Vol. XIII, 110 pp., 62 textfigs.

WALFORD, LIONEL A.
1938. Effect of Currents on Distribution and Survival of the Eggs and Larvae of the Haddock (*Melangramus aeglefinis*) on Georges Bank. Bull. U. S. Bureau of Fisheries, Vol. XLIX, No. 29, pp. 1-75, textfigs. 1-50.

WHEELER, WILLIAM MORTON
1901. The free-swimming copepods of the Woods Hole region. Bull. U. S. Fish Comm., Vol. XIX, 1889 (1901), pp. 157–192, 30 textfigs.

WILSON, CHARLES B.
1932. The copepods of the Woods Hole region. Bull. Smithsonian Inst., U. S. Nat. Mus., 158, 635 pp., 316 textfigs., 41 pls.
1932a. The copepod crustaceans of Chesapeake Bay. Proc. U. S. Nat. Mus., Vol. 80, Art. 15, 54 pp., 5 pls.

WIMPENNY, R. S.
1929. Preliminary Observations on the Fat-Content of the Plankton on the English Herring Grounds in the North Sea. Fishery Invest. Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XI, No. 5, 23 pp., 9 tables.

1937. The Distribution, Breeding and Feeding of some important Plankton Organisms of the South-West North Sea in 1934. Pt. I. *Calanus finmarchicus* (Gunn.), *Sagitta setosa* (J. Müller), and *Sagitta elegans* (Verrill). Fishery Invest. Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XV, No. 3, pp. 3-53, 24 textfigs., 14 tables.

Winsor, Charles P., and Walford, Lionel A.

1936. Sampling Variations in the Use of Plankton Nets. Jour. Cons., Cons. Perm. Int. Expl. de la Mer, Vol. XI, No. 2, pp. 190-204, 1 textfig.

Zimmer, Carl

1909. VI. Die nordischen Schizopoden. Nordisches Plankton, Zwölfte Lief., No. VI, 1909, pp. 1-178, 383 textfigs.