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# PLANKTON OF THE OFFSHORE WATERS OF THE GULF OF MAINE : : : : : : : By Henry B. Bigelow

From BULLETIN OF THE BUREAU OF FISHERIES, Vol. XL, 1924, Part II

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Errata.

Page 33: Footnote 16, drift should read drifts.

Page 93: Line 11, p. 92 should read p. 96.

Page 239: Under the heading "Halithalestris croni (Kroyer)", paragraph 1, line 4, tables, p. 207 should read tables, p. 297.

Page 267: Last line before table, p. 298 should read p. 297.

Page 330: Legend for Figure 92, contour should read contours.

# PLANKTON OF THE OFFSHORE WATERS OF THE GULF OF MAINE

By HENRY B. BIGELOW

*Museum of Comparative Zoology, Harvard University*

With tables of copepods by C. B. Wilson, and tables of diatoms by Albert Mann

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# INTRODUCTION

This memoir is the second part of the report on the oceanographic and biologic survey of the Gulf of Maine, the account of the fishes [1] forming the first.

The vessels of the bureau have carried out the following oceanographic and plankton cruises in the Gulf of Maine since 1912, when the systematic survey was begun:

Schooner *Grampus:* July to August, 1912; July to August, 1913; July to August, 1914; May to October, 1915; and July, August, and October–November, 1916.

Steamer *Albatross:* February to May, 1920.

Steamer *Halcyon:* December–January, 1920–21; March, 1921; and August, 1922.

In addition, tows were taken at intervals during the winter of 1912–13 off Gloucester and between Cape Ann and Cape Elizabeth in April and May, 1913. The *Fish Hawk* also carried out an extensive program of towing in Massachusetts Bay during the winter and spring of 1924–25, but only a few of the catches have been examined.

The locations, hydrographic data, and types of nets employed, and the depths of the hauls have been published for all the stations up to May, 1920, in the following reports:

July–August, 1912, stations 10001 to 10046, in Bigelow, 1914, p. 135.

November, 1912–May, 1913, stations 10047 to 10056, in Bigelow, 1914a, p. 416.

July–August, 1913, stations 10057 to 10061 and 10085 to 10112, in Bigelow, 1915, p. 342.

July–August, 1914, stations 10213 to 10264, in Bigelow, 1917, p. 330.

May–October, 1915, stations 10266 to 10339, in Bigelow, 1917, p. 331.

July–November, 1916, stations 10340 to 10355, 10398, and 10399 to 10404, in Bigelow, 1922, p. 176.

February–May, 1920, stations 20044 to 20129, in United States Bureau of Fisheries Document No. 897 (1921).

For ready reference the locations of all the tow-net stations for these cruises are given on the accompanying charts (figs. 1 to 6); also on figures 7 and 8, the *Halcyon* tow-net stations of the winter and spring of 1920 and 1921, and of August, 1922, the data for which have not yet been published.

As the value of any regional account of the plankton depends largely on the amount of data available, it may be of interest to add that more than 1,000 tows have been made in the Gulf of Maine region since 1912, at various depths from the surface down to the bottom, some with horizontal and others with vertical nets. In a few cases the tows were made with the horizontal closing net (Bigelow, 1913a).

The area covered in this report is the same as that covered in the report on the fishes; that is, the oceanic bight from Nantucket on the west to Cape Sable (Nova

[1] Fishes of the Gulf of Maine, by Henry B. Bigelow and William W. Welsh. Pt. I, Vol. XL, Bulletin, U. S. Bureau of Fisheries, 1924 (1925), 567 pp., 278 figs. Washington. Bureau of Fisheries Document No. 965.

Scotia) on the east. These natural boundaries are continued offshore by Nantucket Shoals on the one side and by Browns Bank on the other, which roughly demark the boreal waters of the gulf from the warmer coastal water off southern

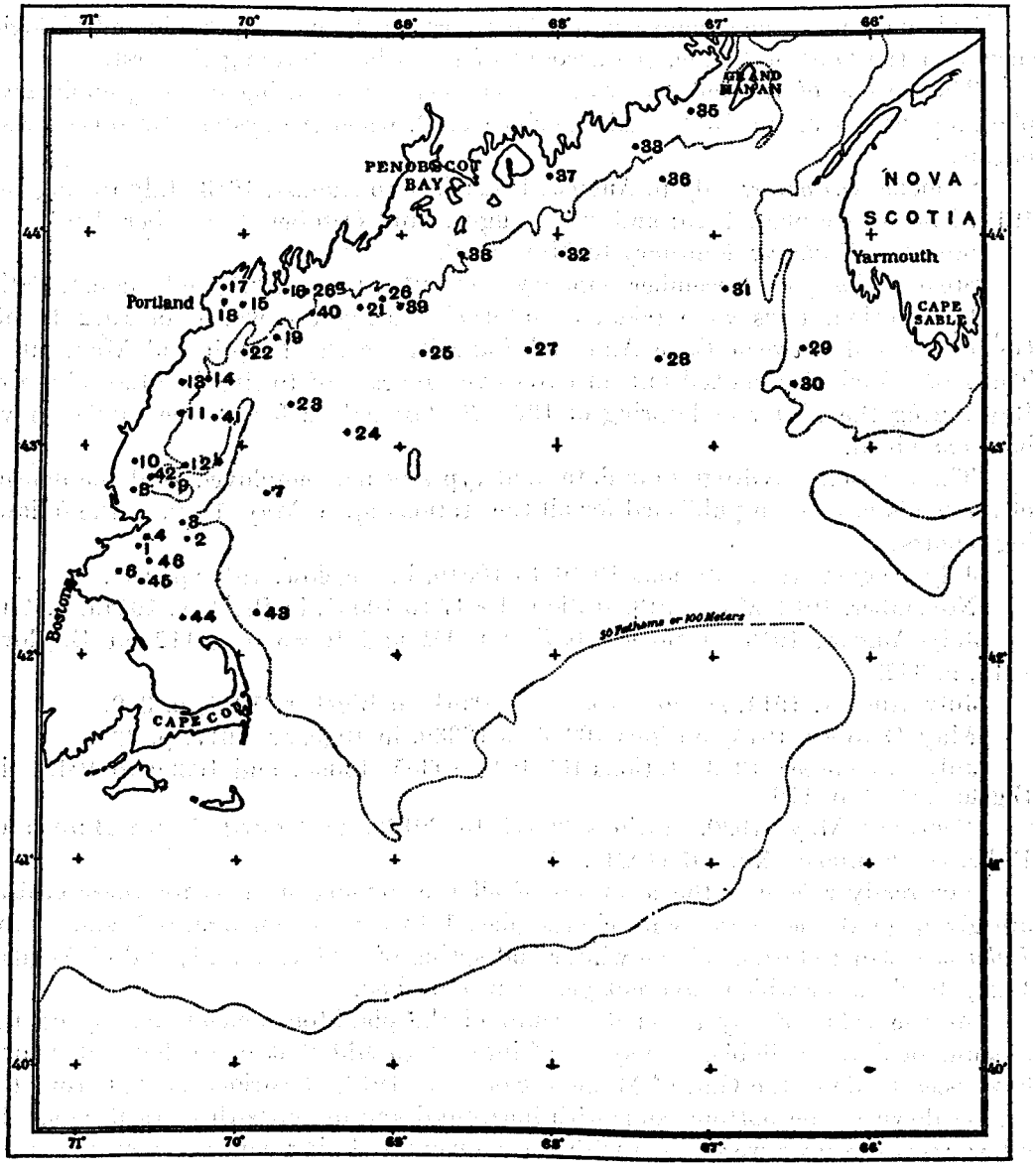


FIG. 1.—Locations from *Grampus* stations 10001 to 10046, July 9 to August 21, 1912

New England, on the one hand, and from the lower sea temperatures along southern Nova Scotia, on the other. Longitudes 65° and 70° W. have been taken as the definite limits east and west. The edge of the continent, at the 200-meter contour, is chosen as the arbitrary offshore boundary, because this zone marks the transition

from the characteristic boreal plankton of the banks water to the tropical oceanic plankton of the much warmer and more saline waters of the so-called "inner edge of the Gulf Stream." The reader will note that, as defined here, the Gulf of Maine

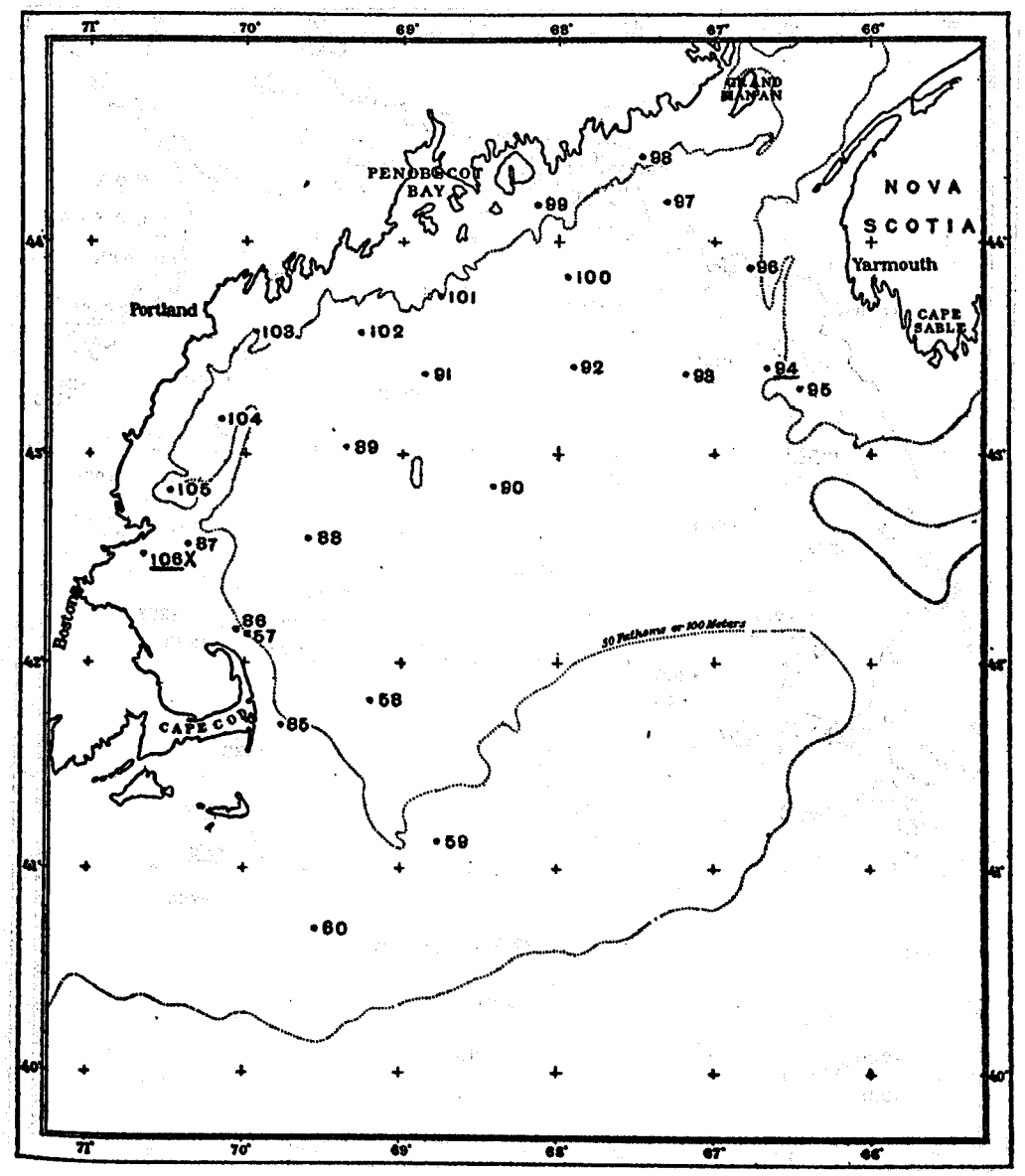


FIG. 2.—Locations of *Grampus* stations 10057 to 10060 and 10087 to 10106, July 8 to August 22, 1913, and general location of stations 10047 to 10056 and 10053 to 10056, November 20, 1912, to April 14, 1913 (X)

includes the whole of the offshore rim formed by Georges and Browns Banks and the two main deep channels—Eastern and Northern—that pierce it.

Brief notes on the plankton collected on the several cruises have already been published (Bigelow, 1914, 1914a, 1915, 1917, and 1922).

The present report gives a general account of the planktonic communities (animal and plant) of the open waters of the gulf outside the outer headlands (such as must precede the intensive survey of the plankton of any region), with such

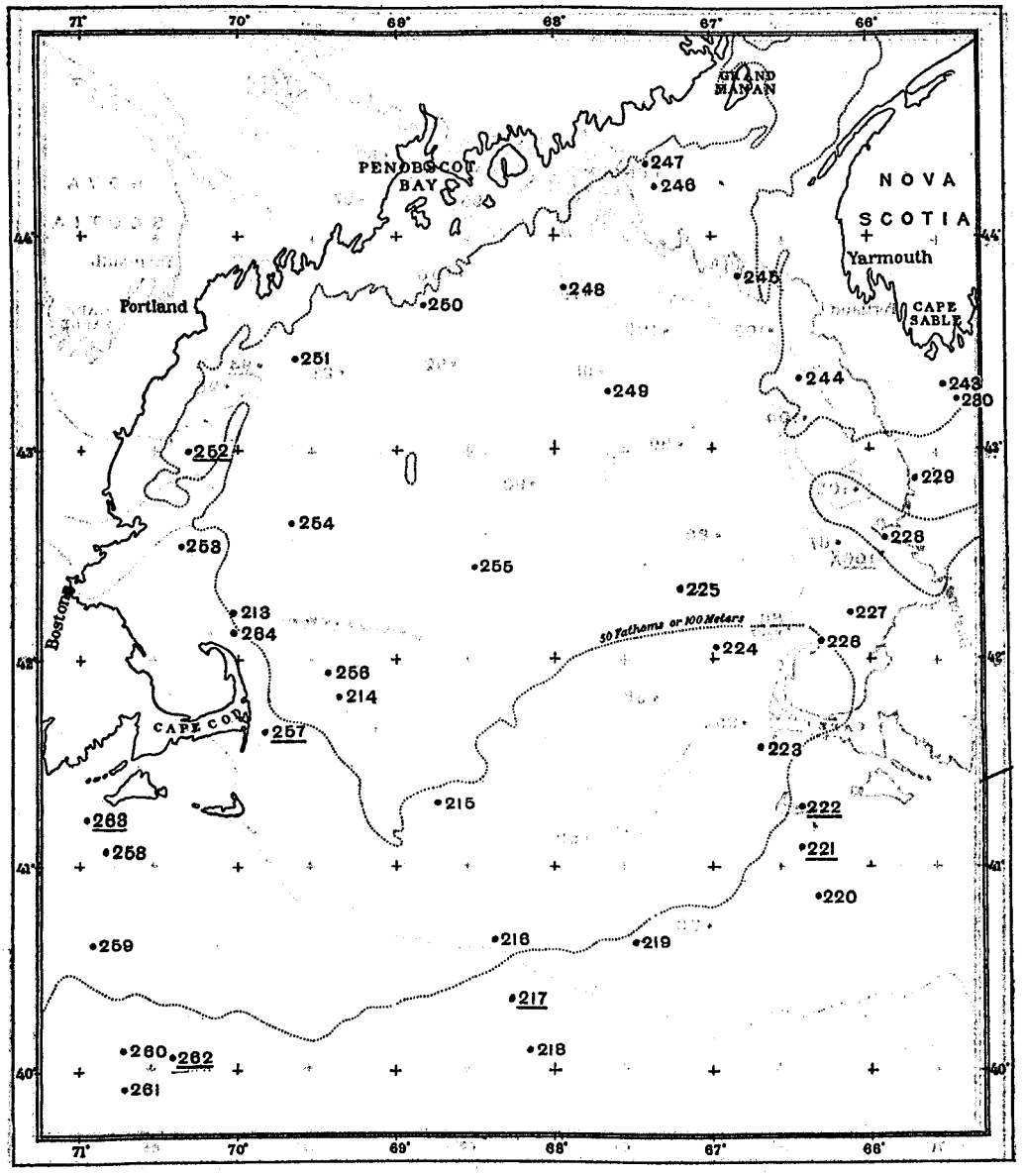


FIG. 3.—Locations of *Grampus* stations 10213 to 10263, July 19 to August 28, 1914. Stations where no tows were made are underlined

notes on the occurrence of the more important groups and species as a preliminary examination of the large amount of material collected has afforded. The plankton of the many harbors and estuarine situations around the shore line of the gulf, and within 1 to 5 miles of the land generally, is barely touched on. almost all our towing

having been done well out at sea; and when this is studied the communities will no doubt prove quite different from those of the open gulf, with neritic forms dominating instead of oceanic, and with larval forms of various parentage playing a far

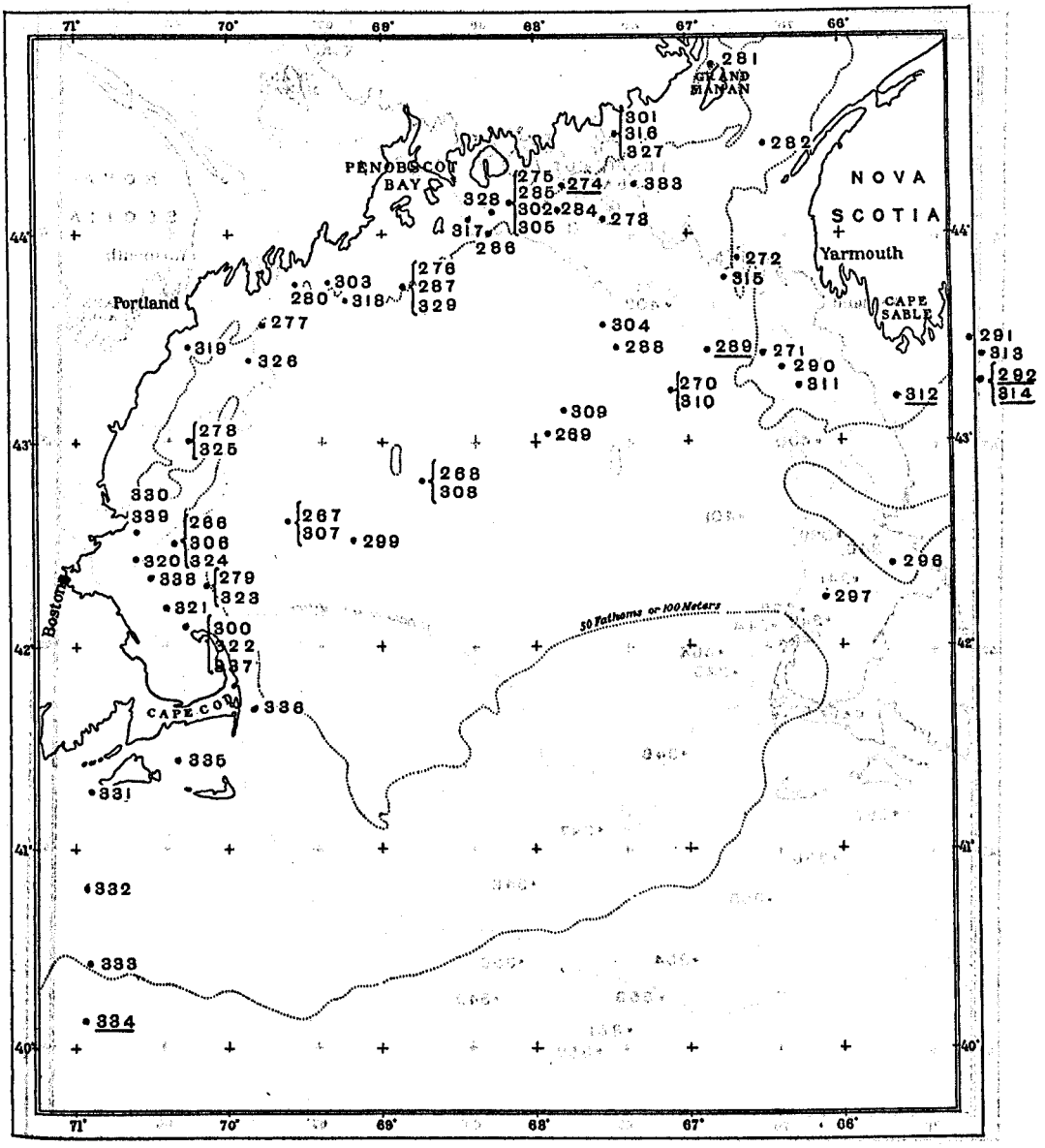


FIG. 4.—Locations of *Grampus* stations 10266 to 10339, May 4 to October 27, 1915. Stations where no tows were made are underlined

more important rôle. This is touched upon later. Fish eggs and larval fishes are not included because they have been already discussed in the first part of this volume.[2]

[2] Fishes of the Gulf of Maine (Bigelow and Welsh, 1925).

It is a pleasure to acknowledge afresh the assistance rendered by the following collaborators, who have undertaken the identification of different groups: W. F. Clapp, the pelagic mollusks of the cruises of 1912 to 1916; Dr. S. F. Clarke,

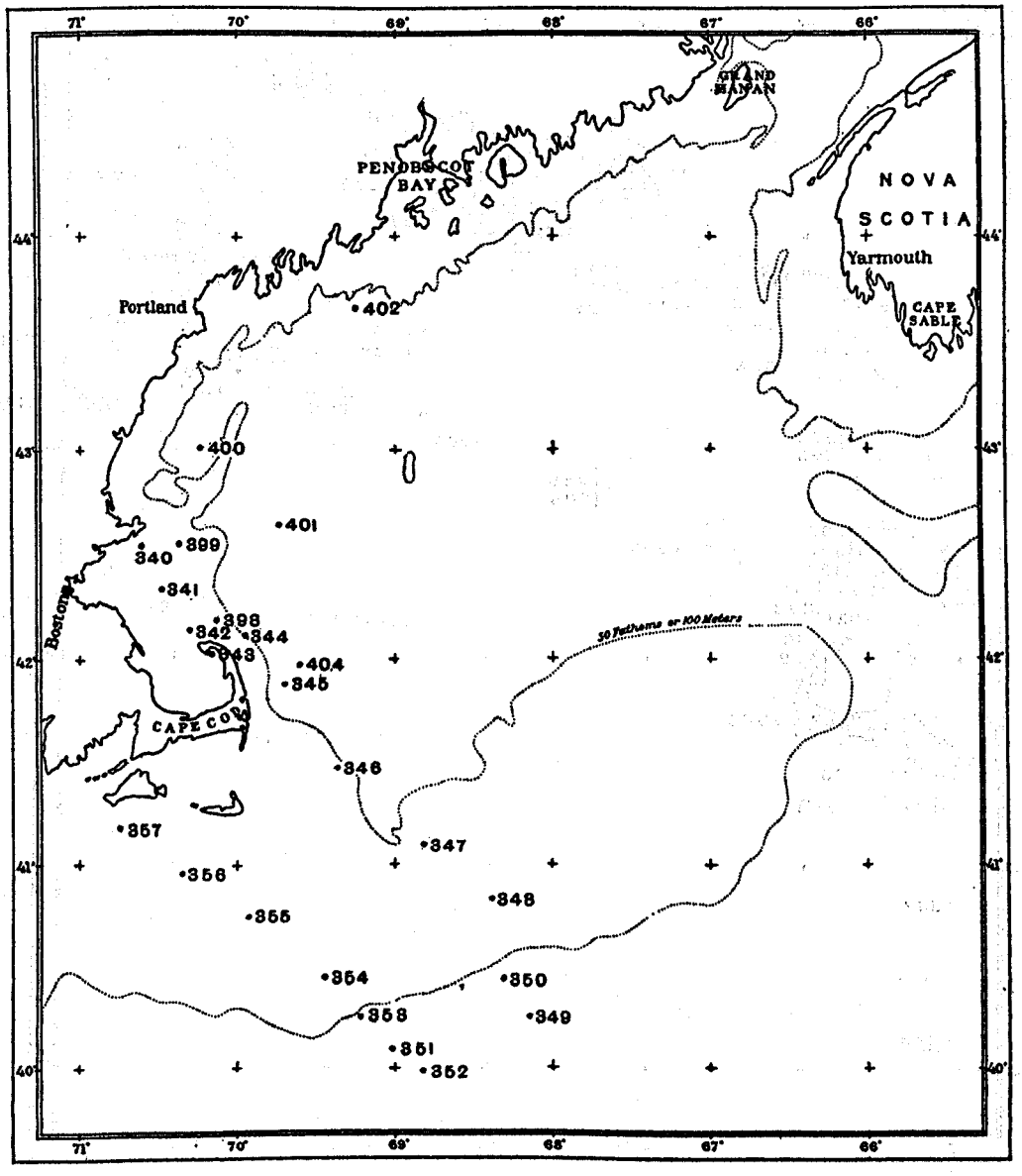


FIG. 5.—Locations of *Grampus* stations 10340 to 10357, July 19 to 26; station 10398, August 29; and stations 10399 to 10404, October 31 to November 8, 1916

floating hydroids, spring of 1913 (in Bigelow, 1914a, p. 415); Dr. C. O. Esterly, the copepods of 1912, 1913, and 1914 (in Bigelow, 1914, p. 115; 1914a, p. 409; 1915, p. 287; and 1917, p. 290); Dr. C. McLean Fraser, floating hydroids, summer of 1913 (in Bigelow, 1915, p. 306); Dr. H. J. Hansen, the euphausiids of 1912 and of

the winter of 1912–1913 (in Bigelow, 1914a, p. 411); Dr. Albert Mann, samples of diatoms at representative stations, listed below (p. 423); A. Pringle-Jameson, the Sagittæ of 1912 and 1913 (in Bigelow, 1914, p. 121; 1914a; and 1915, p. 294); Dr.

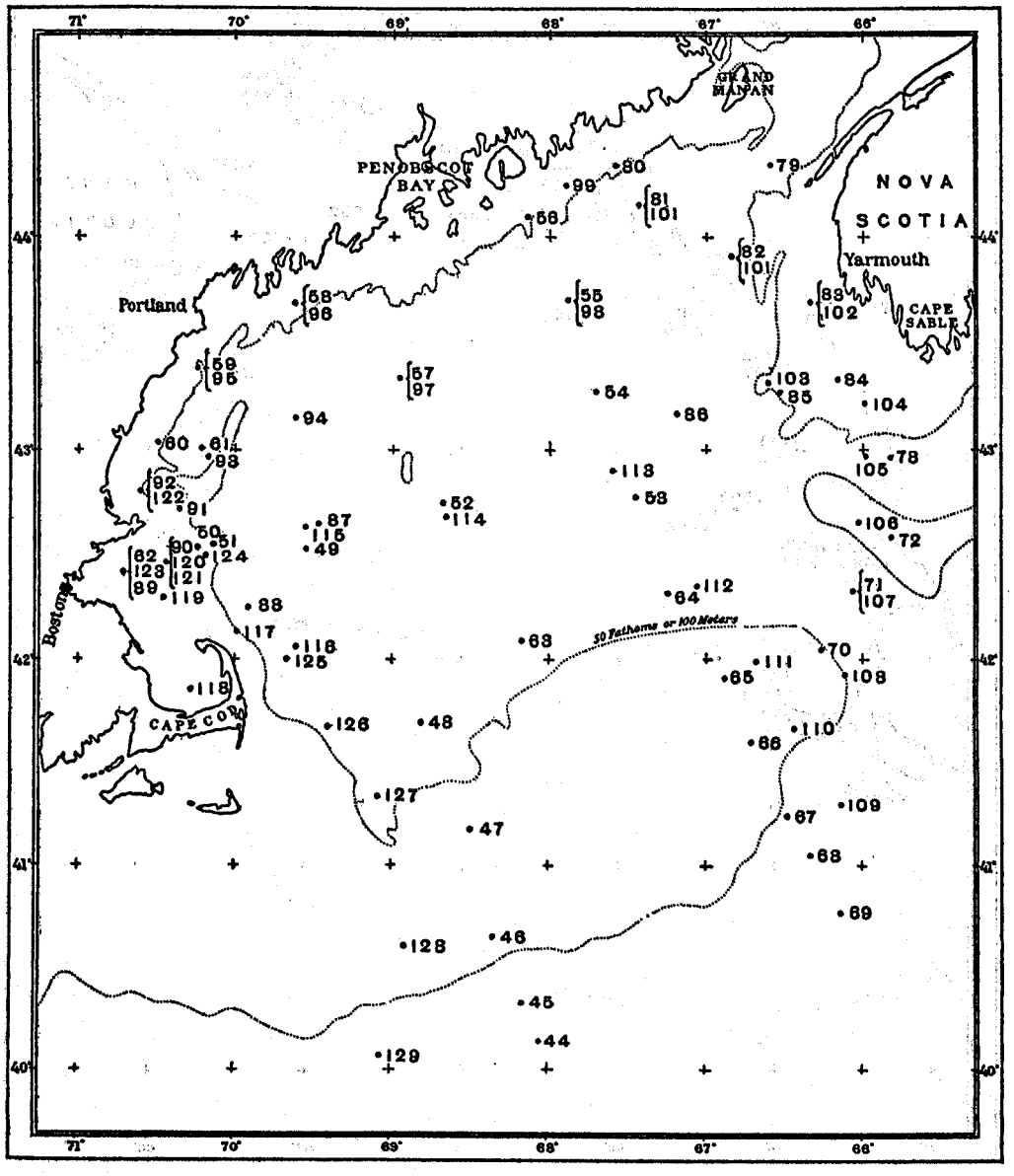


FIG. 6.—Location of *Albatross* stations 20044 to 20129, February 22 to May 17, 1920

William Tattersall, the euphausiids of 1914 (in Bigelow, 1917, p. 281); Dr. C. B. Wilson, lists of the copepods for 1915, 1920, and 1921 (p. 297). Their friendly cooperation lends authority to the following pages.

Dr. W. C. Kendall has contributed his field notes on the towings carried out from the *Grampus* in various parts of the Gulf of Maine during August and September, 1896. Dr. J. P. McMurrich has most generously allowed the use of his

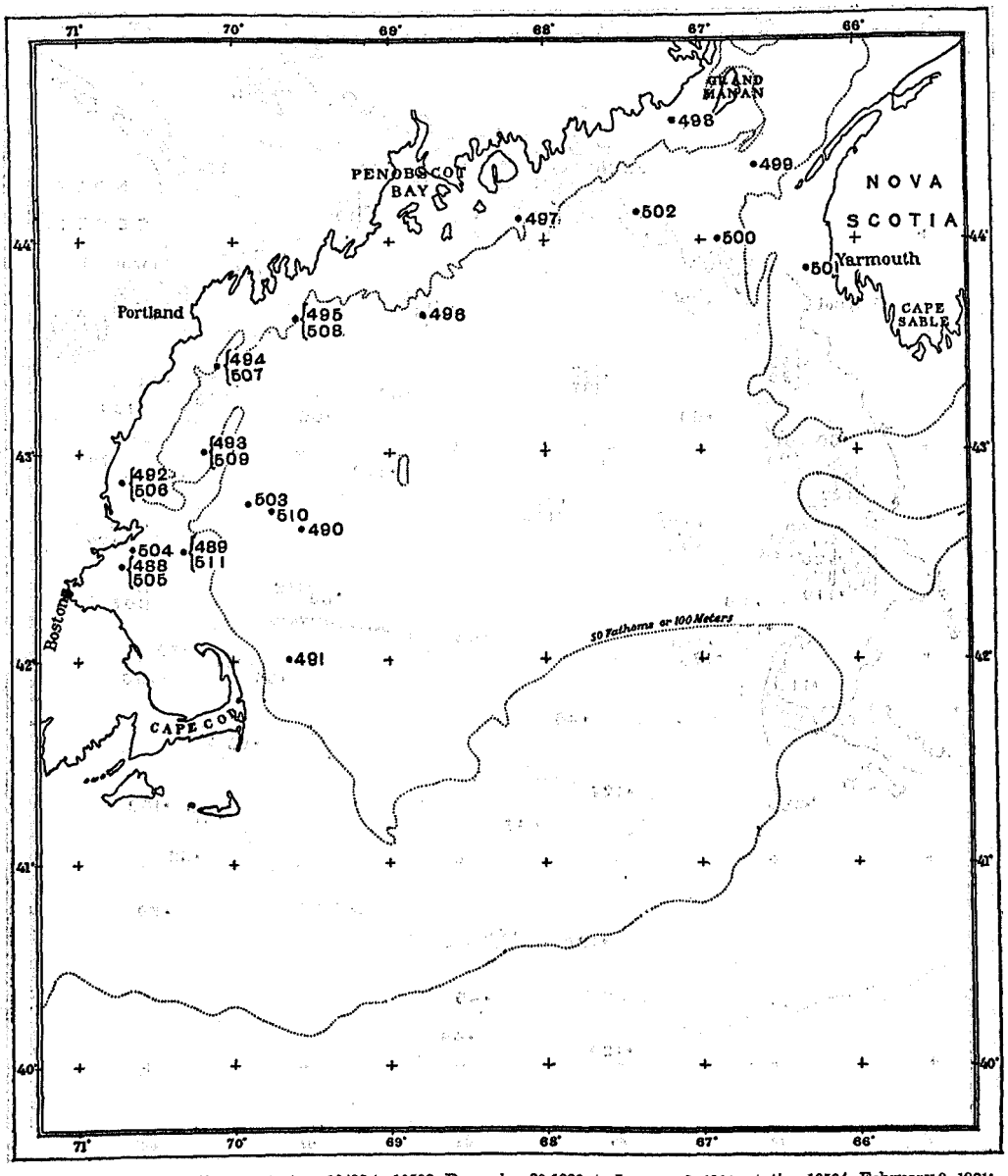


FIG. 7.—Locations of *Halcyon* stations 10488 to 10503, December 29,1920, to January 9, 1921; station 10504, February 9, 1921; and stations 10505 to 10511, March 4 and 5, 1921

unpublished lists of the plankton taken in towings at frequent intervals at St. Andrews, New Brunswick, from November, 1915, to October, 1916, data repeatedly referred to below. I also owe thanks to Dr. A. G. Huntsman, who has offered many

unpublished notes and much information on conditions in the Bay of Fundy region; to Dr. C. J. Fish, who has contributed a preliminary note on the phytoplankton

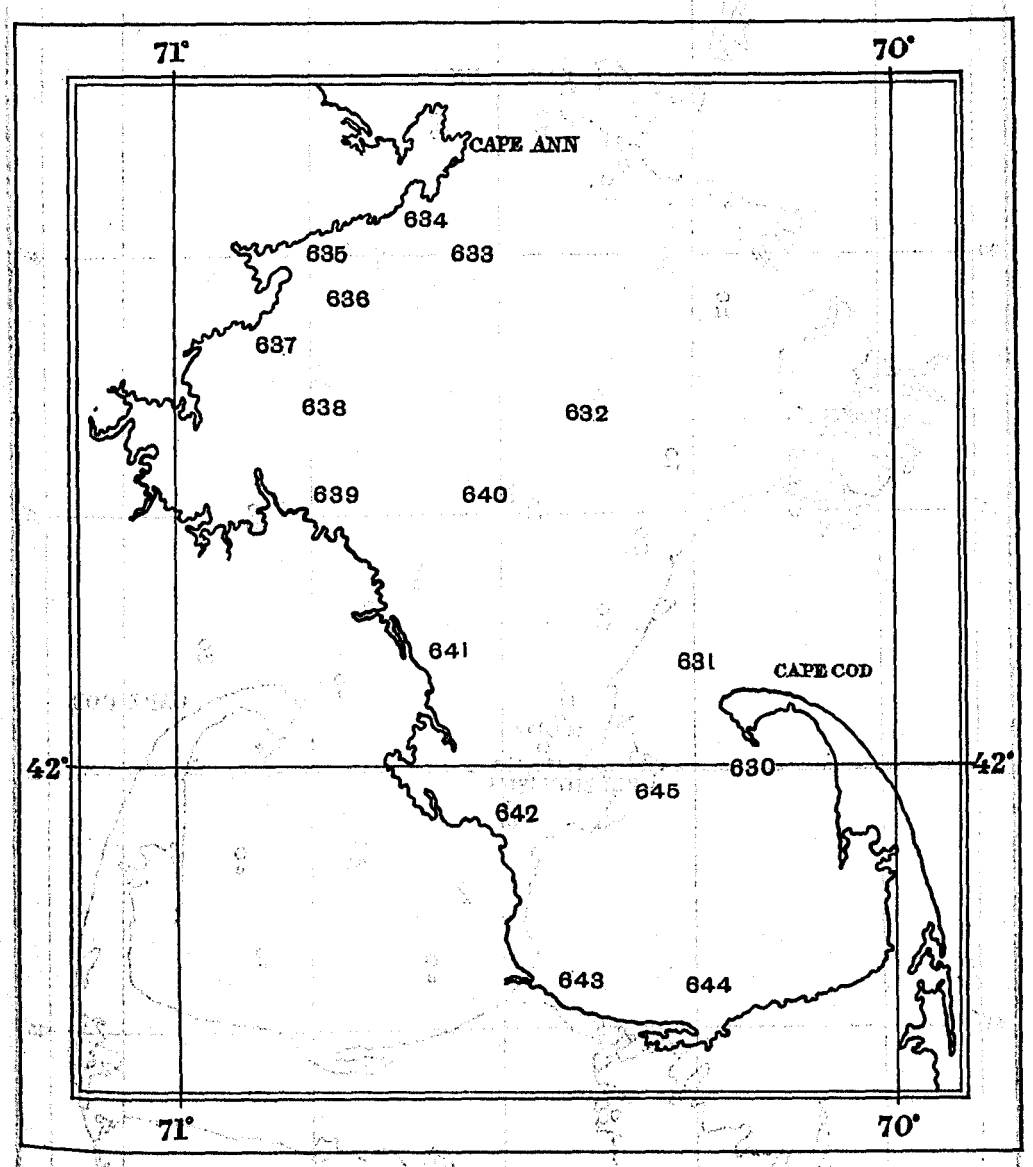


FIG. 8.—Location of *Halcyon* stations 10631 to 10645, August 22 to 24, 1922

collected by the *Fish Hawk* in Massachusetts Bay during the winter and spring of 1924 and 1925; to Dr. A. H. Leim; and to Capt. John McFarland for towings taken from his schooner *Victor*.

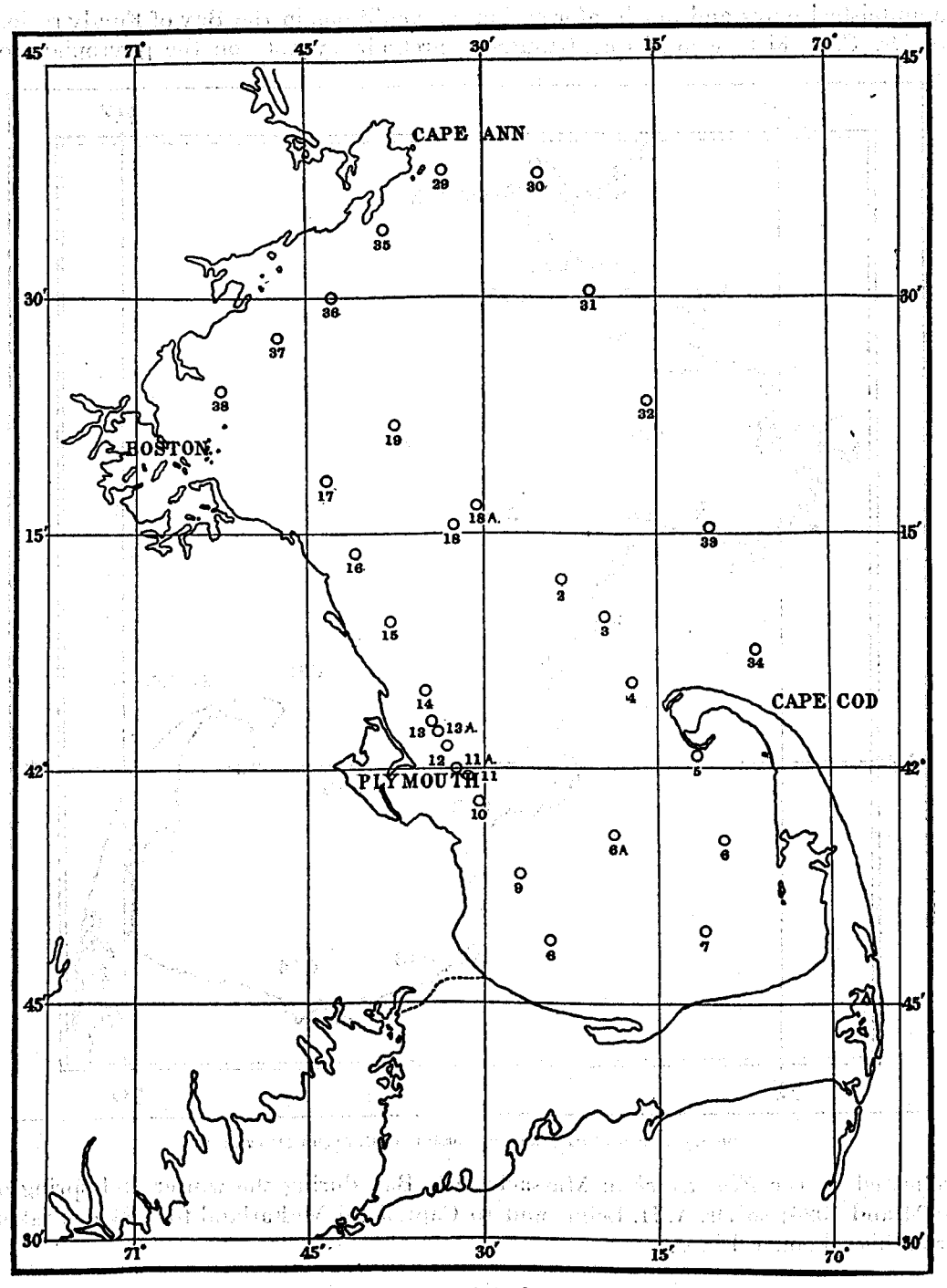


FIG. 9.—Location of *Fish Hawk* stations, 1924-25

# THE PLANKTON

Although of rather recent birth as words go,[3] the term "plankton" filled so obvious a need that it is now in general use to cover a whole assemblage of organisms, plant and animal, related by their manner of life though they may be far apart in the systematic scale. By it we understand all such forms as float or swim freely in the water, but which, however active, are unable to carry out voluntary horizontal journeys of any extent, though certain of them perform considerable vertical migrations under the directive influence of sunlight or of some other physical stimulus. Among the three major faunistic groups into which the inhabitants of the sea may be divided—bottom dwellers, free swimmers, and plankton—the importance of the last in the economy of nature was slowest in gaining general appreciation. Within the last half century, however, biologists have come to realize both that the number of species of this category is past all counting and that the microscopic pelagic plants are the chief producers—that is, are capable of elaborating simple inorganic compounds into complex organic matter—in the sea. They serve as food supply for many larger marine animals at one stage or another, and thus play a most essential rôle in the general nutritive scheme of marine life. As it chances, the planktonic plants (producers) as a whole are unicellular and microscopic; the planktonic animals (consumers) are multicellular and comparatively large, so that the oft-employed terms "microplankton" and "macroplankton" are not empiric, but do classify the plankton roughly as vegetable or animal, more technically as phytoplankton or zoöplankton.

In the following pages I have attempted to place before the reader a general survey of these two great planktonic divisions as they occur in the Gulf of Maine, followed by more particular accounts of the status of such groups of each as loom large in its pelagic communities at one time or another. Many other groups are also represented in the tow nettings, but time and the assistance available have so far allowed examination of those only that are dominant or numerically important in the Gulf at one time or place or another.

Study of the occurrence of buoyant fish eggs is not sufficiently advanced to warrant more than a few preliminary notes here. The present knowledge of the breeding grounds and seasons and of the distribution of the eggs and larvæ of Gulf of Maine fishes is summarized by species in the first part of this report (Bigelow and Welsh, 1925).

[3] The term was coined in 1886 by Hensen.

# SECTION 1.—GENERAL SURVEY OF THE ANIMAL PLANKTON (ZOÖPLANKTON)

Few living zoologists have been as fortunately placed as were we on setting sail on the *Grampus* from Gloucester on our first oceanographic cruise in the Gulf of Maine on July 9, 1912, for a veritable *mare incognitum* lay before us, so far as its floating life was concerned, though the bottom fauna can be described as comparatively well known. Not but what an extensive list of pelagic crustaceans, cœlenterates, and other planktonic animals had been recorded thence, but everything was yet to be learned as to what groups or species would prove predominant in the pelagic fauna; their relative importance in the natural economy of the Gulf; their geographic and bathymetric variations; their seasonal successions, migrations, and annual fluctuations; their temperature affinities, whether arctic, boreal, or tropic; and whether they were oceanic or creatures of the coastal zone. We even had no idea (incredible though it may seem at this place and day) what we should probably catch when we first lowered our tow nets into deeper strata of Massachusetts Bay, for, so far as we could learn, tows had never previously been tried more than a few fathoms below its surface. Nor did we at first realize, when the catch was examined in our floating laboratory, that the little reddish copepods (Calanus) darting to and fro in the glass dish, with a few large Sagittæ (*S. elegans*) and young euphausiids among them, would prove the backbone of the local planktonic fauna. Such, however, has proved to be the case; for station after station, cruise after cruise, year after year, have yielded cumulative evidence that (taken by and large) the calanoid copepods are its predominant members at all seasons, except where deposed from the leading rôle by the local or temporary swarming of some other and usually larger animal. Our first summer's cruise was enough to show that *Calanus finmarchicus* (large among copepods but small if judged by more familiar standards) is the most important member of the plankton of the Gulf of Maine, if bulk and numbers both be taken into account, and that it plays much the same rôle there that it does in North European waters (Bigelow, 1914, p. 99).

Calanus, as "red feed" or "cayenne," is well known to the local fishermen, who are quite aware of its importance as food for fishes.[4] Side by side with Calanus we have everywhere found its relative, *Pseudocalanus elongatus* (p. 275); but even where the latter outnumbers the former, as sometimes happens, it adds but little to the bulk of the catch, so tiny is it. We have so constantly found the copepod *Metridia lucens* (p. 253), the chætognath, or "glassworm," *Sagitta elegans* (p. 308), the amphipod genus Euthemisto (p. 156), the euphausiid genera Thysanoessa (several species, p. 133) and Meganyctiphanes (p. 147), the pteropod *Limacina retroversa* (p. 116), the ctenophore *Pleurobrachia pileus* (p. 365), and (in deep water) the larger copepod Euchæta (p. 230), associated with Calanus, that all these together may be spoken of as the "Calanus community" (figs. 10 and 11), a community that dominates the animal plankton from the Grand Banks on the north to Cape Cod (in winter even to Chesapeake Bay) on the south, and from the coast line, on the one hand, out to the continental slope, on the other.

[4] See page 188 for a further account of this copepod.

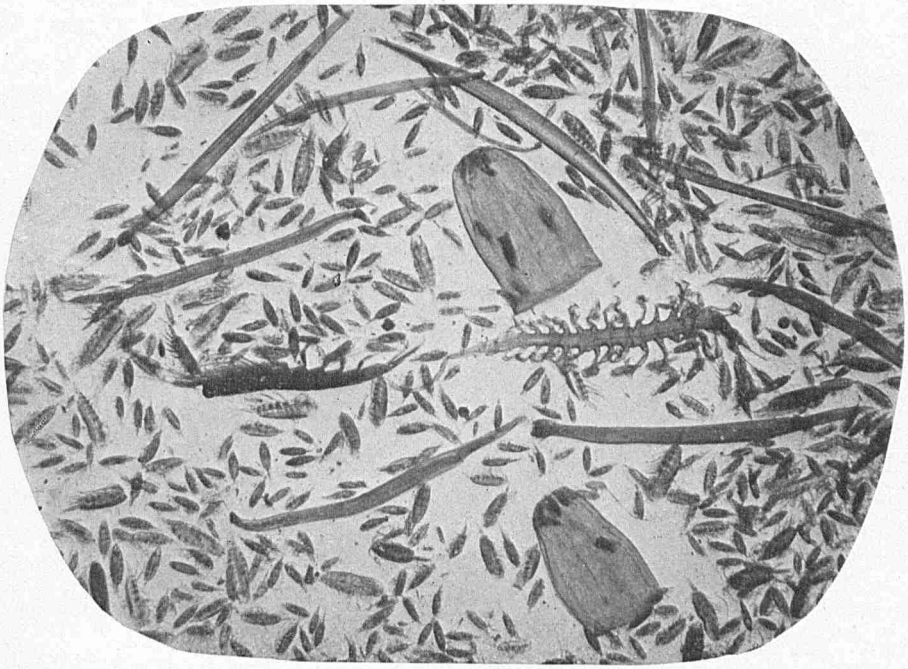

FIG. 10.—Calanus community, chiefly *Calanus finmarchicus*, with *C. hyperboreus*, *Euchæta norvegica*, *Sagitta elegans*, Tomopteris, Thysanoessa, and Aglantha. Western side of basin, March 24, 1920, haul from 200-0 meters (station 20087). × 1.5

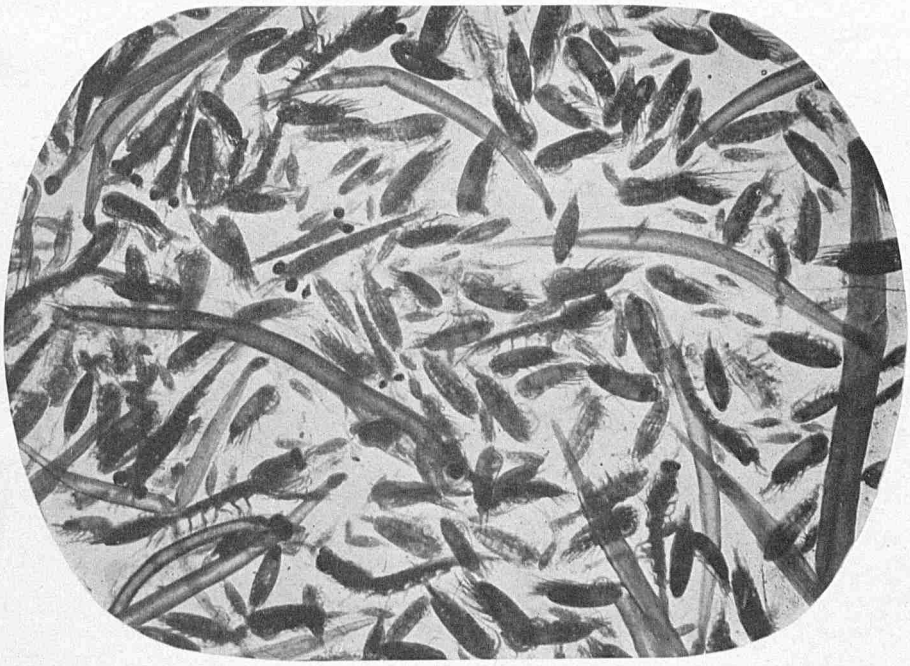

FIG. 11.—Calanus community, chiefly *Calanus finmarchicus*, with *Sagitta elegans*, larval euphausiids, and larval witch flounder (*Glyptocephalus cynoglossus*), Massachusetts Bay, July 19, 1916, haul from 30-0 meters (station 20340). × 3.5

Although copepods usually dominate, the other boreal animals just mentioned are so nearly universal in the Gulf in summer that the planktonic community is then surprisingly uniform qualitatively, with the list of prevalent species varying hardly at all from station to station over its inner parts, as is illustrated by the two following tables of catches made north of the Cape Cod-Cape Sable line during the summers of 1913 and 1914, seasons that may serve as representative because the plankton of the upper water layers was of the same general type during the summers of 1912, 1915, and 1916, as I have pointed out eleswhere (Bigelow, 1917 and 1922).

*Occurrence of representative species in the Gulf of Maine, August, 1913*

| Species | Stations | | | | | | | | | | | | | | | | | | | Per cent of stations for each species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10086 | 10087 | 10088 | 10089 | 10090 | 10091 | 10092 | 10093 | 10095 | 10096 | 10097 | 10098 | 10099 | 10100 | 10101 | 10102 | 10103 | 10104 | 10105 | |
| Calanus finmarchicus | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | 100 |
| Pseudocalanus elongatus | (?) | × | × | × | × | ---- | × | ---- | × | × | × | × | × | × | × | × | × | ---- | × | 80 |
| Metridia lucens | × | × | × | × | × | ---- | × | × | ---- | × | × | × | × | × | × | × | × | × | × | 80 |
| Anomalocera pattersoni | ---- | ---- | × | × | × | × | × | × | × | × | × | × | ---- | × | × | × | × | × | × | 80 |
| Euchæta norvegica | ---- | × | × | × | × | × | × | × | ---- | × | × | ---- | ---- | × | × | × | ---- | × | ---- | 70 |
| Meganyctiphanes norvegica | ---- | ---- | × | ---- | ---- | ---- | × | × | ---- | ---- | × | ---- | ---- | × | × | × | × | ---- | ---- | 40 |
| Thysanoessa inermis [1] | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| Euthemisto compressa | × | × | × | × | × | × | × | × | × | × | × | ---- | ---- | × | × | × | × | × | × | 90 |
| Euthemisto bispinosa | ---- | ---- | ---- | × | × | × | × | × | × | × | × | ---- | ---- | ---- | ---- | × | ---- | ---- | ---- | 50 |
| Hyperoche kroyeri | × | × | × | ---- | ---- | ---- | ---- | ---- | ---- | ---- | × | × | ---- | × | ---- | ---- | ---- | × | ---- | 40 |
| Limacina retroversa | × | × | × | ---- | × | × | × | × | × | × | × | ---- | × | × | × | × | × | × | ---- | 80 |
| Tomopteris catharina | ---- | × | × | × | ---- | × | ---- | × | × | × | × | ---- | × | × | × | ---- | × | ---- | ---- | 60 |
| Sagitta elegans | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | 100 |
| Phialidium languidum | ---- | ---- | × | × | × | × | ---- | ---- | × | × | × | × | × | × | × | × | × | ---- | × | 80 |
| Pleurobrachia pileus | × | × | ---- | × | ---- | ---- | ---- | ---- | × | × | × | × | × | × | ---- | ---- | × | ---- | ---- | 50 |

[1] Data for *Th. inermis* are not available for 1913; it can, however, be assumed to occur in at least 80 per cent of the cases, since it was taken at 14 of our 18 midsummer stations in 1914.

*Occurrence of representative species north of Georges and Browns Banks, July and August, 1914*

| Species | July | | | | | | | August | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10213 | 10214 | 10225 | 10227 | 10228 | 10229 | 10230 | 10245 | 10246 | 10247 | 10248 | 10249 | 10250 | 10253 | 10254 | 10255 | 10256 |
| Calanus finmarchicus | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| Pseudocalanus elongatus | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| Metridia lucens | × | ---- | × | × | × | × | × | × | × | × | × | × | × | × | ---- | × | × |
| Anomalocera pattersoni | ---- | ---- | ---- | ---- | ---- | ---- | ---- | × | × | × | ---- | ---- | × | ---- | × | ---- | ---- |
| Euchæta norvegica | × | × | × | ---- | ---- | ---- | ---- | × | × | × | × | × | ---- | ---- | × | ---- | × |
| Meganyctiphanes norvegica | × | × | × | ---- | × | ---- | ---- | ---- | × | ---- | × | × | ---- | × | × | ---- | × |
| Thysanoessa inermis | × | × | × | ---- | × | × | × | ---- | × | × | × | × | × | × | × | ---- | × |
| Thysanoessa longicaudata | ---- | ---- | × | × | × | × | ---- | ---- | × | ---- | × | × | × | × | × | × | × |
| Euthemisto compressa | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| Euthemisto bispinosa | ---- | × | × | × | × | × | × | × | × | × | ---- | × | × | ---- | ---- | × | × |
| Limacina retroversa | × | ---- | × | ---- | ---- | × | × | × | × | × | × | × | × | ---- | ---- | × | ---- |
| Tomopteris catharina | × | × | × | ---- | × | ---- | ---- | × | × | × | × | × | × | × | × | × | ---- |
| Sagitta elegans | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| Sagitta serratodentata | ---- | ---- | × | × | × | × | × | × | × | × | × | × | × | ---- | × | ---- | ---- |

Notwithstanding the qualitative uniformity of the animal plankton of the waters of the Gulf of Maine in summer, the actual aspect of the catches of the tow nets often differs markedly from station to station, according to the relative abundance of their several components and especially of the copepods. As a rule these (chiefly Calanus, Pseudocalanus, and Metridia, with Euchæta in the deepest layers of

water) are the dominant factor, and it occasionally happens that they practically monopolize the water locally. Such, for instance, was the case in the Eastern Basin on August 13, 1914 (station 10249), when the net from 50 meters captured only 3 or 4 Sagittæ, 2 pteropods (Limacina), 3 or 4 larval rosefish (Sebastes), a few small medusæ (Phialidium), 51 euphausiid shrimps, and an odd Euchæta, among millions of Calanus (3 to 4 liters, by measure; no other copepods were detected in sample examined by Doctor Esterly). Near Mount Desert Rock, too, on the same day (station 10248), a cursory examination of about 3 quarts of copepods, among which Calanus, Metridia, and Euchæta were represented in the proportion of about 30, 5, and 2, revealed only a few Pseudocalanus, 21 *Thysanoessa longicaudata*, odd amphipods (Euthemisto), 24 Meganyctiphanes, 7 *Thysanœssa inermis*, 6 or 8 pteropods (Limacina), 1 worm (Tomopteris), a few Sagittæ, 1 Pleurobrachia, and fragments of the ctenophore Beroë.

Similarly, the only other animals detected in a preliminary examination of the 2 to 3 quarts of copepods[5] captured in the 60–0 meter haul on the eastern part of Georges Bank, on July 23 of that same year (station 10224), were 89 euphausiid shrimps (*Thysanœssa inermis*), a few amphipods (Euthemisto), half a dozen young fish, and one caprellid, the latter being an accidental straggler from the bottom.

The most notable shoal of Calanus we have encountered was off Cape Cod on July 22, 1916 (station 10344), where a 15-minute haul with a net 1 meter in diameter captured 6 quarts at 40–0 meters, together with many thousands of silver-hake larvæ (Merluccius), but nothing else except a few small *Sagitta elegans*, an odd pteropod (Limacina), and an occasional larval crab and euphausiid, though the deeper waters, as exemplified by a haul at 90–0 meters, supported comparatively few copepods but many Sagittæ. We have found Calanus (with its relatives, Pseudocalanus and Metridia) hardly less dominant at enough other localities[6] to prove that it is a common event for these copepods to monopolize the plankton of any part of the Gulf in summer. As a rule, however, the animal plankton is more diversified at all levels by the hyperiid amphipods, euphausiids of several species, pteropods (Limacina), Sagittæ, etc., mentioned above, even though copepods may dominate the planktonic community as a whole (figs. 10, 11, and 12). Some of these other groups may be a major element in the plankton locally. For instance, the chætognaths (*Sagitta elegans*) often rival the copepods in bulk (if not in actual numbers) at the mouth of Massachusetts Bay and in the Isles of Shoals regions; indeed, our second towing station, 12 miles or so off Cape Ann (10002), yielded a swarm of these arrow worms on July 10, 1912 (Bigelow, 1914, p. 100), and we have encountered similar swarms of Sagittæ at other localities since then (fig. 13).

An abundance of the large pelagic shrimps Meganyctiphanes (fig. 14) and Thysanœssa is regularly characteristic of the deep northeastern corner of the Gulf throughout the year and of the Eastport–St. Andrews region in summer (p. 134), while various larval forms (crustaceans, especially) are extremely numerous locally near shore in their appropriate seasons, as noted elsewhere (p. 31). As other instances of the swarming of one characteristic boreal animal or another we may add that the

[5] Sample examined by Doctor Esterly was nearly pure *Calanus finmarchicus*.

[6] Notably off Gloucester on Aug. 9, 1913 (station 10087); in the Western Basin on July 15, 1912 (station 10007); near Platts Bank on Aug. 10, 1913 (station 10089); off the slope of German Bank on Aug, 12, 1913 (station 10095); northeast of Mount Desert Rock on Aug. 13, 1913 (station 10100); and off Cape Elizabeth on Aug. 15, 1913 (station 10104).

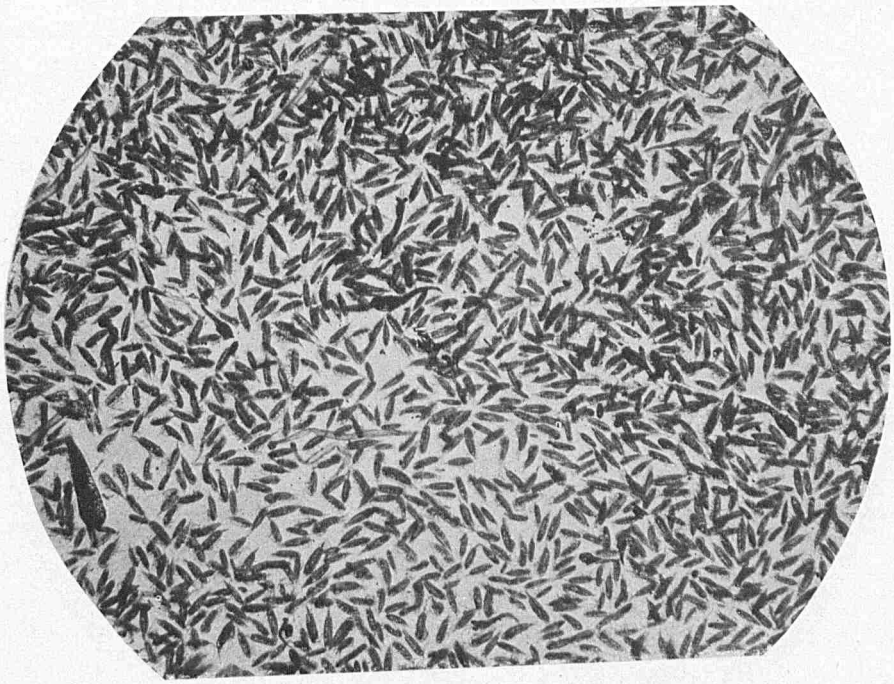

FIG. 12.—A monotonous plankton of *Calanus finmarchicus*, Massachusetts Bay, July 19, 1916, haul from 30-0 meters (station 10341). In connection with Figure 13 it illustrates a striking example of vertical stratification, with Calanus dominating the shoaler and *Sagitta elegans* the deeper levels. × 1.75

FIG. 13.—Plankton dominated by *Sagitta elegans*, Massachusetts Bay, July 19, 1916, haul from 80 meters (station 10341). In connection with Figure 12 it illustrates local abundance of this chætognath at the deeper levels at a station where the plankton at shoaler levels was almost pure Calanus. × 1.75

FIG. 14.—Plankton dominated by the pelagic shrimp *Meganyctiphanes norvegica* and by the glassworms *Eukrohnia hamata* and *Sagitta elegans*, with Calanus and other copepods. Northeast part of basin, March 23, 1920 (station 20081), haul from 140–0 meters. × 1.25

FIG. 15.—Plankton dominated by juvenile amphipods (Euthemisto). Southern slope of Georges Bank, July 21 ,1914 (station 10219), surface haul. × 9

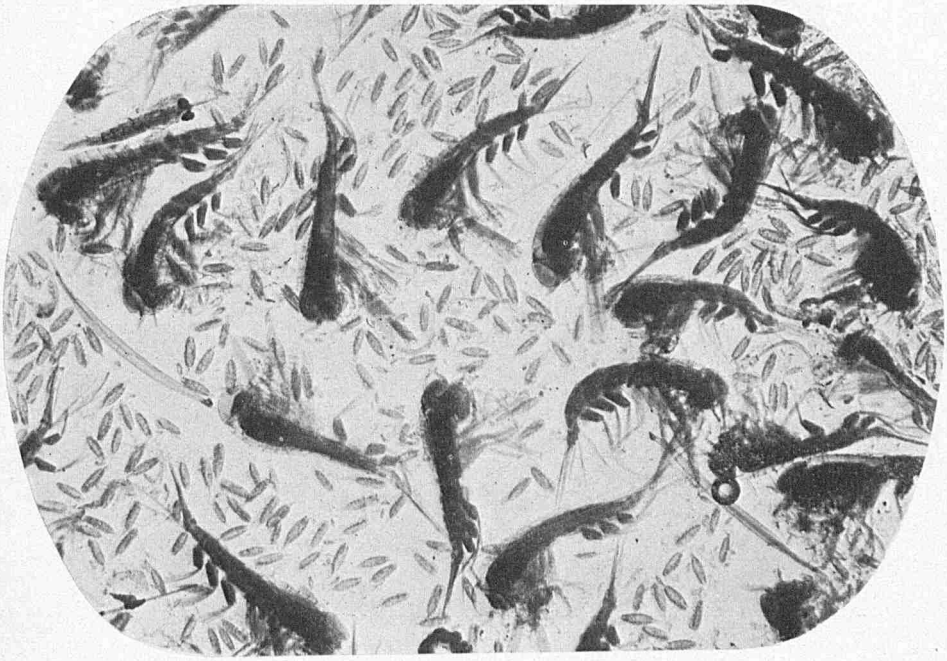

FIG. 16.—Plankton dominated by adult amphipods (Euthemisto) and by *Calanus finmarchicus*. Southwestern edge of Georges Bank, July 24, 1916, haul from 160-0 meters (station 10351). × about 2

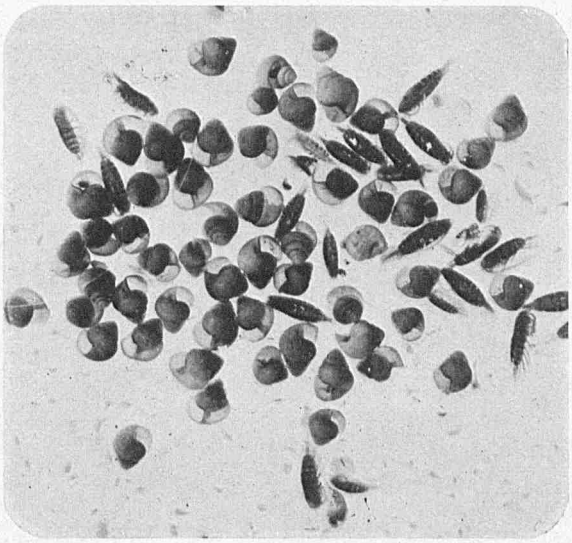

FIG. 17.—Pteropods (*Limacina retroversa*) and *Calanus finmarchicus*, northwest part of Georges Bank, July 20, 1914, haul from 50-0 meters (station 10215). × about 2.5

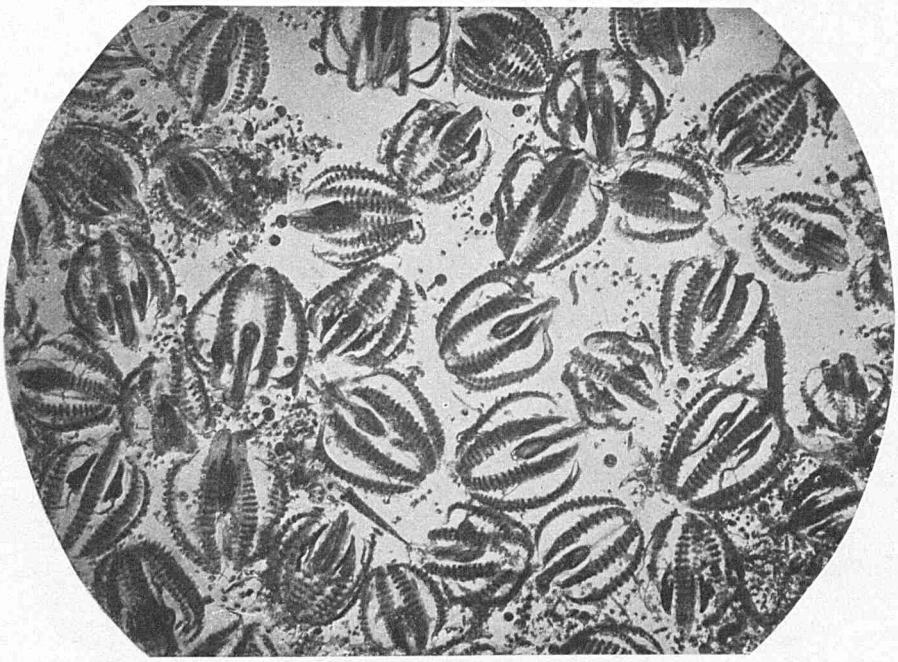

FIG. 18.—Plankton dominated by the ctenophore *Pleurobrachia pileus*, with barnacle (Balanus) larvæ in the "nauplius" stage. Browns Bank, April 16, 1920, haul from 40-0 meters (station 20106). × 1.5

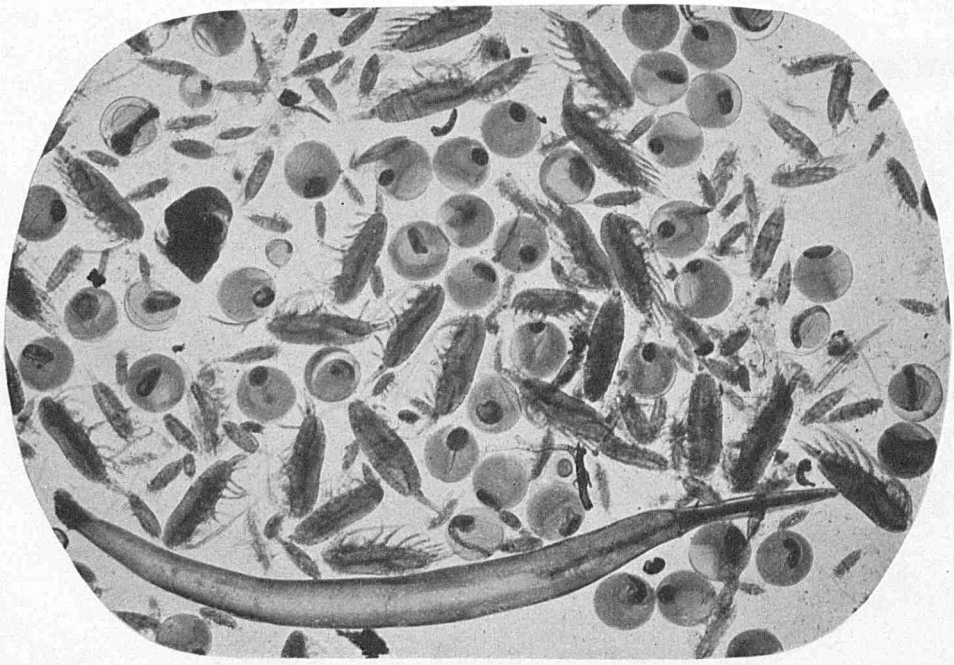

FIG. 19.—An unusually rich catch of haddock eggs, with the glassworm *Sagitta elegans*, the pteropod *Limacina retroversa*, Calanus, and other copepods. Eastern part of Georges Bank, April 17, 1920, haul at the surface (station 20111). × 4

surface waters were alive "with young amphipods (Euthemisto) as well as with young stages of *Calanus finmarchicus*, in the proportion of about one of the former to four of the latter" (fig. 15), off Penobscot Bay and off Mount Desert Island on August 11, 1913 (Bigelow, 1915, p. 274, stations 10091 and 10092); that older Euthemisto (fig. 16) were plentiful (though not rivaling the copepods) off Cape Ann and in the western basin on August 31, 1915 (stations 10306 and 10307), and at several stations along the outer edge of the offshore banks (p. 156); that the pteropod *Limacina retroversa* (fig. 17), which, as a rule, is but sparsely represented in our tow nettings, swarmed off Penobscot Bay on August 11 and 14, 1913 (stations 10091 and 10101); that fragments of a siphonophore (Stephanomia) formed fully half the catch of the 40-meter haul off Cape Cod on July 8 of that same year (station 10058); and that the ctenophore *Pleurobrachia pileus* often fills the water to the exclusion of almost everything else in the neighborhood of German Bank (fig. 18).

In summer and early autumn the large medusæ Cyanea, Aurelia, and Staurophora often gather in vast numbers in narrow lanes or windrows, though usually for brief periods (p. 362), and at this same season the hydroid medusa *Phialidium languidum* is often so abundant on the surface that it fills the tow net to the brim (p. 350). Young fish, too, sometimes occur in numbers sufficient to loom large in the total catch, notable instances of which have been the swarming of young silver hake off Cape Cod, mentioned above (p. 18); likewise of young rosefish (Sebastes) near Cape Elizabeth on July 19, 1912 (station 10019), when several hundreds were taken (Bigelow, 1914, p. 101), off Massachusetts Bay on August 9, 1913 (station 10087), and near Cashes Ledge, September 1, 1915 (station 10308). Occasionally we have encountered notable quantities of fish eggs, particularly of squirrel hake (*Urophycis chuss*), in Ipswich Bay, July 16, 1912 (station 10008); of silver hake (Merluccius) near Monhegan Island and off Mount Desert, on August 4 and 18, 1915 (stations 10303 and 10305); of cunners (Tautogolabrus) at many localities along shore in summer, especially in Massachusetts Bay[7] (station 10340–10343); and of haddock over their spawning grounds on Georges Bank during the early spring (fig. 19).

In summer, generally speaking, copepods are relatively most abundant in the western side of the gulf, less so in the eastern, the result being that, in spite of the qualitative uniformity of the tow nettings from station to station, their general aspect is usually most monotonous off the coasts of Massachusetts and southern Maine and out thence to the western basin, and most diversified in the central parts of the gulf and in its deep eastern trough. The only notable exception to the midsummer dominance of calanoids anywhere in the open gulf north of its offshore banks (local swarmings of other animals, such as those just mentioned, seldom rival the copepods in actual abundance, whether measured by bulk or by numbers) is the Pleurobrachia swarm of the German Bank region, which I have already described in the several preliminary reports on our cruises (Bigelow, 1914, 1915, and 1917). Since we have found this ctenophore in abundance at that same general locality during the successive Augusts of 1912, 1913, and 1914, and again on September 2, 1915, this is evidently a regular phenomenon of summer. Having occasion to recur to it in a later chapter (p. 365), I need add here only that Pleurobrachia, large and small,

[7] The ledges off Cohasset are a very productive nursery for this fish, judging from the quantities of its eggs that are to be found there.

were so abundant on these occasions that every haul yielded quarts of them, and that they fish through the water so thoroughly with their trailing tentacles that a great scarcity of all smaller pelagic animals regularly characterizes this part of the gulf in summer. In fact, a more striking contrast would be far to seek than between the masses of these glassy sea marbles, which have filled our nets there, and the abundant crustacean plankton of the deeper basin a few miles to the westward.

Although spring, not midsummer, is the chief season of reproduction in the Gulf of Maine (p. 41), certain of the planktonic groups of animals breed in sufficient numbers there in July or August for their larvæ to loom large in the summer plankton. This is true of the euphausiids, for we have found their larval stages common in Provincetown Harbor on July 20, 1916 (station 10343); on the surface off northern Cape Cod, August 28, 1914, in company with large Calanus (station 10264; Bigelow, 1917, p. 283). Young euphausiids were also abundantly represented in the horizontal haul at 40–0 meters on August 31, 1915 (station 10306), but so closely restricted to the upper stratum that a haul from 110–0 meters brought back very few among a half liter or so of calanoid copepods. Euthemisto is likewise produced in great numbers well within the gulf in August—witness rich hauls of the newly-hatched larvæ off Penobscot Bay on August 11, 1913 (station 10092), and in the western basin two summers later (p. 160). Copepods, too, breed throughout the summer, as noted below (p. 46), and in sufficient numbers for their young stages to characterize the plankton locally. Most of the medusæ spawn during the late summer or early autumn (pp. 358, 364). We may also point out, what is discussed at some length below, that larvæ of coastwise origin and of the most diverse natures are likewise produced during the warm season, though few of them color the aspect of the plankton more than a few miles out from the land (p. 32).

In a later section the seasonal plankton cycle is discussed in some detail (p. 37); however, it may clarify the account to note here that very little change takes place in the general composition of the Calanus community during the period (July to August) covered by our midsummer cruises, except for the disappearance of the earlier and the appearance of the later maturing species of medusæ (p. 46). For example, the only notable change during the interval between hauls made at the same location off Cape Cod on July 8 (station 10057) and again on August 5 (station 10086) in 1913 was that Staurophora, Stephanomia, and Beroë, which were prominent in the tow on the first occasion, were no longer to be found on the second, the lists being practically identical otherwise.[8] Three years later we found Calanus and its companion copepods as overwhelmingly predominant in the upper 40 meters or so off Cape Cod on August 29 (station 10398), among such boreal animals as Pleurobrachia, Aglantha, *Sagitta elegans*, *Euthemisto compressa*, and larval euphausiids, as we had five weeks previous (station 10344, July 22) in the corresponding stratum of water a few miles to the south. One very notable event does take place during the summer, however; that is, the entrance of *Sagitta serratodentata* into the gulf and its westward dispersal there, which are described in a later chapter (p. 322).

The foregoing remarks have reference chiefly to the inner waters of the gulf—that is, north of the offshore banks that form its southern rim—but the same elements unite to form the general planktonic assemblage over all but the outermost

[8] A typical Calanus community with *Sagitta elegans*, Euthemisto, a few euphausiids, and Limacina.

slope of the latter. Thus, a typical Calanus community, with Clione, Limacina, and the other boreal forms characteristic of the inner parts of the Gulf, occupied the waters over Nantucket Shoals on July 14, 1908 (Bigelow, 1909, p. 201), and at the same time of year in 1913, when we found no decided change in the boreal character of the plankton (Calanus predominating) until we had sailed westward nearly to New York (Bigelow, 1915, p. 269). During the summer of 1914 we again found Calanus, with its usual companions, predominant over the greater part of Georges Bank in July, and across the mid-zone of the continental shelf abreast of Marthas Vineyard in August; also in August, 1915; and from Cape Cod out to the continental slope in July, 1916. But although Calanus is as universal over the offshore banks as within the gulf, it does not dominate the plankton so constantly there. Thus we found *Sagitta elegans* as important, faunally, as were the copepods over the central part of Georges Bank during our summer cruise of 1914, and swarming both over the northeast corner of the bank on July 23 (station 10224 [9]) and in the Northern Channel on July 25 (station 10229), practically to the exclusion of everything else, except for an abundance of adult Euthemisto, which (we may suppose) are sufficiently large and active to protect themselves from the glassworms, voracious though the latter are (p. 107).

Even when copepods, as a group, are the chief factor in the summer plankton over Georges Bank, it is sometimes the little brown *Temora longicornis* (fig. 20), not Calanus, that is the dominant species there. This was the case at a station on the northwestern part of the bank in July, 1913 (station 10059), while the frequency with which Kendall, in his field notes for August, 1896, describes "small brown copepods" (which could only be Temora) as abundant, side by side with "red feed" (Calanus) and "green copepods" (Anomalocera), or even as constituting the bulk of the surface tow, suggests that such dominance on its part is a common event on the northern part of the bank (lat. 41° 45′ to 42°, long. 66° 30′ to 68° 30′). His records suggest that Temora increases in number there with the advance of the summer,[10] which parallels its seasonal history in the Massachusetts Bay region (p. 289).

Hyperiid amphipods (two species of the genus Euthemisto, p. 156) have often been reported as plentiful over the outer part of the continental shelf off Marthas Vineyard. We found them in abundance over the corresponding zone off Nantucket Shoals and over the western end of Georges Bank, side by side with the copepods, in July of 1913 and 1916 and August of 1913 and 1914. They are equally characteristic of the outer parts of the banks eastward across the mouth of the Gulf of Maine and off the Nova Scotian coast, where they breed in abundance (p. 160) and grow larger than within the gulf to the north.

The outer part of the continental shelf is the offshore limit to the occurrence of copepods in abundance abreast of the Gulf of Maine; but the pelagic amphipod genus just mentioned is perhaps most plentiful along the upper part of the continental slope, where it mingles with the oceanic planktonic community of the warmer waters of the Atlantic basin. It has likewise been our experience (though fresh observations may give cause to alter conclusions drawn from a single summer's cruise) that in mid-

[9] The catch of one-half hour's haul of the Helgoland net at 40–0 meters was about 5 liters of *Sagitta elegans*, and very little else except a few Calanus, Temora, Pseudocalanus, 3 or 4 Euthemisto, 2 Limacina, young crabs and other decapods, and some floating hydroid fragments described below (p. 380).

[10] Kendall's tows were taken during the last week in August.

summer Euthemisto is to be expected in abundance over Browns Bank, largely replacing the copepods there, for on July 24, 1914 (station 10228), the surface waters were alive with them, while on June 24, 1915 (station 10296), the tows on the bank yielded large numbers of these amphipods among the still more abundant Calanus (more abundant in bulk as well as in numbers). Euthemisto is also an important factor in the plankton close in to the land off Cape Sable, where they increased in relative abundance in 1914 from July 25 (station 10230), when they were overshadowed by Calanus, until August 11 (station 10243), when they were dominant in the plankton. A seasonal change of the same sort took place in the shoal coastal waters off Shelburne, Nova Scotia, during the summer of 1915; for Euthemisto dominated a very scanty plankton there on September 6 (station 10313), where it had been outbulked both by copepods and by Sagittæ on June 23 (station 10291), though dominating the plankton farther out over the shelf on that day (10293).

Although euphausiid shrimps of one species or another (p. 133) are practically universal within the gulf—may, indeed, be constantly plentiful locally, as off the Eastport-Grand Manan region, and temporarily so elsewhere (p. 133)—we have never found them dominating the water of the gulf at any level except over Browns Bank, where the tow net working at 60 meters depth yielded a quart or more of these pelagic shrimps [11] on July 24, 1914 (station 10228), diversified only by an occasional Sagitta, three *Beroë cucumis*, a few copepods, and no amphipods at all, notwithstanding the abundance of the latter at the surface at this same station. Though not strictly within the limits of the gulf, I may add that four days later euphausiids occurred in great numbers over the slope abreast of Cape Sable [12] (station 10233), and in this same general region on March 19, 1920 (station 20076, fig. 21). It is not safe to assume, however, that these shrimps are constantly abundant over Browns Bank in summer, for we found none at all there on our only other visit during the warm half of the year (June 24, 1915, station 10296), but in their stead made a very rich haul of calanoids (3 to 4 liters bulk), with a few Euchæta, many large Euthemisto, small Sagittæ, and occasional tropical organisms, such as Phronima and *Salpa zonaria*.

To close this brief survey of the chief planktonic communities of midsummer, I must remark that a sprinkling of Gulf Stream animals—sometimes, indeed, a typically tropical plankton—is to be expected all along the upper part of the continental slope at that season, corresponding to the high temperature of the Gulf Stream, the inner edge of which lies but a few miles farther offshore. This tropical plankton and such members of the general bathypelagic community of the Atlantic basin as approach the slope are the subject of a later section (p. 53).

The accompanying photographs (figs. 10 to 21), illustrate certain of the more characteristic communities as they occur in nature, and the distribution of the more characteristic communities, for July-August, 1914, is outlined on the chart (fig. 22).

The great majority of the species of pelagic animals that unite to form the bulk of the zooplankton of the gulf are endemic in origin, breeding sufficiently regularly and abundantly within its limits to maintain the local stock by local production. This generalization, which the reader will find discussed in more detail under the accounts of several of the species concerned, applies to most of the com-

[11] Chiefly *Meganyctiphanes norvegica*, *Thysanœssa inermis*, *Th. longicaudata*, with fewer *Th. gregaria* and *Nematoscelis megalops*.
[12] Chiefly Euphausia and Nematoscelis and fewer *Th. longicaudata* at 100 meters; Nematoscelis at 400 meters.

FIG. 20.—Plankton dominated by the small brown copepod *Temora longicornis*, with a few of the larger *Calanus finmarchicus*, juvenile Euthemisto, and glassworms (*Sagitta elegans*). Western part of Georges Bank, July 9, 1913, haul from 25–0 fathoms (station 10059). × 9

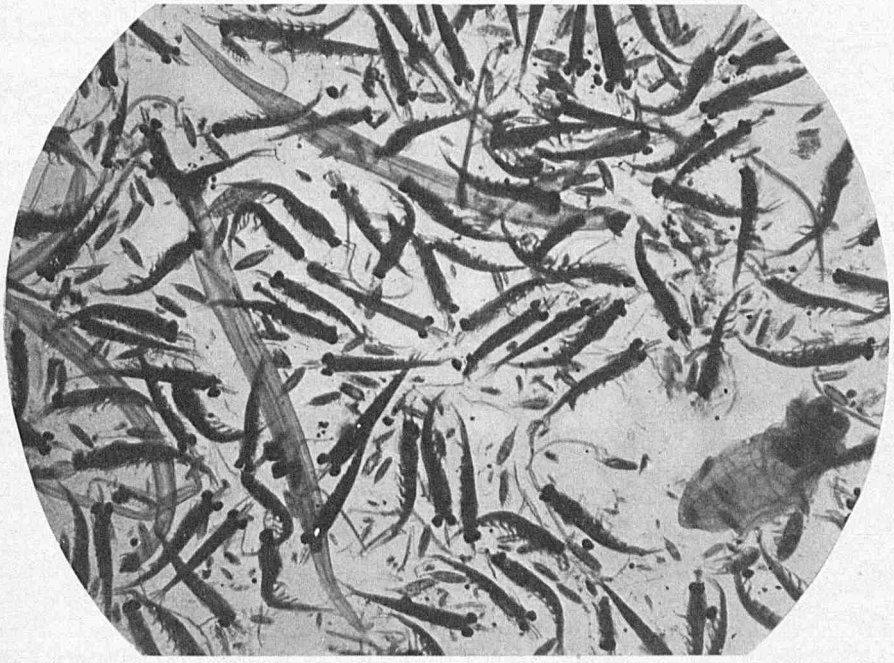

FIG. 21.—Plankton dominated by the pelagic shrimp *Thysanoessa longicaudata*, with *Calanus finmarchicus*, glass worms (*Sagitta elegans*), and the naked pteropod *Clione limacina*. Outer part of continental shelf off Shelburne, Nova Scotia, March 19, 1920, haul from 100–0 meters (station 20076). × 1.75

mon copepods, notably to *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Metridia lucens*, Euchæta, and to sundry others (see the chapter on copepods, p. 167); likewise to *Sagitta elegans* (p. 308), both the local species of Euthemisto (*E. compressa*

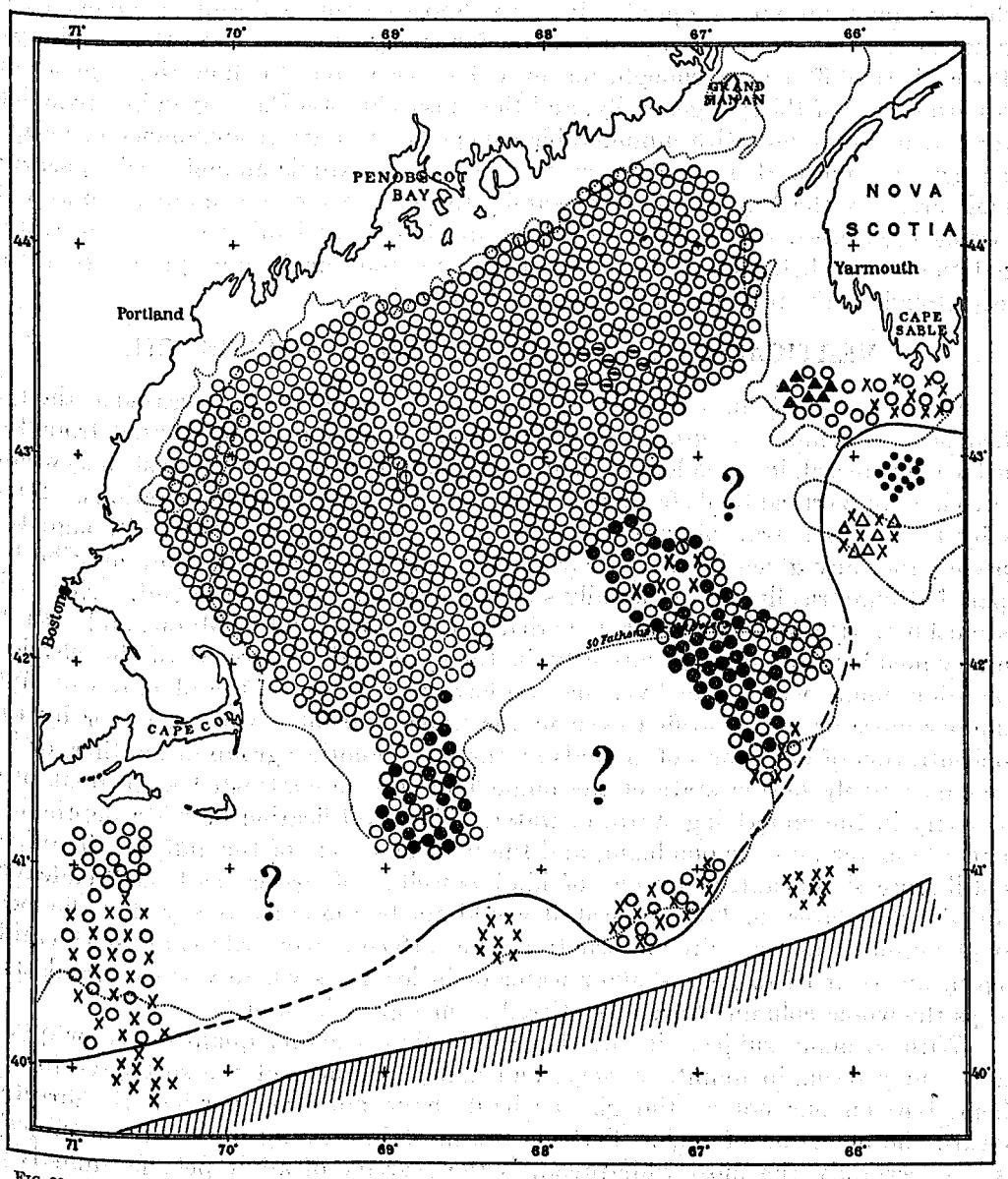


FIG. 22.—Distribution of the more characteristic types of animal plankton in the offshore waters of the Gulf of Maine, July and August, 1914. ○, calanoid copepods dominant; ●, glass worms (Sagittæ) dominant; X, amphipods (Euthemisto) dominant; △, euphausiid shrimps dominant; ▲, ctenophores (Pleurobrachia) dominant; ⊖, hydromedusæ (Phialidium) dominant; P, swarm of pteropods (*Limacina retroversa*)

and *E. bispinosa*, p. 156), the euphausiid shrimps Meganyctiphanes and probably *Thysanœssa inermis* (p. 139), and the pteropod *Limacina retroversa* (p. 124), to mention only a few. It also applies to a whole category of animals of coastwise nativity

It does not follow from this, however, that all parts of the gulf are equally favorable as marine nurseries. On the contrary, few if any animals breed indifferently or equally plentifully over its whole area, and different parts of the gulf may run the whole gamut from extreme productivity to almost complete sterility for one species or another. Our work has not progressed far enough to give more than a glimpse of such local differences; enough, however, has been done to show that the southwestern corner of the gulf generally, and the Massachusetts Bay region in particular, stand at one extreme, with innumerable copepods and a great abundance of pelagic fish eggs produced there (not to mention other planktonic animals), while certain small areas in the Bay of Fundy exemplify the other, where few if any animals with floating eggs breed successfully. Broadly speaking, our hauls have demonstrated that the coastal belt, out to the 100 or 150 meter contour, is more prolific than the deep trough in the production of planktonic animals.

## VERTICAL DISTRIBUTION OF THE ZOÖPLANKTON

In the foregoing lines the various planktonic communities are treated as though their several component groups or species were indifferently distributed from the surface downward, independent of depth; the various lists, that is, are such as would be yielded by vertical hauls from surface to bottom at the respective stations. Such is by no means a true picture, however, for it often happens that, although the species from any given locality occur side by side geographically, they may be far apart bathymetrically, and especially so in the deeper parts of the gulf. Nor is it astonishing, with a pelagic fauna as varied as that of the Gulf of Maine, and with its sundry members responding variously in their vertical occurrence to the physical conditions under which they live, that we have usually found the plankton of midsummer more or less stratified even in the upper 100 meters or so, either by the concentration of one group of animals at one level, another group at another, or by a comparatively barren state of the immediate surface contrasted with great productivity in the underlying strata of water. The stratification between depths less than 100 meters, on the one hand, and the bottom waters of the gulf, on the other, is still more significant, being one of kind as well as of degree, as I shall endeavor to make clear later (p. 26). Indeed, it would not be too much to say that the local zooplankton is never quite uniform from the surface downward to any considerable depth, unless it be in very shallow water or in localities where vertical circulation keeps the whole column effectively stirred from top to bottom.

With so many subjects involved, stratification, whether quantitative or qualitative, may occur in infinite variety, and many instances of the sort have forced themselves on our notice, though our hauls have not been particularly directed toward the detection of such. Perhaps the most interesting phase of the subject, as it is certainly the most widespread, is the scarcity of adult pelagic animals of the Calanus community, including most of the species which together make up the preceding plankton lists (p. 17), at the surface during the daylight hours of summer. No matter what nets we have used on the surface between sunrise and sunset in the offshore waters of the gulf at this season, they have usually yielded very little zoöplankton of any kind, and often practically nothing except larval

forms and the smallest Crustacea and phytoplankton. In fact, had we relied on surface hauls by daylight alone, we would hardly have suspected the existence of the abundant and varied planktonic fauna which peoples its deeper water layers. True, we have occasionally made rich catches of Calanus, with its companion animals, right on the surface in the middle of the day, as, for example, near Gloucester on July 22, 1912 (station 10012), near Lurcher Shoal on August 12, and off Penobscot Bay and Cape Elizabeth on August 14, 1914 (stations 10245, 10250, and 10251), and near Seguin Island on August 4, 1915 (station 10303)[13]; while the extraordinary abundance of Calanus that characterized the 40–100 meter stratum in the western side of the gulf during late July, 1916 (p. 18), was reflected in the presence of considerable numbers of these little crustaceans on the surface at the time, by day as well as by night. However, such occurrences have been exceptional. Huntsman, similarly, has characterized "the presence of Calanus en masse at the surface between 3 and 4 p. m., under a bright sun," in the Bay of Fundy in September as an unusual event (Willey, 1919, p. 181). On the other hand, surface tows made in the gulf during the hours of darkness, especially if near midnight, have usually yielded an abundance of the calanoid copepods (even including the deep-water genus Euchæta). And the geographic locations of the stations where we have made rich surface catches by night point to a general diurnal migration of the Calanus community—upward after dark, downward about daylight—in the inner parts of the Gulf of Maine in summer, such as Esterly (1911 and 1912) and Michael (1911) describe for the San Diego region,[14] and with all the major planktonic groups sharing in it more or less, though perhaps none so regularly as the copepods. The data bearing on this point are not extensive, no particular attention having been paid to it in arranging the stations. We have occasionally found the surface practically barren some hours after sunset and before the first sign of sunrise, even at localities where the deeper waters supported a rich and varied plankton, as was the case in the western basin on August 9, 1913 (station 10088), and again on the 22d of that month a year later (station 10254).

Of course, there is nothing novel in a vertical migration of this kind, similar phenomena having long been known and widely heralded in other seas; nor is it necessary to seek far afield to find a parallel in New England waters, for Peck (1896) long ago described the copepods as deserting the surface of Buzzards Bay almost completely during the daytime, to reappear there after dusk.

It is unfortunate that our hauls have not been arranged to show at what precise time after sunset the copepods rise to the surface in largest number or how soon after midnight they sink again, a question of great interest from the physiological standpoint (p. 204). Few data have been gathered as to the actual vertical range through which this migration takes place in the Gulf of Maine; that is, how far up and down any individual animal may swim, or how universally or regularly the members of any group of animals indulge in it. It must be very widespread occasionally, at least among the copepods, for at times we have towed them in great numbers right

[13] In an earlier report (Bigelow, 1914a) it was stated by error that a large haul of Calanus was obtained on the surface by day at station 10027; actually this station was occupied at about midnight.

[14] Data on the euphausiids, amphipods, pteropods, etc., will be found summarized in the accounts of these several groups.

on top of the water after dark, notably near Mount Desert Rock on August 16, 1912 (station 10032), where the 4-foot net, towed for half an hour, yielded nearly 3 liters of plankton, chiefly copepods, with *Calanus finmarchicus* dominating, besides Euchæta, *Centropages typicus*, Metridia, Anomalocera, and Pseudocalanus; also the shrimps Meganyctiphanes, *Thysanœssa inermis*, *Th. longicaudata*, *Th. gregaria*, and Nematoscelis; the pteropods Limacina and Clione; Euthemisto of both species; the two common chætognaths *Sagitta elegans* and *S. serratodentata;* Tomopteris; Stephanomia; and larval redfish in lesser number; in short, a typical Calanus community. A second instance of this sort came to our notice off southern Cape Cod on July 22, 1916 (station 10346), when the surface net yielded about as much Calanus (nearly a liter), with a sprinkling of Pseudocalanus and Metridia, an odd Euthemisto, *Sagitta elegans*, and Clione, as did the 30-meter net, although the mouth area of the latter was four times the greater, and it was towed for an equal period. As a rule, however, this vertical migration does not bring nearly so large a proportion of the zoöplankton to the top of the water at any time during the night, for our catches have almost always been far richer (more varied, as well) at some little depth than immediately on the surface. This is illustrated by a station off Cape Cod on August 23, 1914 (station 10256), where the catch of Calanus, Euchæta, Meganyctiphanes, Euthemisto, *S. elegans*, and Stephanomia was several times larger in the 130–0 meter haul than in the surface haul, even after allowing for the use of nets of different diameters.

Whatever the precise physiological stimulus may be which causes so many of the copepods and other pelagic animals to rise at sunset and to sink again soon after midnight—and this is still an open question (p. 204)—its results are certainly confined to a far shoaler stratum in the Gulf of Maine, where it is never necessary to lower the net deeper than 40–100 meters to find the Calanus community at full strength at any time of day, than in the San Diego region off southern California, where Calanus in particular congregates as deep as 200 fathoms by day, to swim upward nearly or quite to the surface in the darkening hours (Esterly, 1911). Nor is it probable that the daily vertical migration in the Gulf of Maine often covers more than 100 fathoms even for Euchæta, which sinks considerably deeper in the daytime than does Calanus but less often reaches the surface at night. Until more extensive data are available it is idle to do more than touch on this interesting question.

Apart from these vertical diurnal migrations our hauls have afforded glimpses of vertical stratifications of three other sorts (sometimes all three of them are exemplified at a given station): (1) As between young and adult communities as a whole; (2) between the adults of the several groups, genera, or species, even within the rather narrow depth limits (say, 10 to 100 meters) where the Calanus community as a whole attains its most abundant development; and (3) between the planktonic communities of the upper 100 meters or so, on the one hand, and of the deepest water of the gulf, on the other. Perhaps as illustrative a case as any that has come under our notice, and one typical of the western side of the gulf as a whole in early summer, is afforded by a station off Cape Cod on July 8, 1913 (station 10057), where it was the surface hauls alone that yielded any considerable number of copepod nauplii and eggs; the haul at 15–0 fathoms (27–0 meters) caught swarms of Calanus and many

euphausiids and hyperiids, but only a few Sagittæ; the haul from 60-odd meters contained almost no euphausiids, hyperiids, or pteropods, but yielded large numbers of Sagittæ, and Euchæta was taken in it alone. Thus, the Calanus, euphausiids, and pteropods were mostly above 30–50 meters, the Euchæta and Sagittæ below that depth, with Beroë, Pleurobrachia, and Stephanomia more evenly distributed (Bigelow, 1915, p. 267).

A similar bathymetric segregation as between the copepods and the large adult Sagittæ prevailed in Massachusetts Bay on July 19, 1916 (station 10341; figs. 12 and 13), when the haul at 30 meters yielded a practically pure Calanus plankton with many larval fishes and some young euphausiids but very few Sagittæ, whereas the net working at 80 meters captured a swarm of large *S. elegans* but not nearly so many Calanus as the shoaler haul. This condition must have been general over a considerable area at the time, for we had much the same experience two days later off Cape Cod (station 10344), where Calanus and young silver hake were extraordinarily abundant at 40 meters (the largest catch of young fishes we have ever made—Bigelow and Welsh, 1925, p. 394), but evidently concentrated in a narrow depth zone centering at about that level, for both were practically absent on the surface, on the one hand, and very much less numerous in the 90-0 meter catch, on the other, whereas Sagittæ, equally absent from the surface, were scarce in the 40-meter hauls but abundant in the catch from 90 meters.

A depth relationship of the same sort (between copepods and euphausiids) obtained on August 9, 1913, off Cape Ann (station 10087), where the 30-0 meter haul brought back a rich gathering of the former (chiefly Calanus, with many Pseudocalanus) and many larval rosefish, but only an occasional euphausiid, whereas we captured a considerable number of the latter (small Thysanœssa) at 80–0 meters, but only a fraction as many copepods as at 30 meters, and an occasional Sebastes. On the other hand, lest the reader conclude that the Sagittæ and the euphausiids invariably congregate below the densest shoals of copepods when stratification occurs between these groups, I may point out that we found the 40-0 meter haul on the northwest slope of Georges Bank, July 20, 1914 (station 10215), practically monopolized by *S. elegans* and *Limacina retroversa*, with very few copepods, whereas a rather rich haul from 70–0 meters brought in about as great a bulk of copepods (about equal numbers of Calanus and Pseudocalanus) as Sagittæ, but no Limacina at all. Similarly, there were about six times as many Calanus and Pseudocalanus at 110–0 meters as at 40–0 meters off Cape Ann on August 31, 1915 (station 10306), with just the reverse holding in these same hauls for Euthemisto and for young euphausiids. The latter, indeed, were almost wholly confined to the shoaler level, where they about equaled the copepods in bulk if not in numbers. The copepod plankton of the western basin must also have been much denser below than above 100 meters on May 5, 1915 (station 10267), when the vertical haul from 250–0 meters yielded great numbers, whereas the catch of the horizontal net working at 85 meters and up to the surface was scanty (total catch less than ¼ liter).

As still another instance of vertical stratification in summer, I may mention our station of August 12, 1914, on German Bank (10244), where the surface water contained an abundance of small Euthemisto but only a few Calanus (besides the Pleuro-

brachia so common there, p. 19), whereas the haul from 40 meters yielded copepods chiefly, with only occasional Euthemisto.

No doubt a more intensive examination of the zoöplankton of the Gulf of Maine will multiply such instances indefinitely, but enough have been mentioned to show that a definite vertical segregation may occur at certain times and places between animals having the same faunal status. On other occasions the contents of hauls at different depth levels, between, say, 10 and 100 meters, are often almost precisely alike, as was the case near Lurcher Shoal on August 15, 1912 (station 10031), when copepods, euphausiids, Sagittæ, Staurophora, Euthemisto, and even Salpæ (p. 56) occurred in proportions so similar in hauls from 50–0 and from 100–0 meters that it would have been difficult to distinguish samples of the one catch from the other had it not been for the presence of the large copepod Euchæta in the deeper one. Many other instances of this same sort might be mentioned also.

Our experience has been that young and larval forms of all sorts, from fish eggs to copepod nauplii, are usually most plentiful at or very near the surface. For example, in May, 1920, which is the season of their greatest abundance, nauplii were far more abundant in the surface catch and in closing-net hauls from 10–15 meters in Massachusetts Bay (stations 20120, 20121, and 20124) and off the Merrimac River (station 20122) than in the deeper catches. It is safe to say that the great majority of the copepods breeding in the Gulf of Maine pass through their early stages in the upper 40 meters of water. Similarly, the nauplius and cyprid larvæ of the common barnacle, so prominent in the plankton for a brief period in spring (p. 43), are usually condensed at and near the surface, rarely at some lower level (station 20105, figs. 23 and 24). Larval and even half-grown euphausiids are also far more plentiful above than below 50 meters; and this is even more true of larval amphipods (Euthemisto), which live close to the surface at first (p. 163), to sink to deeper levels with advancing age; likewise of young *S. elegans*, as described elsewhere (p. 316). Since most of the fish produced in the gulf live in this same zone during their first weeks, it may, not inaptly, be named the nursery of the gulf.

Certain conspicuous adult animals are also as typically characteristic of the surface of the gulf as are the innumerable larval forms. Such, for instance, is the large blue copepod Anomalocera which may often be seen darting to and fro in the sunlight immediately in the surface film and which seldom sinks more than a few fathoms. The small brown copepod *Temora longicornis* likewise occurs in greatest numbers near the surface; for instance, a surface tow near Nantucket Lightship, on July 9, 1913 (station 10060), "yielded thousands, while the haul from 20 fathoms caught only 25 specimens, and it was not taken at all in hauls from depths greater than 23 fathoms" during that summer (Bigelow, 1915, p. 294). Much the same rule holds for the little copepod *Centropages typicus*, of which "the surface haul at station 10088 yielded ten times as many specimens as the haul from 80 fathoms, though made with a net of only one-sixth the mouth area" (Bigelow, 1915, p. 293), and which we twice found common at the surface during August, 1914, but not at all in the catches at 25 meters and deeper (Bigelow, 1917, p. 291). It is our surface hauls, too, that most often yield Evadne and appendicularians; indeed, we question whether the latter ever sinks to any great depth in the Gulf of Maine. One of the

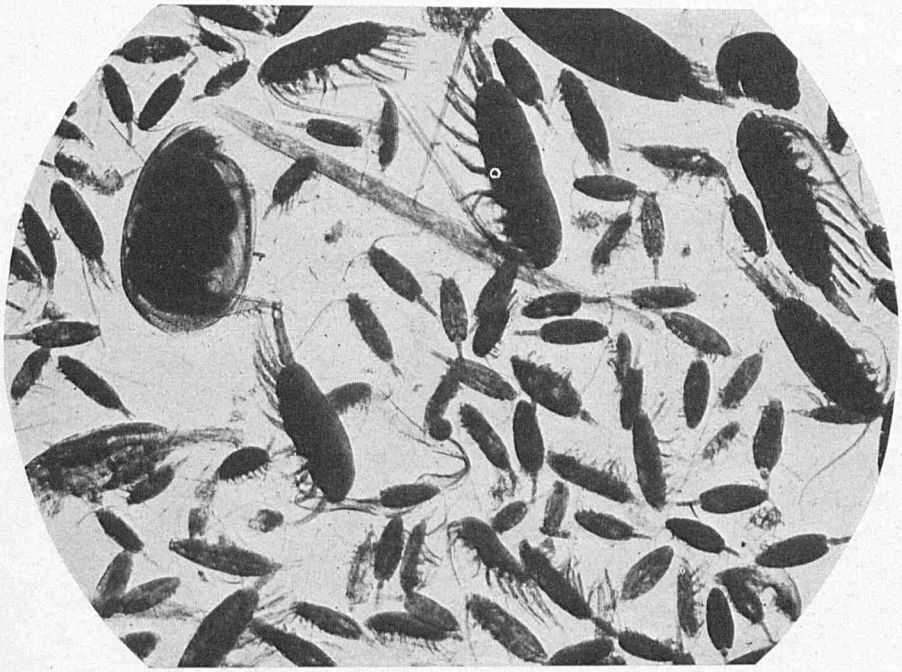

FIG. 23.—Plankton at the surface, northern channel, April 15, 1920 (station 20105), dominated by the copepods *Calanus finmarchicus*, Acartia, and Metridia. In connection with Figure 24 it illustrates vertical stratification of the plankton. × 10

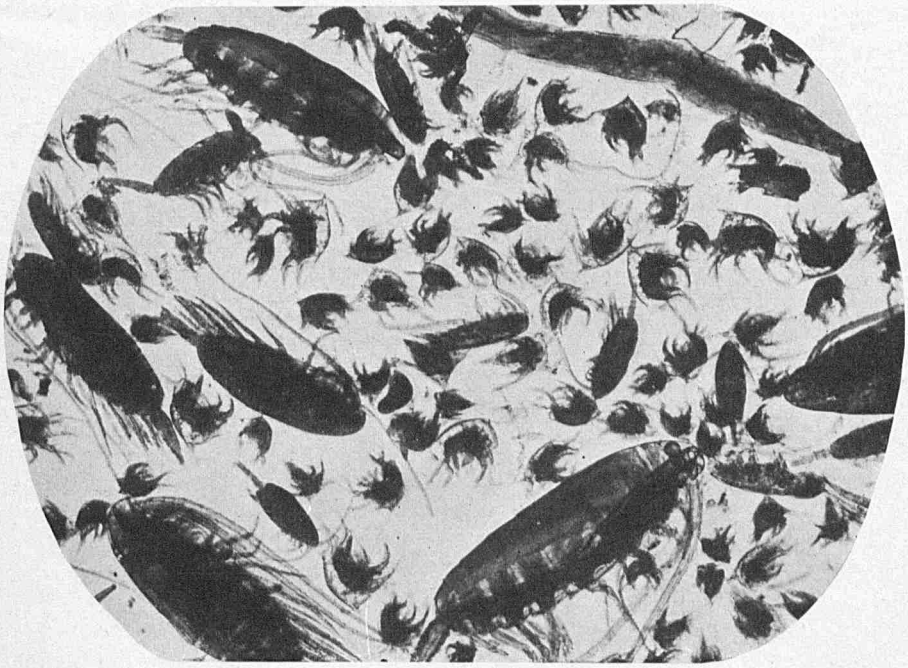

FIG. 24.—Plankton of the deeper levels, at the same station as the surface haul in Figure 23. This deep haul (150–0 meters) was dominated by the "nauplius" larvæ of barnacles (Balanus), with fewer Calanus and other copepods. × 10

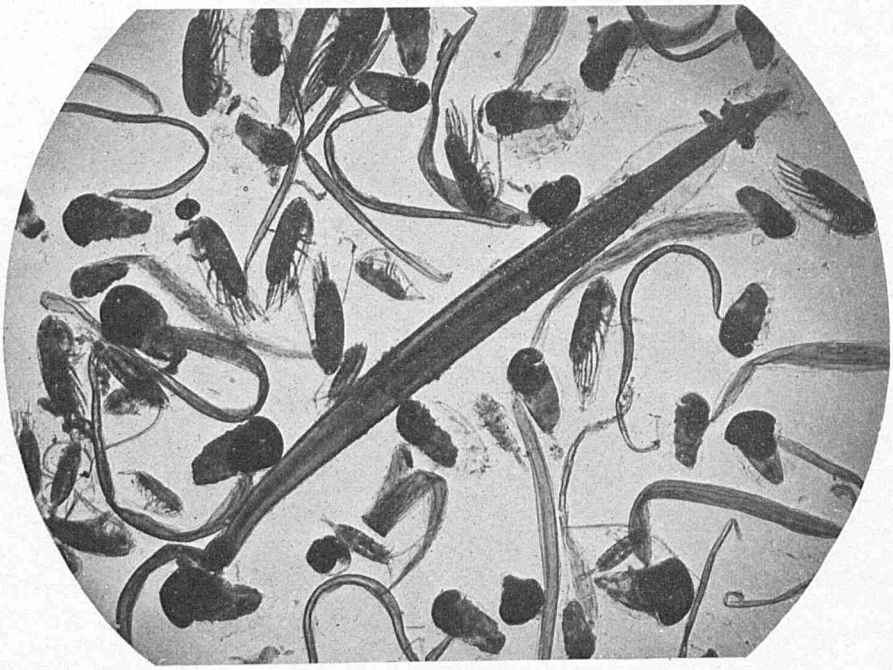

FIG. 25.—Surface plankton dominated by Oikopleura at a station on the continental slope southwest of Georges Bank, May 17, 1920 (station 20129), where the deeper water (fig. 26) was dominated by euphausiids and copepods. × 3.5

FIG. 26.—Plankton in the 100–0 meter haul, dominated by *Calanus finmarchicus* and other copepods, and by euphausiid shrimps (Thysanoessa) at a station off the southwest slope of Georges Bank, May 17, 1920 (station 20129), where the surface catch (fig. 25) was dominated by Oikopleura. × 4

most striking instances of vertically stratified plankton we have ever encountered resulted from a swarming of large appendicularians (fig. 25) on the surface and down perhaps to 40 or 50 meters over the southern edge of Georges Bank on May 17, 1920 (station 20129), overlying a moderately abundant Calanus and young euphausiid community in the deeper strata down to about 100 meters (fig. 26).

Various medusæ, among them the largest (Aurelia and Cyanea), likewise seek the surface even in bright sunlight, while smaller species, notably the common hydroid medusa *Phialidium languidum*, sometimes swarm there in such numbers as to fill our tow nets to the brim. In fact, the latter seldom, if ever, sinks more than a few meters deep. Ctenophores, too, of several species, come up to the top on smooth days, where they can be seen drifting along like crystal balls (p. 372), and on occasion even the large euphausiid shrimps may swarm on top of the water, day as well as night, probably to avail themselves of a particularly succulent food supply; in the Eastport region, for instance, in summer (p. 147), and in the Isles of Shoals-Boon Island region in spring (p. 145), though they are no more characteristic of the superficial layers elsewhere and at other seasons than are the adult Sagittæ. Since most of the deep-water members of the plankton (e. g., Euchæta, the largest of local copepods, and the chætognath *Eukrohnia hamata*) have occasionally been taken on the surface in the Gulf of Maine (pp. 235, 328), any number of this faunal group may be expected to appear at that level occasionally.

It needed very few hauls from the deep trough of the gulf to show that there is a decided cleavage in composition between the zooplankton of the upper and of the lower water layers, with the 100 to 150 meter level roughly delimiting the two. No hard and fast line can be drawn between these communities, for the gap is bridged, on the one hand, by such occasional excursions of the deep-water dwellers upward even to the surface as have just been mentioned and, on the other, by the presence of Calanus, Metridia, *Thysanoessa inermis*, Tomopteris, *Sagitta elegans*, Euthemisto, Limacina, etc., in decreasing numbers right down to the bottom, even in the deepest parts of the gulf, a fact demonstrated by the closing-net hauls listed below (p. 50). Nevertheless, the two communities are so characteristic in general aspect that it is usually possible to tell at a glance whether any particular sample came from much above or far below 100 meters. The features making this possible are the abundance and regular occurrence of *Euchæta norvegica* in the deep basin of the gulf. This copepod is so much larger than any of its relatives and is made so conspicuous by the blue egg clusters of the female that it gives a distinctive appearance to the entire catch. It is regularly accompanied by the chætognath genus Eukrohnia (p. 328); more rarely by the larger glass worm *S. lyra* (p. 327); frequently by the large pelagic decapodous shrimp Pasiphæa; and locally by large numbers of the euphausiid shrimp *Meganyctiphanes norvegica* (the latter, however, occurring in shallow water also). On the other hand, this "Euchæta" community includes only a sparse representation of Euthemisto, Calanus, or Pseudocalanus, and practically no Pleurobrachia or pteropods.

Unfortunately we have made only one successful closing-net haul deeper than 100 meters during all our summer cruises, for it was not until the spring of 1920 that our closing apparatus for horizontal hauls was developed to a dependable state;

hence, except for that one instance, the catches in the deep summer hauls have all been contaminated by the Calanus community captured by the open nets on their journeys up and down. For this reason I can not claim that the Euchæta, Eukrohnia, etc., taken at any given station necessarily came from the deepest levels. But the Euchæta community has been consistently represented in our midsummer hauls below 100 meters, no matter in what part of the basin of the gulf these have been made (see the following tables, pp. 40 and 50), and as we have never found it in any abundance in hauls shoaler than 100 meters it would be merely academic to dispute the general thesis that it is actually characteristic of the deepest stratum of the Gulf of Maine.

Whether the occasional excursions of Eukrohnia and Euchæta to the surface, such as I have just mentioned (p. 29) and discuss at greater length elsewhere (pp. 235, 328), are sporadic events induced by some temporarily or locally active vertical circulation, or whether they are more regular concomitants of regularly recurrent physical states than now appears probable, the fact remains that it is only below 100 meters—that is, in the saltest water of the trough of the gulf, which is never very cold—that the Euchæta community occurs regularly.[15] The Euchæta community similarly characterizes the corresponding level along the continental slope abreast of the gulf.

The use of the closing net is requisite to show in what relative amounts these deep-water animals are mingled with Calanus and its companions in the deeper strata of the inner parts of the gulf. In one such haul just mentioned (off Cape Cod, August 29, 1912, station 10043) at a station where Calanus outnumbered Euchæta at least 2,000 to 1 in the 20–0 meter haul (Bigelow, 1914, p. 116), these two copepods were about equally numerous at 125 to 120 meters, with Euchæta bulking the larger, thanks to its great size. The total volume of the catch was small, however (less than one-half liter), and we have never found the deep-water Euchæta community even approaching the swarms of Calanus of the upper 100 meters, or so, in volume of plankton present in the water. Unfortunately we lack precise data on this point.

To recapitulate, three chief bathymetric pelagic communities of animals can be distinguished in the Gulf of Maine in summer, not, of course, sharply outlined, but still sufficiently so to be recognizable. First is that of the surface, with its juveniles, small copepods, etc., which receives accessions of large copepods, Sagittæ, euphausiids, etc., by night and rarely by day; second, the general boreal community of the upper and mid depths, with Calanus, Metridia, and Pseudocalanus, Euthemisto, Thysanoessa, and *Sagitta elegans* as its index species; third, the Euchæta community of the deepest waters of the gulf. The distinctions between these communities, and especially between the last two, are greatest when and where the water is most stratified in density and temperature—that is, in the southwestern part of the gulf in midsummer—least when and where the water is most uniform vertically. This is the case in all parts of the gulf during late winter and early spring; and throughout the year in regions of very active vertical circulation, such as the neighborhood of Eastport, the St. Andrews region at the mouth of the Bay of Fundy, and locally on the offshore banks.

[15] See p. 236 for precise temperatures and salinities.

To answer a question that has often been asked me by zoologists as well as laymen, I may remark that there is no level in the Gulf of Maine but supports a varied pelagic fauna.

## NERITIC AND OCEANIC PLANKTON

None of the criteria by which the plankton can be subdivided ecologically (e. g., relation to temperature, season of reproduction, depth of habitat, etc.) is more fundamental than whether its members do or do not depend on the coast line with its shallows and great supply of foodstuffs; that is, whether they are neritic or oceanic. This distinction is as interesting to the oceanographer as to the biologist, a knowledge of the mutual distribution of the two groups on the high seas often going far to reveal the mutual relationships and fluctuations of waters of coastal and of offshore origin.

The pelagic larvæ of various familiar bottom-dwelling animals (a host in themselves), including most of the worms, bivalve and gastropod mollusks, decapod crustaceans, barnacles, starfishes, and sea-urchins, so abundant in the bays and shallow waters along the coasts of the Gulf of Maine, belong to the neritic category. The adults of many medusæ, including the largest and most conspicuous species as well as others minute, are equally neritic, for they pass through a fixed stage in shallow waters during early life. Here, also, fall certain small phyllopod crustaceans (e. g., Evadne), which, though pelagic for most of their lives, survive unfavorable seasons in the form of resting spores on the bottom, a life history analogous to that of many diatoms, which consequently fall in the neritic category also, as do various other pelagic plants less prominent in the plankton. There is also a whole series of planktonic animals, particularly among the copepods, bound to the neighborhood of the coast by some unknown bond (perhaps by dependence on a particular food supply), and hence to be classed as neritic, although they are pelagic throughout life both as larvæ and as adults. Here, too, must be classed the pelagic eggs of all the species of fish that spawn in shallow water, such as cod, haddock, pollock, silver hake, cunners, and flounders of sundry species.

Contrasted with this coastwise population of the open sea are all the oceanic animals and plants, which are not only free floating or swimming throughout life but show no apparent relation to the coast line in their distribution—to borrow a nautical term, they form its "blue water" population.

It is, of course, impossible to draw a hard and fast distinction between the neritic and oceanic categories, the border line being bridged in too many instances by the many pelagic forms occurring indifferently both near shore and out at sea, and also by animals that are dependent on the bottom in deep water at some stage of existence but not in shallow water; for example, by the hydromedusan genus Calycopsis, which probably passes through a fixed stage but has never been found nearer shore than the continental slope. However, the division holds fairly well for the Gulf of Maine.

In northern seas, generally, neritic elements form a large part, if not practically the whole, of the plankton of sheltered bays and estuaries and off river mouths—

indeed, in all locations where conditions may be described as estuarine—and dominate for a mile or two out from the coast line generally. No detailed study of the plankton of any such situation tributary to the Gulf of Maine has yet appeared, but Willey's (1913 and 1915) and McMurrich's (1917) observations at St. Andrews, with the lists contributed by Doctor McMurrich (p. 12) and the record that might be collected from many sources of the abundance of various medusæ and of larval forms of many kinds inshore, show that the gulf is no exception to the general rule.

The complexion of the plankton at Woods Hole recently described by Fish (1925) may serve as an indication of the preponderance of neritic forms that may be expected in the Gulf of Maine bays and harbors and close along its coast line generally. Thus, Fish classifies 42 of the characteristic diatoms as neritic and only 16 as oceanic, while at least 13 out of 15 hydromedusæ described by him as "occurring commonly in surface towings" (Fish, 1925, fig. 26) are characteristic of the neritic group and only one oceanic. Two neritic scyphomedusæ occur in abundance. Only two of the many annelids listed from his tows (Sagitta and Tomopteris) are truly pelagic when adult, for the others swim only during the breeding season or as larvæ.

Molluscan larvæ are at times abundant in the Woods Hole plankton. The neritic phyllopods Evadne and Podon are characteristic of the local tows, as are the larvæ and sometimes the adults of neritic mysids. Fish found barnacle larvæ abundant in their season, bottom-dwelling amphipods were taken in large numbers in the tow during their breeding season, and the larvæ of decapod Crustacea—shrimps, prawns, crabs, and hermit crabs—are dominant. On the other hand, no euphausiid is a permanent member of the local plankton, though several species have been recorded at Woods Hole. Thus, aside from the copepods, the oceanic element of the Woods Hole plankton is wholly overshadowed by the neritic.

If one were to turn to the Gulf of Maine *de novo*, one might naturally expect the plankton of its central portion to be so largely recruited from the coastal zone that neritic elements would loom large there also, judging from the form, length, and complexity of the shore line with the abundant and varied bottom fauna which it supports; from the confinement of the gulf by the extensive and shallow offshore banks on the ocean side; from the great volume of river water that pours into it; and from the fact that the tides are strong enough in places to stir the water thoroughly. Our first summer's cruise (in 1912) was enough to show that this is not the case but that the pelagic communities of the gulf a few miles out to sea are predominantly oceanic, except over the offshore banks.

Our subsequent cruises have corroborated this for summer, autumn, and winter for all the years of record, and for the whole offshore basin of the gulf, where we have never found neritic forms, plant or animal, playing a rôle of any importance in the plankton except for a brief period in spring, as pointed out below.

The rarity of animals of coastwise origin or affinity in the open gulf in summer (except within a trivial distance of land and over the shallow banks) will appear from the following facts of distribution, already summarized in an earlier report (Bigelow, 1917, p. 251).

The most conspicuous planktonic inhabitants of the gulf, of neritic nature, are the two large scyphomedusan genera Aurelia (p. 362) and Cyanea (p. 357). Their value as indices of coast water has long been appreciated in north European seas, and they are both so large that they are usually visible as they float on or near the surface, if present in any numbers; consequently, notes on their local presence or absence, as seen from the vessel, afford a closer record of their distribution than do the actual captures of specimens at the tow-net stations. Both of these medusæ are abundant along the shores of the gulf in summer, but Aurelia is so closely confined to the immediate vicinity of the land that we have seldom seen it more than a mile or two outside the 100-meter contour (or more than 15 miles from land), while the zone within which it occurs regularly, if not abundantly, extends hardly 10 miles seaward beyond the outer headlands and islands (p. 363); nor have we found it on Georges Bank, though the shallowness of the water there suggests this as a possible breeding ground for it. Cyanea, the common "red jellyfish," which often grows to a breadth of 3 feet across the disk and sometimes to a tremendous size (A. Agassiz, 1865), is not so closely confined to the immediate vicinity of the land as is Aurelia, for it occurs regularly in the coastal zone, on Nantucket Shoals, and on Georges Bank, which must be important centers of production for it, judging from the abundance of the young medusæ there in spring and summer (p. 359). However, it is a rare occurrence to find a Cyanea outside the 100-meter contour in the Gulf of Maine (on July 15, 1912, we captured a very large Cyanea in a haul from 120–0 meters in the western basin). The hydromedusa *Melicertum campanula*,[16] so abundant all along the coasts of the Gulf of Maine (p. 341), is an even more precise neritic indicator than Aurelia, for it is still more closely confined to the coastal zone, not because the waters of the open sea are fatal to it (its abundance in Massachusetts Bay proves the contrary), but because it passes through its fixed stage only in sheltered localities, estuaries, etc., and because its free-floating (medusa) stage is of shorter duration. Although Melicertum often swarms in localities as open to the ocean as Massachusetts Bay and the outer parts of Penobscot Bay, as well as in more inclosed waters, a single example from the western basin (August, 1913, station 10088) is our only record of it more than 15 miles from land.

The medusæ of the genus Sarsia, which are plentiful in season (p. 43) in bays and estuarine situations all along the shallow coastal zone of the gulf, where they are detached from their hydroids in great numbers in spring, are similarly restricted to the coast line, for we have never taken them in the offshore parts of the gulf and rarely more than 4 or 5 miles from land. This is equally true of many other small hydroid medusæ, most of which appear in the gulf for a brief period only, and then far more numerously close to shore than outside the outer islands.

As I have pointed out elsewhere (Bigelow, 1917, p. 252), an interesting example of neritic occurrence among Cœlenterates is afforded by the hydroid colonies we have found floating in considerable numbers over Nantucket Shoals and Georges Bank in July of 1913, 1914, and 1916, and in February, 1920, as well (p. 379). These are so closely confined to the immediate vicinity of the localities where they are torn from the bottom that we have never found them or their free medusæ (which sometimes swarm on the banks) anywhere in the deeps of the gulf to the north.

[16] Large catches of Melicertum 38 miles off Cape Cod and near Browns Bank on August 12 and 19, 1926, prove that it drift farther offshore.

There are other species of hydroid medusæ that are not so closely confined to shoal water, probably because they are able to pass through their fixed stage at greater depths and consequently at a greater distance from land. Staurophora and Phialidium, for example, bear much the same relationship to the 100-meter contour in their distribution (p. 345) as Aurelia, Melicertum, and other forms more dependent on shoal water bear to the immediate coast line.

Other typical examples of the neritic habit are afforded by the larvæ of various decapods among the pelagic Crustacea, young crabs, in particular, being instructive because so conspicuous and so easily recognized in the tow. These (provisionally identified as the common rock crab, *Cancer amœnus*[17]) are produced in great numbers all along the coast line of the Gulf of Maine in summer, and occasionally they have occurred in swarms in our summer hauls near land, for instance, off Rye, N. H., and in Ipswich Bay, Mass., on July 23, 1915. Crab larvæ of some species are equally plentiful on Georges Bank, where we encountered hosts of them on July 23, 1916 (station 10347), and where Dr. W. C. Kendall towed them in abundance and found them providing the young mackerel with a rich food supply at various localities along the northern edge of the bank during August, 1896. They are so closely limited to the vicinity of the land and to the shallow waters of the offshore banks, however, at least so far as occurrence in any numbers is concerned, that I have usually sought them in vain in towings made in the central parts of the gulf, even during their season of abundance; nor have we found crab larvæ over Platts Bank or near Cashes Ledge, though they may be expected there, these doubtess being as good crab grounds as is Georges Bank. The presence of an abundance of crab zœæ in the surface water of the western basin on August 22, 1914 (station 10254), was an exception to the general rule and interesting because the considerable depth (268 meters) at the locality in question makes it almost certain that these young crabs were not hatched there but had drifted out from the rocky banks and ledges off Cape Ann, 25 or 30 miles to the west and northwest, which is visible evidence of the circulation in this part of the gulf at the time.[18]

Hermit crab (Pagurid) larvæ may also swarm locally over the offshore shoals, as was the case near Nantucket Lightship on July 25, 1916 (station 10355), when they were plentiful in the tow from 30 meters (the total depth of water being 36 meters), though represented by occasional examples only at 16 meters and on the surface. We have not detected them in any of our hauls in the basin of the gulf, nor are the macruran larvæ of various species (which are almost invariably present in the coastal waters of the gulf in summer) of any importance in the plankton more than a few miles from land.

The larval (naupliid and cyprid) stages of the common barnacle, which appeared in myriads along the coast north of Cape Ann in April, 1913 (Bigelow, 1914a), and again off Cape Sable during the same month of 1920 (p. 40), are strictly confined to shallow waters, for we have never detected them outside the 100-meter contour. This applies equally to many other metazoan larvæ; those, for example, of the common sea anemone (Metridium), which appear in some numbers in our coastwise catches

[17] See Connolly (1923) for account of the larval stages of this crab.

[18] Crab larvæ also were plentiful 38 miles off Cape Cod and on Georges Bank August 12 to 19, 1926.

in spring. In fact, we have never found the young stages of any bottom-dwelling animals numerically important in the plankton in the basin of the gulf. This fact is interesting because, although the fauna of these deep bottoms is neither so varied nor so rich in actual numbers of specimens as that of the coastal belt, the various mollusks, decapods, worms, and echinoderms that occur there no doubt contribute their larvæ to the waters above them, but are so overshadowed by the shoals of Calanus, etc., that only close examination of large amounts of plankton would reveal their presence.

The phyllopod crustacean genus Evadne deserves mention in this connection; not for any faunal importance in the Gulf of Maine, but because its peculiar life history makes it an infallible index of coastal water, as European students have long recognized (Gran, 1902; Apstein, 1910; Herdman and Riddell, 1911). Probably Evadne, which is seasonal in its appearance in northern coastal waters as a whole, would be found in summer in bays and sheltered waters all around the gulf, for it occurs regularly at the mouth of the St. Croix River in the Bay of Fundy (Willey, 1913), on the one hand, and at Woods Hole, on the other. So seldom does it stray seaward in any numbers, however, that the nine stations where it was detected in 1915 (the first season when special watch was kept for it, and when towing was carried on from May until October), all lay within 10 miles of land, and most of them closer in.

In this connection it is interesting that several of the pelagic shrimps (Meganyctiphanes) taken in the eastern basin on August 7, 1915 (station 10304), were carrying numbers of Evadne (among other prey) clasped between their thoracic legs (p. 108), although none of these little Cladocera were taken in the tows made at that station. From what distance could their captors have brought them?

In an earlier paper (Bigelow, 1917, p. 253) I have briefly summarized the status of neritic copepods in the Gulf of Maine in the following words:

> It is less easy to divide the copepods than other Crustacea into the neritic and oceanic categories, because they are pelagic at all stages. Hence (barring brackish water species), what is neritic in one sea may prove to be oceanic in another. Nevertheless, since they constitute the bulk of the plankton of the Gulf of Maine, I may point out that species which are generally classed as neritic in the North Sea region play only a very subordinate rôle, if they occur at all, in the central part of the gulf, our summer lists containing only five which are so classed by Farran (1910), [T.] Scott (1911), Herdman and Riddell (1911), and Gough (1905 and 1907); viz, Acartia, *Tortanus discaudatus*, *Centropages hamatus*, Eurytemora, and Temora.

We have only one or two records for each of the first four outside the outer islands; none from offshore parts of the gulf (Bigelow, 1914 and 1915). The fifth (*Temora longicornis*) is apparently less closely confined to coastal waters in the western than in the eastern side of the Atlantic, for in the summer of 1913 it was generally distributed over the gulf (p. 287), though there was no corresponding expansion of other neritic organisms. As a rule it is common only locally near land and over Nantucket Shoals and Georges Bank, a distribution roughly paralleling that of Cyanea.

Dr. C. B. Wilson's examination of the copepods of the cruises of 1915, 1920, and 1921 somewhat enlarges the neritic list at the offshore stations, but supports the general thesis that, as a rule, the more oceanic species greatly predominate outside the outer islands.

The pelagic eggs of the many species of fish that spawn on the banks or in shallow water alongshore in the gulf are as rarely found in our tow nettings outside the 100 or 150 meter contours as are other neritic organisms. Cod, haddock, and several species of flatfish may serve as examples of this; likewise the silver hake (Bigelow and Welsh, 1925, p. 488, fig. 217, and p. 244); while the eggs of the cunner are closely confined to the coast line and to the vicinity of the outer islands and shoals (Bigelow and Welsh, 1925, p. 284).

The locality records for the neritic animals just summarized, and for sundry others belonging to the same category, are concentrated in a rather narrow coastal zone paralleling the periphery of the gulf and over its shallow southern rim, with neritic forms very seldom of any importance in the planktonic community more than a few miles out at sea in summer, except for the shallow offshore banks. The fact that most of the animals of this category, if not wanting in the central basin of the gulf, are at least so scarce there as to have been overlooked, is sufficient evidence that the plankton of the coastwise belt has little tendency to disperse seaward at that season, but that the eddylike circulation parallels the coast, which is corroborated by drift bottles and by oceanographic evidence generally.

With few exceptions the scarcity of pelagic animals of neritic origin in the offshore parts of the gulf leaves the planktonic communities that people its open waters (not only in the central basin but right up to the outer headlands) composed of animals and plants not only independent of the bottom at all times but most of which are equally oceanic as opposed to neritic in European waters, as appears from the very extensive records accumulated by the International Committee for the Exploration of the Sea. However, they are not the product of the Atlantic basin outside the continental slope, as the term "oceanic" might imply, but of the banks water that washes the continental shelf on both sides of the Atlantic, and to which they are confined off the North American littoral by the high temperatures of the tropical water farther offshore.

The diatom plankton encountered over the basin in May, 1915, typified by *Chætoceras densum* and *Rhizosolenia semispina*, belongs to this category (p. 434; Gran, 1915; Ostenfeld, 1913; Herdman and Riddell, 1911), while the Ceratium community, which usually occupies the Gulf of Maine as a whole throughout the summer (p. 391), is also characterized by species (*Ceratium tripos* and *C. longipes* var. *atlantica*) usually regarded as oceanic in the North Sea region (Paulsen, 1908; Jørgensen, 1911) and in the Norwegian Sea (Gran, 1902). This is equally true of most of the pelagic animals most constantly characteristic of the plankton of the gulf; for example, of the copepods *Calanus finmarchicus*, Pseudocalanus, Euchæta, and Metridia (Damas, 1905; Gran, 1902; Farran, 1910; Herdman and Riddell, 1911); of the amphipods *Euthemisto bispinosa* and *E. compressa* (Tesch, 1911; Sars, 1895); of the pteropod *Limacina retroversa* (Paulsen, 1910); and of the euphausiid shrimp *Thysanoessa inermis* (Tattersall, 1911; Kramp, 1913a), to mention only a few of the most typical. While two of the most important of its members, faunistically (*Sagitta elegans* and *Meganyctiphanes norvegica*), are intermediate between oceanic and neritic in their biologic status in the North Sea region (Apstein, 1911; Kramp, 1913a), in the Gulf of Maine they cover practically the same range as the more typically oceanic forms just mentioned. Off the European coast most of these species—in fact, the Calanus commu-

nity as a whole—are not only charactersitic of the waters over the continental shelf, but also of the neighboring parts of the ocean basin, and spread right across the North Atlantic from the Norwegian Sea and Iceland, on the one side, to Newfoundland and Nova Scotia, on the other (Herdman and Scott, 1908; Murray and Hjort, 1912). Passing southward from the region of the Grand Banks, however, the band of cool banks water next the coast is a sort of cul-de-sac for them, with the tropical water ("Gulf Stream") limiting their spread on the offshore side as definitely as the coast line does on the inner side.

The contrast in distribution between the neritic and oceanic elements of the zooplankton of the Gulf, which I have just outlined, prevails throughout the summer, autumn, and winter; and although in spring neritic diatoms, such as Thalassiosira, appear in swarms over deep water as well as along the shore, when the rivers are in flood and the outpouring of land water is evidenced far out from the coast by lowered salinity, they are decidedly more abundant in the coastal zone than in the basin even at the time of their widest dispersal, a fact discussed below in the general account of the phytoplankton. Neither are larvæ of coastwise origin of much more importance in the plankton over the basin in spring (as exemplified by our tow nettings of March, April, and May of the years 1915 and 1920) than in summer. Probably this is because the water has hardly warmed appreciably by freshet season, so that the vernal wave of reproduction has only begun on the part of the littoral and bottom fauna.

## SEASONAL FLUCTUATIONS IN THE PLANKTONIC COMMUNITIES

Seasonal fluctuations in the plankton are greatest in regions where neritic larvæ, or forms dependent on the bottom at some time of year, bulk large in the pelagic community, and in seas where the pelagic fauna or flora is largely recruited from extralimital sources by ocean currents, which may vary in strength or in origin from month to month. In the Gulf of Maine the presence or absence of the various crustacean larvæ, or of fish eggs, may govern the composition of the catch for the particular season close in to the land, as examples of which I may cite the swarming of Balanus cyprids near the Isles of Shoals (p. 44) and of haddock eggs on Georges Bank (p. 44), both in spring. This applies more generally to the North Sea, the Irish Sea, and the Baltic than to the Gulf of Maine, where the communities of planktonic animals are, as a whole, more oceanic; and since few constant or even regularly seasonal members of the zooplankton of the gulf are immigrants, but nearly all of them are endemic, the seasonal cycle of the plankton is a simpler problem for us than for students of the North Sea region. It can hardly be emphasized too strongly that very few immigrants, whether from the north, the south, or from the open ocean, penetrate the Gulf of Maine in numbers sufficient to color its plankton community (*Sagitta serratodentata* is an exception, p. 58), instructive though the regular or sporadic occurrence of animals of exotic origin may be for the light they throw on the sources of its waters. This question is discussed below (p. 51).

In the case of the pelagic flora, a very pronounced alternation of the prevalent planktonic types does take place from season to season, and one characteristic of northern seas as a whole; viz, a tremendous flowering of diatoms in spring, giving

place to a rich Peridinian flora in summer, which is succeeded in turn by the limited flowering of diatoms in autumn, as described in the chapter devoted to the phytoplankton (p. 383).

No such seasonal alternation of dominance by one or other group takes place among the planktonic animals of the gulf, however, though there is a very pronounced oscillation in the total amount of zooplankton present there at different times of year and in the abundance of its several members relative to one another. Thus, we have never failed to find the Calanus community dominating the pelagic fauna generally in the southwest part of the gulf, whether our trips thither were made in the heat of summer, the cold of winter, in autumn, or in spring. Nevertheless, even in this region the varying seasons of reproduction of different animals, which determine the presence or absence of their larvæ and the abundance or scarcity of the adults, with the local irregularities of distribution that always obtain for the larger pelagic forms, added to the general ebb and flow in the abundance of the zoöplanktonic community as a whole, cause such variations from month to month as appear in the following lists of the more abundant species in tow-net catches made at the mouth of Massachusetts Bay in spring, summer, autumn, and winter. The case is made still more complex by sporadic fluctuations in the abundance of one species or another, for which we are not yet able to account.

*Tow-net catches at the mouth of Massachusetts Bay*

[D, dominating the plankton; X, occurred]

| | Mar. 1, 1920, station 20050, 75–0 meters | Apr. 9, 1920, station 20090, 60–0 meters | May 4, 1920, station 20120, 40–0 meters | July 9, 1916, station 10341, 0 and 80–0 meters | Oct. 31, 1916, station 10399, 60–0 meters | Feb. 13, 1913, station 10053, 20–0 meters |
|---|---|---|---|---|---|---|
| Cod eggs | | | | | | X |
| Haddock eggs | | | X | | | |
| Cod or haddock eggs | X | X | | | | |
| Silver hake (Merluccious) eggs | | | | X | | |
| Silver hake (Merluccius) larvæ | | | | X | | |
| Butterfish (Poronotus) eggs | | | | X | | |
| Plaice (Hippoglossoides) eggs | | X | X | | | |
| Plaice (Hippoglossoides) larvæ | | | X | X | | |
| Dab (Limanda) larvæ | | | | X | | |
| Witch (Glyptocephalus) larvæ | | | | X | | |
| Oikopleura | | | | | X | X |
| Decapod larvæ | | | X | | | |
| Thysanoessa inermis | | | | X | | |
| Thysanoessa raschii | | | | X | | |
| Meganyctiphanes norvegica | | | | X | | |
| Euphausiid larvæ | | | X | | | |
| Euthemisto compressa | X | | | | | X |
| Euthemisto bispinosa | | | | | X | X |
| Calanus finmarchicus | D | D | D | D | D | D |
| Calanus hyperboreus | | X | | | | |
| Pseudocalanus elongatus | | | X | X | X | X |
| Metridia lucens | | | | X | X | X |
| Anomalocera pattersoni | | | | X | | |
| Euchæta norvegica | | | | X | | X |
| Temora longicornis | | | | | D | |
| Centropages hamatus | | | | | X | |
| Tortanus discaudatus | | | | | | X |
| Copepods, juvenile | X | X | D | | X | |
| Copepod nauplii | | | D | X | | |
| Sagitta elegans | D | X | X | D | X | X |
| Sagitta serratodentata | | | | | | X |
| Tomopteris catherina | X | | | | | X |
| Limacina retroversa | | | X | | X | X |
| Staurophora mertensii | | | X | | | |
| Tima bairdii | | | X | | | |
| Aglantha digitale | | | | X | X | |
| Pleurobrachia pileus | | X | | | | |
| Beroë cucumis | | | | | | X |
| Anemone (Metridium) larvæ | | | X | | | |

The most striking event in the seasonal cycle of the zoöplankton of the Gulf of Maine (if a negative one) is that a very decided decrease, amounting on occasion almost to complete disappearance of the pelagic fauna, takes place early in spring over the whole area of the gulf, coincident with the tremendous vernal flowering of diatoms (p. 385), an event the precise date of which varies locally and from year to year. The quantitative aspect of this change is discussed elsewhere (p. 82), but it also exerts an adventitious influence on the qualitative composition of the plankton, for with all its members sharing in the impoverishment, the rare as well as the common, the less abundant forms practically disappear and the scanty catches become extremely monotonous.

We first observed this impoverishment in Massachusetts Bay during the late winter and early spring of 1913, when the zoöplankton fell to so low an ebb, quantitatively, as the water began to warm from its winter minimum, that the total volume of the catch of a net about 1.2 meters in diameter, towed for half an hour at 40–0 meters on March 4, was only about 15 cubic centimeters. In this catch an occasional *Pseudocalanus elongatus*, 12 *Sagitta elegans*, 9 *Tomopteris catharina*, an odd Euthemisto, and some haddock eggs were the only variants detected among the *Calanus finmarchicus*, of which the general mass consisted. On April 3, following, the net yielded only a few dozen copepods, one Euthemisto, and two Clione, with a few unrecognizable siphonophore bells and Balanus nauplii; while the catch of planktonic animals made on April 14 was no more varied (a few Calanus, one Tomopteris, one *S. elegans*, one Beroë, one young Staurophora, and a few Balanus nauplii), whereas the water was thick with diatoms on both these occasions.

Subsequent experience during the spring of 1920 has shown that this vernal impoverishment of the zoöplankton, which takes place to a greater or less degree in the upper strata of water over the entire area of the gulf, is especially characteristic of the coastal belt and of Georges Bank, where it culminates in March. It involves no qualitative alteration in the plankton, however, for the spring community, sparse though it be near land, is of essentially the same type as the more abundant pelagic population of midsummer, with the same groups and species (notably *Calanus finmarchicus*) predominant. Practically all the common oceanic animals of midsummer except *Sagitta serratodentata*, which is a seasonal immigrant (p. 320), may be found represented in late winter and spring, if a sufficient mass of plankton be examined from any given locality in the gulf, though many are so rare then that the net is more apt to miss than to catch them. Winter adds few extralimital visitors to the local pelagic fauna, never (in our experience) enough to give a distinctive aspect to the plankton.

The essential qualitative unity between the zoöplankton of summer and that of spring may be illustrated by the horizontal hauls off Cape Elizabeth on March 4, 1920 (station 20059), which yielded *Calanus finmarchicus* (dominant), *Sagitta elegans*, *Thysanoessa inermis*, *Th. raschii*, haddock and plaice eggs, Pleurobrachia, and *Tomopteris catharina*, although the water was then so barren that the vertical net caught nothing at all (p. 82). The typical boreal fauna was still more fully represented on the same day off Penobscot Bay (station 20057), although the plankton was hardly denser there numerically, viz, by *C. finmarchicus* (dominant), Pseudocalanus,

Euchæta, *Sagitta elegans*, Eukrohnia, Euthemisto of both species, Clione, *Limacina retroversa*, Tomopteris, Meganyctiphanes, *Thysanoessa inermis*, and *Th. longicaudata*. This is a list that might be expected in summer or autumn, and the same was true of the hauls made in Massachusetts Bay during the winter of 1912–1913, mentioned above (p. 39). The plankton is as uniform, qualitatively, from season to season in the deeper parts of the gulf as the following table shows for a location in the western basin about 30 miles off Cape Ann.

*Zoöplankton in the western basin, various months*

[D, dominant; X, occurred]

| | February, station 20049 | March | | April, station 20115 | May, station 10267 | June, station 10299 | July, station 10007 | August | | | December, station 10490 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Station 20087 | Station 10510 | | | | | Station 10088 | Station 10254 | Station 10307 | |
| Calanus finmarchicus | D | D | D | D | D | D | D | D | D | D | D |
| Calanus hyperboreus | | | X | X | X | | | | | | X |
| Pseudocalanus elongatus | | | | | X | X | | X | X | X | X |
| Metridia lucens | | | | | X | X | | X | X | X | X |
| Metridia longa | | | | | | | | X | | | |
| Euchæta norvegica | X | D | X | D | X | X | X | D | D | X | X |
| Anomalocera pattersoni | | | | | X | | | X | X | X | |
| Centropages typicus | | | | | | | | X | | | |
| Pasiphæa | | X | | X | | | | X | X | X | |
| Meganyctiphanes norvegica | X | X | X | X | | | X | X | X | X | |
| Thysanoessa inermis | X | X | X | | | | X | X | X | X | |
| Thysanoessa longicaudata | | X | X | | | | | (?) | X | | |
| Thysanoessa gregaria | | | | | | | | | X | | |
| Euthemisto compressa | | X | | | | X | X | X | X | X | |
| Euthemisto bispinosa | | | | | | | | | | X | |
| Limacina retroversa | | | X | | | | | X | | X | X |
| Clione limacina | X | X | X | X | | | X | | | | |
| Sagitta elegans | X | X | X | X | X | X | D | X | X | X | X |
| Sagitta serratodentata | | | | | | | | | X | X | |
| Sagitta lyra | | X | | X | | | | X | X | | |
| Eukrohnia hamata | | X | X | X | | | | | X | | X |
| Tomopteris catharina | | | X | X | X | | | X | | | X |
| Aglantha digitale | X | X | X | X | | | X | | | | |
| Beroë cucumis | | X | | X | | | X | | | X | |
| Stephanomia | | | X | | | | X | X | X | | X |
| Phialidium languidum | | | | | | | | X | X | | |

Broadly speaking, our March hauls have paralleled those made in midsummer in the relative importance of the several groups of animals in different parts of the gulf, as well as in the qualitative composition of the catches. Thus, Pleurobrachia was dominant on German Bank both on March 23 and on April 16, 1920 (stations 20085 and 20103), just as it usually is in summer and autumn, and its area of abundance extended from abreast of Yarmouth, on the north, to the shoals off Cape Sable, to the south, on both these visits. On both these spring visits there was a second center of abundance for Pleurobrachia on Browns Bank, where our June and July tows have yielded only an occasional specimen; but although the area of abundance for Pleurobrachia in this general region was more extensive in March and April, 1920, than we have found it in summer, these ctenophores were less plentiful in actual number; nor had they so thoroughly exterminated the other smaller animals, for we found the German Bank–Cape Sable swarm accompanied by copepods in fair numbers on the April visit, besides barnacle (Balanus) nauplii (in abundance), *Sagitta elegans*, euphausiids, Euthemisto, and Tomopteris.

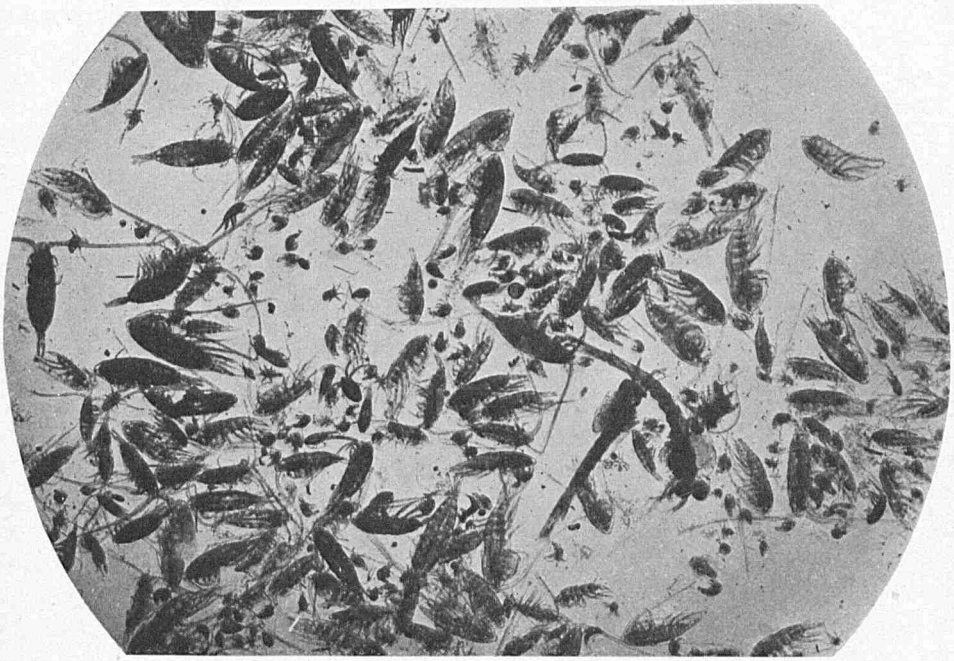

FIG. 27.—Surface catch illustrating abundance of larval copepods in the "nauplius" stage, in Massachusetts Bay in May (station 20121, May 4, 1920). × 9

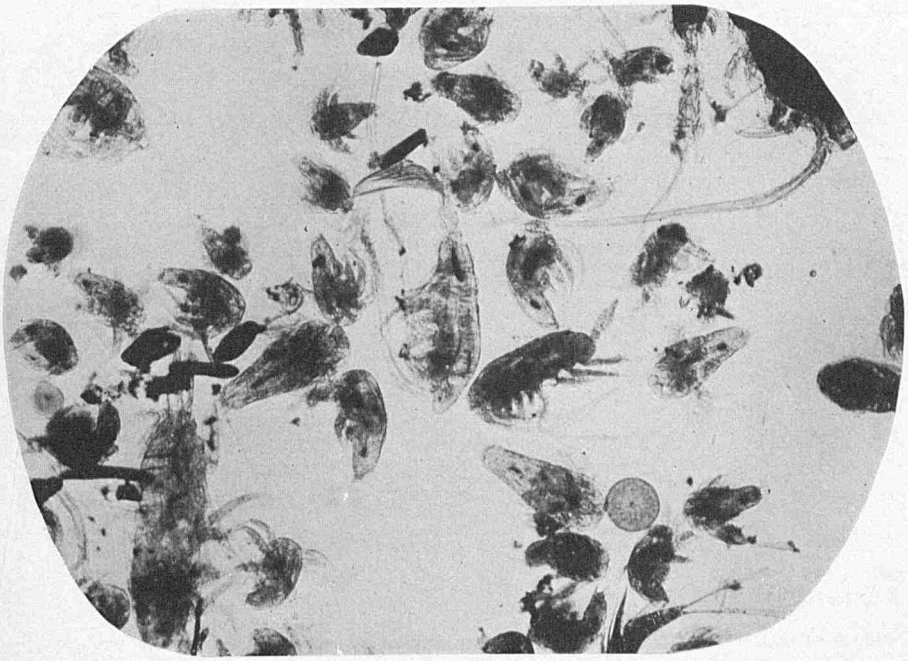

FIG. 28.—The same, more highly magnified. × about 100

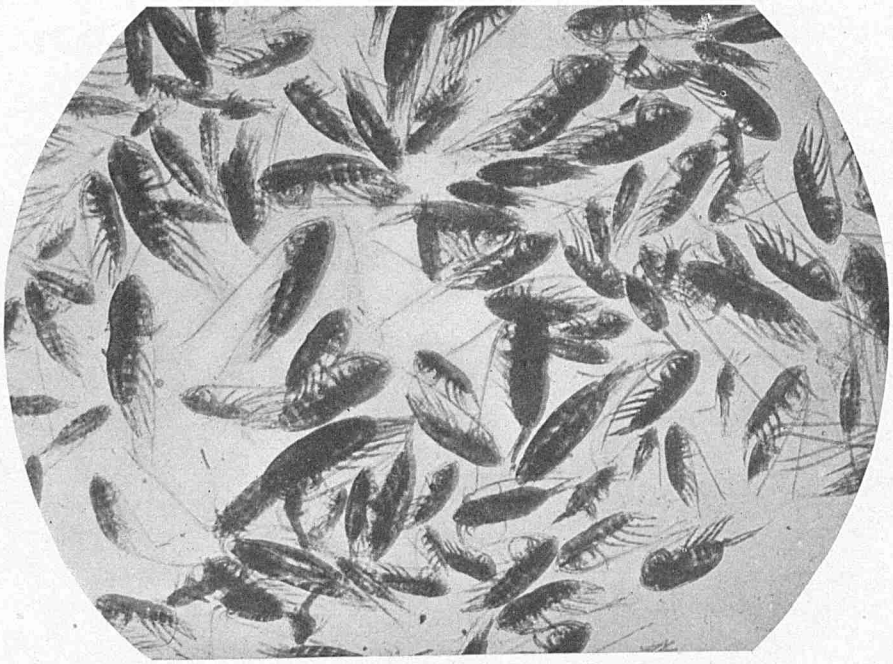

FIG. 29.—Plankton dominated by half-grown *Calanus finmarchicus*, Massachusetts Bay, May 4, 1915 (station 10266), vertical haul from 125–0 meters. × 9

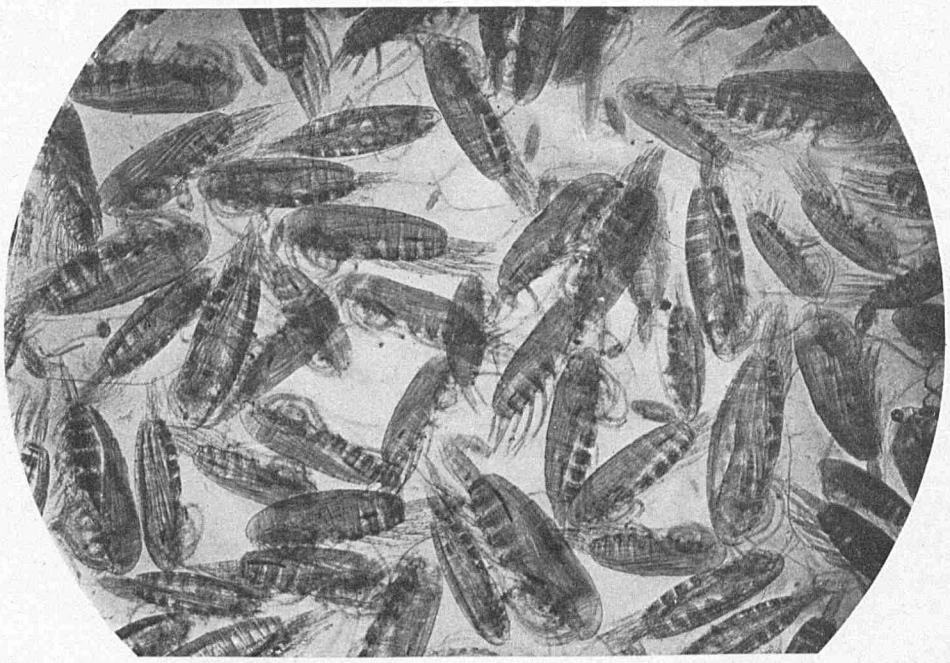

FIG. 30.—Plankton dominated by large *Calanus finmarchicus* off Cape Cod, July 22, 1916, haul from 40–0 meters (station 10344). This sample is from the most productive catch of Calanus yet made in the Gulf of Maine. × 9

Similarly, the spring cruise of 1920 suggests that *S. elegans* may be expected to rival the copepods in abundance over a large part of Georges Bank in February, March, and April, just as it does in July; for it was a large element in the catch at a station on the southwest part of the bank on February 22 (station 20046), on the northeast part on April 17, and had been so plentiful at a third station on the eastern part of the bank on March 11 (station 20066) that the "glass worms," with a great abundance of haddock eggs, dominated the catch (fig. 19). In short, Georges Bank is apparently a center of abundance for *S. elegans* throughout the year (p. 310), and the presence of a shoal of large *Limacina retroversa* on the northern part of the bank on March 11, 1920 (station 20065), reproduced our experience of July 20, 1914, though the exact localities in question were about 80 miles apart.

Late in the winter and early in the spring the scanty zooplankton of the gulf is chiefly composed of fully adult animals, a fact made evident by the predominantly large size of its calanoid copepods and Sagittæ, giving the catches a distinctive aspect when compared with those of July or August. The recrudescence which characterizes the advance of spring results primarily from the local propagation of its several component groups, not of replenishment by immigrants from any extralimital source. This has been proved by repeated observations.

In Massachusetts Bay this vernal augmentation is earliest apparent at stations close in to the land, in the shape of a sudden appearance of hosts of copepod nauplii (figs. 27 and 28). This event commences some time late in March off the mouth of Boston Harbor, for we found few nauplii there on the 5th of that month in 1920 (station 20062), but an abundance of them on the 5th of April (station 20089), besides many copepods in the older larval stages. As the season advances this vernal wave of reproduction on the part of the copepods spreads seaward; and the nauplii appeared in multitudes at the mouth of the bay during the last half of April, 1920, where we had found only an occasional copepod—egg, nauplius, or juvenile—on March 1 or April 9. In 1920 the swarms of larval copepods, together with the various other larvæ that appear about the same time, produced a decided increase in the volume of animal plankton present in the water of the Massachusetts Bay region by the first week in May. This was our experience in 1913, also, when W. W. Welsh found the water in Gloucester Harbor reddened for areas of about a square yard, several yards apart, with what proved to be swarms of copepod nauplii and young copepods on May 3. The peak of production of copepods, however, is so soon passed in Massachusetts Bay that our nets brought back proportionally more of the older juveniles and fewer nauplii off Gloucester on May 16, 1920, than 12 days earlier, while the hauls off Magnolia, Mass., on May 17, 1913, yielded only a few copepod nauplii but an abundance of the later stages (chiefly Calanus, with some Eurytemora), besides many crab larvæ in the zœa stage.

The vernal replenishment of the zoöplankton follows much the same course in the coastal belt immediately north of Cape Ann as in Massachusetts Bay, with a few copepod nauplii among the swarming diatoms off the mouth of the Merrimac River as early as March 4 in 1920 (station 20060). The nauplii were again noted there on April 9, and on May 7 hauls made close by with the closing net yielded

nauplii (besides copepod eggs), larval Anemones, and young Staurophora down to 30 meters, overlying a sparse adult Calanus–Sagitta–Pleurobrachia community in the deeper strata of water.

There is some evidence that the wave of reproduction of copepods continues to spread offshore with the advance of the season until it covers the southwestern part of the gulf generally; and it certainly endures later into the spring in the open gulf than in Massachusetts Bay, for the presence of nauplii showed that in 1920 these little crustaceans were breeding actively from Cape Cod to Georges Bank as late as May 16 and 17. In the spring of 1915 nauplii were abundant on the surface off the Cape, with older stages deeper down, as late as the 26th of the month (station 10279), although they had been almost entirely replaced by the older larvæ and by half-grown Calanus (fig. 29) as early as the 4th of that month off Gloucester (station 10266). Similarly, the presence of copepod nauplii in the sink off the Isles of Shoals on May 14, 1915 (station 10278), coupled with a decided increase in young copepods between April 26 and May 14 to 16, 1913 (Bigelow, 1914a, p. 407), though with diatoms still abundant there on both these occasions,[19] suggests that copepods do not begin to multiply this far offshore until well into May, although reproduction is under way more than a month earlier than this inshore off the Merrimac River.

We have no evidence that the coastal waters east of Penobscot Bay ever see a local reproduction of copepods comparable to the waves of production just described for Massachusetts Bay.

As to local production of copepods along the eastern (Nova Scotian) side of the gulf, I can only say that our hauls near Lurcher Shoal on March 23 (station 20082), and again off Yarmouth, on German Bank, and near Cape Sable on April 13 to 15, 1920 (stations 20102, 20103, and 20104), yielded nauplii and older larval copepods in some numbers, which probably marks the beginning of a period of active propagation, for in 1915 we found both nauplii and the older juvenile stages of Calanus plentiful on the surface of the eastern basin near by on May 6.

The vernal wave of production of these little crustaceans reaches its apex by the end of May or the first of June in the northern and eastern parts of the gulf, for we found a typical Calanus plankton reestablished off Boothbay (station 10280), in the Fundy Deep (station 10282), and off Mount Desert Island (station 10284) by May 31 to June 11 in 1915.

An important problem in the natural economy of the gulf is how far the vernal augmentation of the zoöplankton of the offshore parts of the gulf—say, outside the 100-meter contour—is due to local propagation there and how far to a migration of the copepods out from the coastal zone where they are produced in such enormous numbers. To answer this question definitely demands a more critical study of our towings than opportunity has yet allowed. One thing is clear, however. None of our offshore hauls at any season has ever yielded copepod nauplii or the later larval stages in numbers to compare with their abundance in Massachusetts Bay. It is equally suggestive that in May, when the coastwise copepod plankton is juvenile, large Calanus have invariably been an important element in the total copepod catches in the deep basin, just as is the case in summer, which points to the coastwise waters

[19] In 1913 they were diminishing in numbers locally by that time.

of the gulf, especially its southwestern part including the Massachusetts Bay region, as the chief source of the copepod plankton of its center. It is probable, also, that Georges Bank is an important nursery for copepods, since nauplii occurred in some numbers among the adult calanoids off its northern slope on March 11, 1920 (station 20064).

The vernal increase in the numbers of copepods present in the Massachusetts Bay region, and wherever else reproduction takes place actively, is many times greater than the bulks of the catches might suggest, the production of young coupled with the dying off of the parent stock giving the copepod plankton of the coastal waters a juvenile character in spring with relatively few large adults. Thus, there were only about 8,000 adult Calanus per square meter among some 500,000 copepods, mostly young Calanus, off Gloucester on May 4, 1915 (station 20066)—that is, a little less than 2 per cent. After the peak of production is past, however, and with the growth of its product toward maturity, the percentage of large Calanus and adults of other species once more increases, until they form about one-third of the copepod population at the mouth of Massachusetts Bay by the end of June or first week in July (Bigelow, 1922, p. 136). During the late summer, when the stock of copepods of all species and ages dwindles, adults may locally amount to as much as one-half or two-thirds of the total (fig. 30).

Coincident with the vernal propagation of copepods various young medusæ commence their period of pelagic existence, as, for example, Staurophora, which appears in swarms in Massachusetts Bay in May. Although we have never found young medusæ more than a minor factor in the zooplankton of the gulf outside the outer headlands in spring, they often dominate inclosed waters for a brief period in May. This, for instance, was the case in Gloucester outer harbor on May 3, 1913, when *Sarsia tubulosa, Bougainvillea superciliaris, Rathkea blumenbachii, Tiaropsis diademata,* Obelia, and Staurophora were all abundant, and Æquorea and Cyanea tolerably common—all of them, no doubt, liberated close at hand, and certainly very recently, for none was found there a month earlier. We also found young hydromedusæ swarming in the harbor of Yarmouth, Nova Scotia, in May, 1915, and this probably applies to similar situations all along the complex coast line of the gulf from Cape Cod to Cape Sable; also to the shallow waters of Georges Bank, where young Hybocodon and Staurophora are sometimes sufficiently plentiful to "color" the tow in April (Bigelow, 1914a, p. 414).

The larvæ of echinoderms, worms, and mollusks of many kinds likewise appear in the plankton along shore in spring. Most of these, in fact most of the pelagic animals of coastwise origin, are confined to estuarine situations in the Gulf of Maine, to sounds and bays among the islands, or to a coastal belt only a few miles wide at most, as noted above (p. 32), and hence may be passed over without further comment here. The early stages of the common rock barnacle (genus Balanus), however, are so abundant and so conspicuous that they deserve a word of mention. In 1913, as I have elsewhere described (Bigelow, 1914a), barnacle nauplii[20] were taken in large numbers in the Isles of Shoals-Boon Island region[21]

[20] Here let me correct an error in an earlier paper, namely, that "barnacle" eggs were taken in the tow in March and April of 1913 (Bigelow, 1914a, p. 108). Barnacle eggs are not set free to float, but are nursed by the mother until the nauplii hatch out. For accounts and figures of the early stages of Balanus see Hœck, 1909.

[21] No doubt young barnacles are as common in Massachusetts Bay as in any part of the gulf, though somehow we have chanced to miss their season there.

on April 5; the cyprid stage in abundance on the 9th, with only a few nauplii; while by the 19th cyprids alone were taken. These dominated the surface plankton during the last week of April, after which their numbers diminished, though some persisted in that region until mid-May.

The reproduction of barnacles is at its height at about the same season along the eastern shores of the gulf, for their nauplii occurred at all our stations over the shallows from Yarmouth to Browns Bank on April 13 to 15, 1920—abundantly in the North Channel (station 20105; fig. 24). At St. Andrews, in the Bay of Fundy, where because of the violent tides the surface waters warm slowly in spring, barnacle larvæ (either nauplii, cyprids, or both) are recorded by Doctor McMurrich in his plankton lists as early as the last week of January, regularly after mid-February, reaching their maximum abundance during April, occurring in diminishing numbers until June 8, and occasionally still later in that month. In 1917, according to Willey (1921), barnacle nauplii dominated the plankton at St. Andrews on April 7; nauplii and cyprids in subequal numbers formed nearly the entire catch on May 1; and cyprids alone on the 17th. The season is about the same for them in the Irish Sea.

The spring season, likewise, sees striking additions to the plankton of the coastwise and shoaler waters of the gulf generally, in the shape of buoyant fish eggs. Haddock eggs in particular are produced in such numbers locally during March and April (which is the height of the breeding season) that they may be a considerable element on the more prolific spawning grounds, such as the eastern part of Georges Bank, the neighborhood of the Boon Island ground, and locally in Massachusetts Bay. The extremely characteristic eggs of the plaice (*Hippoglossoides platessoides*) appear early in March (that is, slightly later than those of the haddock) and are taken until mid-June, with the height of the spawning season during April and May. Rusty-flounder (Limanda) eggs are first seen in the tow toward the end of April, most numerously in June and July, and rarely as late as mid-September. The spawning season of the witch flounder (Glyptocephalus) likewise follows hard on that of the haddock. Spring is the season most prolific in fish eggs in the Gulf of Maine, but they are seldom numerous except in the immediate vicinity of the spawning grounds, or anywhere over the central deeps of the gulf, outside the 100-meter contour.[22]

The most obvious effect of the very active reproduction of copepods just described, coupled with the scarcity of most other planktonic animals in the offshore waters of the gulf at the time, is that soon after its inception the zooplankton in the more productive centers of propagation becomes almost pure copepod; and, whether by local breeding or by drifting out from the coastal belt, as seems more likely, their numbers so multiply offshore as the water warms with the advance of the season that they overwhelmingly dominate the pelagic community of the whole gulf north of a line from Cape Cod to Browns Bank in May and during the first half of June. Since, furthermore, the other planktonic groups of animals that assume faunal importance later on in the year (e. g., Sagittæ, amphipods, euphausiids) do not commence multiplying actively until later in the season, it is during late spring and the first weeks of summer that the zooplankton of the upper 100 meters (empha-

[22] For the chief spawning grounds and breeding seasons of Gulf of Maine fishes see Bigelow and Welsh (1925).

sizing this depth limit for reasons which will appear presently) of the offshore parts of the gulf is the most monotonous.

Although our records for this season are not all that might be desired, it seems certain that copepods (Calanus in particular) reach their high-water mark early in June, the exact date varying locally and with the forwardness of the season. So completely did the calanoids (chiefly *C. finmarchicus*) monopolize the upper strata of water right across from Cape Cod to Cape Sable during May, 1915, that the only other animals to be found among a liter of copepods off Cape Ann on May 4 (station 10266) were a few *Sagitta elegans*, one young fish, two tiny Euthemisto, a few euphausiid larvæ, and a few fish eggs, with the zoöplankton of the western basin (station 10267), where diatoms were still swarming, so monotonous that a haul from 85 meters yielded nothing but copepods and one Tomopteris. Nor was the catch more varied in the central deep (station 10269), only one euphausiid, one Euthemisto, six or seven large Clione, and an occasional Limacina being detected among the copepods in the 85-meter tow on May 6, while we found only a few Euthemisto, euphausiids, and Sagittæ, with an arctic planktonic element to be discussed elsewhere (p. 59), among swarms of copepods in the eastern basin on that same day (station 10270).

In that year (which was apparently a typical one) the plankton of the upper 100 meters was as monotonously calanoid in June as it had been in May. In the Grand Manan Channel, for example, on the 4th (station 10281), the 50-meter catch consisted of copepods varied only by 1 Euthemisto, 2 Clione, 1 Aglantha, 1 young fish, 1 fish egg, 2 *Sagitta elegans*, and a single specimen of Tomopteris. Much the same condition prevailed in the Fundy Deep on the 10th (station 10282); likewise near Mount Desert Island on the 11th (station 10284), when a cursory examination of more than 2 liters of Calanus and other copepods in the 70–0 meter haul revealed only one Clione and a single Sagitta as the sole variants. On the 26th of June, too, the upper strata of the western basin were similarly occupied by a calanoid plankton in extraordinary abundance (about 40,000 large Calanus per square meter).

In the western and northern parts of the gulf, where copepods monopolize the water more completely at their peak season than they do the deep basin offshore, it is an unusual event for Sagittæ, amphipods, euphausiids, or pteropods, etc., to be of any importance in the plankton in spring or early summer, with the notable exceptions of the swarms of the euphausiid shrimp *Thysanoessa raschii* near the Isles of Shoals in April and May, 1913, and (with its relative, *Th. inermis*) on April 9, 1920 (station 20093), described below (p. 145); with the exception, too, of Meganyctiphanes, which is so plentiful in the northeast corner of the trough off Grand Manan that we captured no less than 1½ liters there on June 10, 1915 (station 10283), in half an hour's haul at 100–0 meters, and of Pleurobrachia, which swarms on German Bank in May and June just as it does in summer (p. 19). Even where copepods so dominate the contents of the net, however, that nothing else strikes the eye at the first glance, a more careful examination of the catch will reveal some few amphipods, euphausiids, Sagittæ, etc.

June 19 is the earliest date on which we found large Euthemisto in any abundance in 1915 (eastern basin, haul from 85–0 meters, station 10288). The interesting

hydroid medusa *Mitrocoma cruciata* reaches maturity during this same month, when it may appear near shore in numbers sufficient to give a distinctive aspect to the tow, as was the case at the mouth of Penobscot Bay on June 14, 1915 (station 10287 p. 348). For the sake of clarity I should point out, at the risk of repetition (p. 389), that diatoms still swarm along a narrow coastwise belt east of Penobscot Bay in June.

The advance of summer (from June on) sees an actual decrease in the number of copepods, owing, no doubt, to the destruction wrought among them by fishes and other enemies (p. 97). In part this decrease is made good by constant reproduction, evidence of which was afforded by an abundance of copepod nauplii near Cape Cod on July 8, 1913 (station 10057, surface), on July 7, 1915 (station 10300), and on August 29, 1916 (station 10398); likewise by the presence of large numbers of juvenile Calanus [23] between Cape Ann and the Isles of Shoals in July, 1912. The offshore banks also serve as a copepod nursery in July—at least locally—for copepod eggs, nauplii, and juveniles abounded on the surface near Nantucket Lightship on the 25th of that month in 1916 (station 10355), while the presence of young Calanus at various stages in development in most of the summer towings proves that this copepod breeds more or less regularly throughout the summer. Our experience, however, does not suggest that sufficient reproduction takes place during the warm months to maintain the local stock of calanoid copepods against depletion by the many dangers to which it is subjected.

As copepods dwindle in numbers the other groups of common boreal animals increase, lending an increasing diversity to the plankton of the offshore parts of the gulf during the summer, most noticeably in the western side, where the plankton is most monotonously calanoid in May and June, thus producing the midsummer state already described (p. 17). Events notable in this gradual alteration are a great production of Euthemisto, resulting from local centers of reproduction such as I have just mentioned (p. 20); the active propagation of euphausiids (p. 20); a general penetration toward the western and northwestern shores of the Gulf on the part of the pteropod *Limacina retroversa* (p. 119); the appearance of shoals of the white and red jellyfishes (Aurelia and Cyanea) in the coastal belt as they disperse and drift seaward from their estuarine nurseries (pp. 360, 362); the presence of large Stauro-phora, often in abundance (p. 342); and the offshore swarming of the hydroid medusa *Phialidium languidum* (p. 350). It is during the summer, too, that the large and conspicuous arrow-worm *Sagitta serratodentata* first appears in any number in the gulf as a visitor from warmer waters to the south and east outside the edge of the continent, and spreads its range northward and westward as described elsewhere (p. 322). The copepod population, also, becomes diversified as the summer advance by increasing numbers of Anomalocera and Centropages, not only within the gulf but also on Georges Bank, where the former (which we did not find in spring) is practically universal and comparatively abundant in August.[24] The ctenophore *Pleurobrachia pileus* reaches its maximum abundance on the German Bank ground

[23] Identified by Dr. C. O. Esterly.
[24] The "green copepod" of Doctor Kendall's field notes.

and may almost completely monopolize the water there during the summer. In June and July, too, the eggs or larvæ, or both, of sundry summer-breeding fishes, such as silver hake, rosefish, cunner, and witch flounder, appear in the appropriate parts of the gulf to take the place of such spring spawners as the haddock and plaice.

As summer passes into autumn *Sagitta serratodentata* continues to spread westward right into Massachusetts Bay (p. 322). The hyperiid-amphipod genus Euthemisto likewise works inshore in September and October, so that it is more numerous in the bay then than at any other time of year, and Pleurobrachia may swarm locally, notably off the coast of eastern Maine and at the mouth of the Bay of Fundy. It is during late summer or early autumn, too, that Phialidium is most plentiful and that Salpæ and other tropical forms (p. 53) are most often encountered in the gulf.

Hand in hand with the autumnal cooling of the surface, the small *Phialidium languidum* disappears first and then the larger scyphomedusæ, either dying at the close of their natural period of life or being destroyed by the fury of the autumn storms. The large, blue copepod Anomalocera likewise vanishes from the waters of the gulf (p. 184). On the other hand, ctenophores may be locally abundant until well into the autumn, witness the swarms of Pleurobrachia that appeared off Cape Cod during October, 1916 (p. 367); and the small brown copepod *Temora longicornis* becomes so plentiful locally near the land at this season that it dominated the surface catch off Cape Ann on October 31, 1916 (station 10399), when a sample of the copepods consisted of over 100 Temora with but 2 Centropages and 1 Calanus. Doctor McMurrich, likewise, found Temora most regularly and in greatest abundance in October, November, and the first half of December at St. Andrews (p. 289), but in the open Gulf no definite seasonal periodicity has been established for it (p. 289).

Centropages was the most numerous copepod on the surface off Cape Cod in November, 1916 (station 10404), but all our deeper hauls in autumn have been dominated by Calanus, Pseudocalanus, and Metridia, with Euthemisto of both species, *Sagitta elegans*, Meganyctiphanes, Thysanoessa, and Limacina. In fact, they have paralleled the community characteristic of summer. So few of the bottom dwellers of the Gulf breed in October or November that their larvæ are practically nonexistant in the plankton at that season; but the presence of juvenile Calanus in the western basin on November 1 (station 10400), of young Aglantha and young *Sagitta elegans*, of eggs probably referable to the latter, and of an abundance of small as well as large Limacina off Massachusetts Bay at that time (stations 10399 and 10403) proves that all these pelagic animals reproduce in the Gulf during October, though probably not in any great abundance.

I have already pointed out that no general alteration takes place in the zooplankton of the Massachusetts Bay region during late autumn and early winter, for our tows gave us much the same yield off Cape Ann at the end of November and in December, 1912, and in January, 1913,[25] as is to be expected there in August, September, or October—that is, Calanus dominant, with such other copepods as Pseudocalanus, *Metridia lucens*, Centropages, and Euchæta; the chætognaths, *Sagitta elegans* and occasional *S. serratodentata; Euthemisto compressa* and *E. bispinosa;* the common

[25] These hauls are described in an earlier report (Bigelow, 1914a, p. 404)

boreal pteropod *Limacina retroversa;* and the ctenophores Pleurobrachia and Beroë. This also applies to tow-net catches at 12 stations between Cape Cod and Yarmouth (Nova Scotia) for the midwinter of 1920 and 1921, listed below. These lists vary somewhat from station to station, as is always to be expected, but there is no characteristic qualitative difference between the western and the eastern stations, the Calanus community (and chiefly *C. finmarchicus*) dominating the same general assemblage of boreal animals as occurs in summer at the localities in question.

| Species [1] | Location, date, and depth of hauls | | | | | |
|---|---|---|---|---|---|---|
| | Off Boston, Dec. 29, 1920, station 10488, 15–0 meters | Off Cape Ann, Dec. 29, 1920, station 10489, 75–0 meters | Western Basin, Dec. 29, 1920, station 10490, 240–0 meters | Off Cape Cod, Dec. 30, 1920, station 10491, 125–0 meters | Off the Merrimac, Dec. 30, 1920, station 10492, 20–0 meters | Off Isles of Shoals, Dec. 30, 1920, station 10493, 75–0 meters |
| Acartia clausi | × | × | | × | × | × |
| Calanus finmarchicus | × | × | × | × | × | × |
| Calanus hyperboreus | | | × | | | |
| Pseudocalanus elongatus | × | × | | × | × | × |
| Metridia longa | × | × | | × | × | × |
| Metridia lucens | × | × | | × | × | × |
| Centropages typicus | × | × | | | | × |
| Euchæta norvegica | | | × | | | |
| Meganyctiphanes norvegica | | | × | × | | |
| Thysanoessa inermis | | | × | | | |
| Thysanoessa longicaudata | | | × | | | |
| Euthemisto compressa | | × | | 1 | | |
| Sagitta elegans | × | × | × | × | × | |
| Eukrohnia hamata | | | × | | | |
| Limacina retroversa | × | | × | × | × | × |
| Clione limacina | | 1 | 2 | 3 | | 1 |
| Tomopteris catharina | | 1 | × | | | |
| Aglantha digitale | | | × | × | | |
| Pleurobrachia pileus | | | × | 1 | | |
| Beroë cucumis | × | × | | × | | |
| Stephanomia | × | × | × | × | | × |

| Species [1] | Location, date, and depth of hauls | | | | | |
|---|---|---|---|---|---|---|
| | Off Cape Elizabeth, Dec. 30, 1920, station 10494, 75–0 meters | Off Seguin Island, Dec. 31, 1920, station 10495, 60–0 meters | Off Matinicus Island, Jan. 1, 1921, station 10496, 100–0 meters | Off Mount Desert, Jan. 1, 1921, station 10497, 50–0 meters | Fundy Deep, Jan. 4, 1921, station 10499, 150–0 meters | Off Lurcher Shoal, Jan. 4, 1921, station 10500, 60–0 meters |
| Acartia clausi | × | × | | × | × | |
| Calanus finmarchicus | × | × | × | × | × | × |
| Calanus hyperboreus | | | × | × | × | |
| Pseudocalanus elongatus | × | × | × | × | × | |
| Metridia longa | × | × | × | × | × | × |
| Metridia lucens | × | × | × | × | | × |
| Centropages typicus | | × | × | × | | × |
| Euchæta norvegica | | | × | 3 | × | 1 |
| Meganyctiphanes norvegica | × | | | × | × | × |
| Thysanoessa inermis | × | | | × | × | × |
| Thysanoessa longicaudata | 1 | | | | | |
| Thysanoessa raschii | 1 | | | | | 1 |
| Euthemisto compressa | | | | | × | 4 |
| Euthemisto bispinosa | | | | 1 | | |
| Sagitta elegans | × | × | × | × | × | 1 |
| Eukrohnia hamata | 1 | | 1 | 1 | × | |
| Limacina retroversa | | × | × | × | | × |
| Clione limacina | | 1 | 1 | 7 | | |
| Tomopteris catharina | 12 | 1 | | | 4 | |
| Aglantha digitale | | | | | × | |
| Pleurobrachia pileus | | | | × | | |
| Beroë cucumis | | | | | × | |
| Stephanomia | | | | × | | |

[1] For complete lists of the copepods at these stations see p. 304.

The winter plankton of 1920–1921 differed from that of 1912–1913 in the rarity of the amphipod genus Euthemisto, both species of which not only occurred regularly during December, January, and February, 1912 and 1913, but usually in considerable numbers. *Sagitta elegans*, though it occurred regularly, was also far less numerous in the midwinter of 1920–1921 than at that season in 1912–1913, when it was an important factor in the tows made in Massachusetts Bay from December until February. Whether these differences were actually the result of annual fluctuation in the stock of these two animals present or whether both are normally more abundant in Massachusetts Bay and its vicinity than in other parts of the gulf in winter remains to be learned.

Other features of the winter plankton of the gulf worth mention are that the buoyant eggs of the American pollock (*Pollachius virens*) appear in great numbers from November until February over its restricted breeding grounds; that cod eggs are to be expected throughout the winter (Bigelow and Welsh, 1925, p. 424) if the nets be towed near where the fish are spawning—seldom otherwise or in large numbers; and that some few copepods (probably Calanus) continue to reproduce right through the cold season, for their nauplii were detected at most of our December–January stations of 1920 and 1921, most plentifully in Massachusetts Bay. Euthemisto, too, must breed then (though probably in small numbers) to account for very young specimens taken off Gloucester on December 29, 1920. In this connection I may also call attention to numbers of large *Calanus hyperboreus* (5 per cent of all the copepods) among a very rich catch of *C. finmarchicus* in the western basin on December 29, 1920 (station 10490, p. 304), and of Stephanomia bells in the eastern basin and in the shoal water off Yarmouth (Nova Scotia), which was nearly barren otherwise, on January 5. On the other hand, the arrow-worm *Sagitta serratodentata* vanishes from the gulf sometime during late winter, our latest seasonal record of it being for January 16, 1913 (off Gloucester).

Judging from the tow-net hauls made during 1913, the zooplankton of the Massachusetts Bay region continues decidedly uniform in composition throughout January and February, when the successive hauls reproduced one another with monotonous regularity, until early in March, when the quantity of animal plankton present in the water decreased to its annual minimum (p. 39) coincident with the vernal augmentation of vegetable plankton described elsewhere (p. 385), a change soon followed by the wave of reproduction on the part of the copepods which I have just discussed. It may safely be assumed that this is equally true of the northeastern part of the gulf, for although, unfortunately, we have no plankton records from its outer waters during the period January 9 to February 22, Doctor McMurrich found *Calanus finmarchicus* and Pseudocalanus, with *Temora longicornis* and the neritic copepod genus Acartia, the chief animal constituents of tow-net catches during this season of the year at St. Andrews.

The seasonal planktonic cycle in the deep waters of the gulf below 100 meters calls for separate discussion, because the Euchæta community is largely below the reach of the wide fluctuations of temperature to which the inhabitants of the shoaler strata of the gulf are subject. Data on this for the early winter consist of two tow-net hauls, one from 240 meters in the western basin, December 29, 1920

(station 10490), and the other from 150 meters in the eastern basin on January 5, 1921 (station 10502). On the former occasion the only members of the Euchæta community detected among a great abundance of large *Calanus finmarchicus* and *Calanus hyperboreus* (p. 304) were a few Euchæta and Eukrohnia; on the latter date the whole catch was extremely scanty (not over one-tenth liter), consisting chiefly of débris of the siphonophore genus Stephanomia, with Calanus and other copepods, among which there were a few Euchæta, Meganyctiphanes, *Thysanoessa inermis*, *Th. longicaudata*, *Sagitta elegans*, pteropods (*Limacina retroversa*), two *Euthemisto compressa*, but none of the deep-water chætognaths. These hauls suggest that a decided impoverishment of the deep-water plankton takes place during the autumn, but this may have been accidental. The Euchæta community probably persists unaltered in qualitative composition throughout the winter, as widespread over the deep trough then as it is in summer, judging from the following catches made with the closing net in the central and eastern parts of the basin on March 2 to 3, and in the Fundy Deep on March 22, 1920.

[D, dominant; M, many; ×, occurrence]

| Species | Station 20052, central basin, 160 meters | Station 20053, southeast part, 175 meters | Station 20055, east basin, 180 to 140 meters | Station 20079, Fundy Deep, 180 meters |
|---|---|---|---|---|
| Calanus finmarchicus | D | × | D | × |
| Metridia lucens | × | × | × | × |
| Euchæta norvegica | M | × | × | M |
| Meganyctiphanes norvegica | 11 | 2 | 2 | 22 |
| Thysanoessa inermis | | | 1 | × |
| Pasiphæa | 1 | | 1 | 2 |
| Euthemisto compressa | 1 | 1 | 1 | 1 |
| Euthemisto bispinosa | 1 | | | 1 |
| Tomopteris catharina | × | | × | 1 |
| Sagitta elegans | M | M | × | × |
| Sagitta lyra | | | 1 | [1] 1 |
| Eukrohnia hamata | | 12 | × | 20+ |
| Limacina retroversa | × | × | | |
| Clione limacina | | | 2 | [1] 1 |
| Beroë | × | 1 | 1 | [1] 1 |
| Aglantha | | | 2 | |

[1] In open-net haul from 200 meters.

*Occurrence of characteristic animals in the Eastern Basin, various localities and months* [1]

[D, dominant; M, many; ×, occurrence]

| Species | Location, date, and depth of hauls | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Station 20081, 140–0 meters, Mar. 22, 1920 | Station 20086, 150–0 meters, Mar. 23, 1920 | Station 20112, 200–0 meters, Apr. 17, 1920 | Station 10270, 150–0 meters, May 6, 1920 | Station 10288, 200–0 meters, June 19, 1915 | Station 10246, 150–0 meters, Aug. 12, 1914 | Station 10093, 170–0 meters, Aug. 12, 1913 | Station 10310, 175–0 meters, Sept. 2, 1915 | Stations 10500 and 10502, 150–0 meters, Jan. 4 and 5, 1921 |
| Calanus finmarchicus | D | D | D | D | D | D | D | D | D |
| Metridia lucens | | | | × | | × | × | × | |
| Euchæta norvegica | × | × | × | D | M | M | × | M | × |
| Meganyctiphanes norvegica | D | D | × | M | × | M | × | | × |
| Thysanoessa, various species | | × | × | × | × | × | × | × | × |
| Pasiphæa | × | | × | | | | | | × |
| Euthemisto compressa | | | × | × | | × | × | × | |
| Euthemisto bispinosa | | | | | | × | × | × | |
| Tomopteris catharina | × | × | | × | × | | × | | × |
| Sagitta elegans | × | × | × | | | × | × | | |
| Sagitta maxima | × | × | × | | | × | × | × | |
| Eukrohnia hamata | × | × | × | | | × | × | × | × |
| Limacina retroversa | | | | × | × | × | × | × | |
| Clione limacina | × | × | × | × | | | | | |
| Beroë | × | × | × | × | | | | × | |
| Aglantha | × | | | | | × | | | |

[1] For further lists of the copepods see p 297.

A similar community (notably Euchæta and the deep-water chætognaths) also occupied the deeper water layers in the western basin in February and March, 1920 (p. 40), and deep hauls made there and in the southeastern part of the basin that April gave much the same yield. Judging from hauls made in 1915, however, the deep-water chætognaths *Eukrohnia hamata* and *Sagitta maxima* disappear altogether from both the western and the northeastern deep troughs in May, not to reappear there until August,[26] a phenomenon interesting for its bearing on the lines of immigration of these two species, neither of which breeds in the gulf, and as evidence of the seasonal fluctuation of the bottom current. But it is possible that they persist in the southeastern deep and in the eastern channel.

It is probable that the Euchæta community of the western basin is at its lowest ebb in May or June, for if the euphausiid shrimp *Meganyctiphanes norvegica* was not wholly wanting there during those months in 1915, it was at least so rare that the nets did not chance to pick up any specimens, although it was plentiful in the eastern trough at the time. Meganyctiphanes repopulates the deep waters of the western side of the gulf by midsummer, however, for we have found it there at all our stations for July and August (p. 151), and the mammoth copepod *Euchæta norvegica* is as constant, though not as abundant, an inhabitant of the deepest waters of the gulf, season in and season out, as Calanus is of the upper strata.

## IMMIGRANT PLANKTONIC COMMUNITIES

Besides the endemic boreal animals so far discussed (chiefly the Calanus community), which are the most important members of the animal plankton of the Gulf of Maine, various immigrants enter it from time to time, as might be expected in any maritime area where waters of diverse origin meet and mix, the details of such immigrations varying with the ocean currents that give them birth and in which their participants normally pass their existence.

According to their adaptability to the temperatures and salinities which they meet in the gulf, these involuntary visitors exhibit every degree of success as colonists, from inability even to survive for more than a few days or weeks to perfect success in existing, growing, and breeding. The majority, however, occupy a middle ground—able to live and grow to large size in the gulf but not to reproduce themselves there because of unfavorable temperatures or salinities, or at most breeding so seldom that their continued presence in the gulf depends absolutely upon successive waves of immigration from outside. Associated with their essentially exotic origin, most of these immigrants are decidedly seasonal in their appearance within our limits.

To place clearly before the reader the faunal status of such wanderers, I must emphasize here (what is perhaps the most essential factor in the biology of all pelagic animals below the rank of fishes, and a truism to the oceanographer) their utter inability to carry out voluntary migrations of more than a few miles at most from place to place by swimming, for want of a continuous directive stimulus, though they often perform extensive vertical movements. The horizontal migrations of

[26] Possibly in July, a month for which we have but one deep station.

planktonic animals, so often recorded and occasionally so extensive, are invariably the result of actual and corresponding movements of the water masses in which they live. Utterly at the mercy of tide and current, they drift as helplessly as buoys with the latter, able to escape from an unfavorable environment only by swimming up or down in response to light or to gravity. For them there is no such thing as the geographic migration in the true sense, with which we are familiar among birds and fishes.

It follows from this that to state the currents or the more diffuse movements of water that enter the Gulf of Maine is to list the sources from which occasional visitors can reach it. These are, first, but least important, the surface stratum of tropical water, popularly known as the Gulf Stream, lying close outside the continental edge, proverbial both for high temperature and salinity and for the tropical pelagic fauna it carries with it, and which enters the gulf regularly, though in small amounts, as a component of the general surface indraught into its eastern side, besides flowing directly across Georges Bank on rare occasions. Second, and equally characteristic both hydrographically and biologically, is the ice-cold water of the Cabot or Nova Scotian current that flows past Cape Sable in considerable volume in spring, carrying arctic inhabitants. Greater in amount than either of these, though not always so clearly characterized by its plankton, is the complex mixture between coastal, northern, and tropical oceanic waters, which is constantly being manufactured along the outer edge of the continental shelf and over the upper part of the continental slope, and which composes the major part of the influx into the eastern side of the gulf. To this the name "cold wall" has often been applied. Finally, the mid-depths of the Atlantic basin contribute an occasional straggler, which must enter via the deepest trough of the Eastern Channel. None of these sources, except the third, adds appreciably to the gulf plankton, in which, as I have pointed out, endemic animals are overwhelmingly preponderant; but so important are the exotic forms as indicators of the respective waters that give them birth that they deserve more attention than their numerical strength of itself would warrant.

Several of the commonest and most characteristic inhabitants of the different ocean currents are among the largest and most easily recognized. For example, the presence of a Salpa or of a bit of gulf weed (Sargassum) anywhere in the Gulf of Maine is as sure evidence of an actual influx of Gulf Stream water as if the latter could actually be seen, and the same is true of the Arctic pteropod *Limacina helicina* for northern waters. Note, also, that whatever the origin of an exotic immigrant, whether Tropic or Arctic—or any driftage, for that matter—it travels the same route, once it is caught up in the inflow into the eastern side of the gulf, a fact well illustrated by the striking resemblance between the distribution (within our limits) of the cold-water Aglantha, on the one hand (p. 353), and the whole category of tropical organisms, on the other (fig. 31). So close, in fact, is the parallel, that the one chart might almost be substituted for the other, so far as the inner parts of the gulf are concerned, were the seasonal element ignored. Immigrants in the upper strata, whatever their source, rarely reach the central part of the gulf unless their numbers be fortified and their period of existence within our limits lengthened by local reproduction; but those entering in the deeper strata of water do follow the troughs (p. 64).

## TROPICAL VISITORS

The term "tropical visitors" is used here for such animals as are native to the Gulf Stream and are able to survive only in its warm surface waters outside the edge of

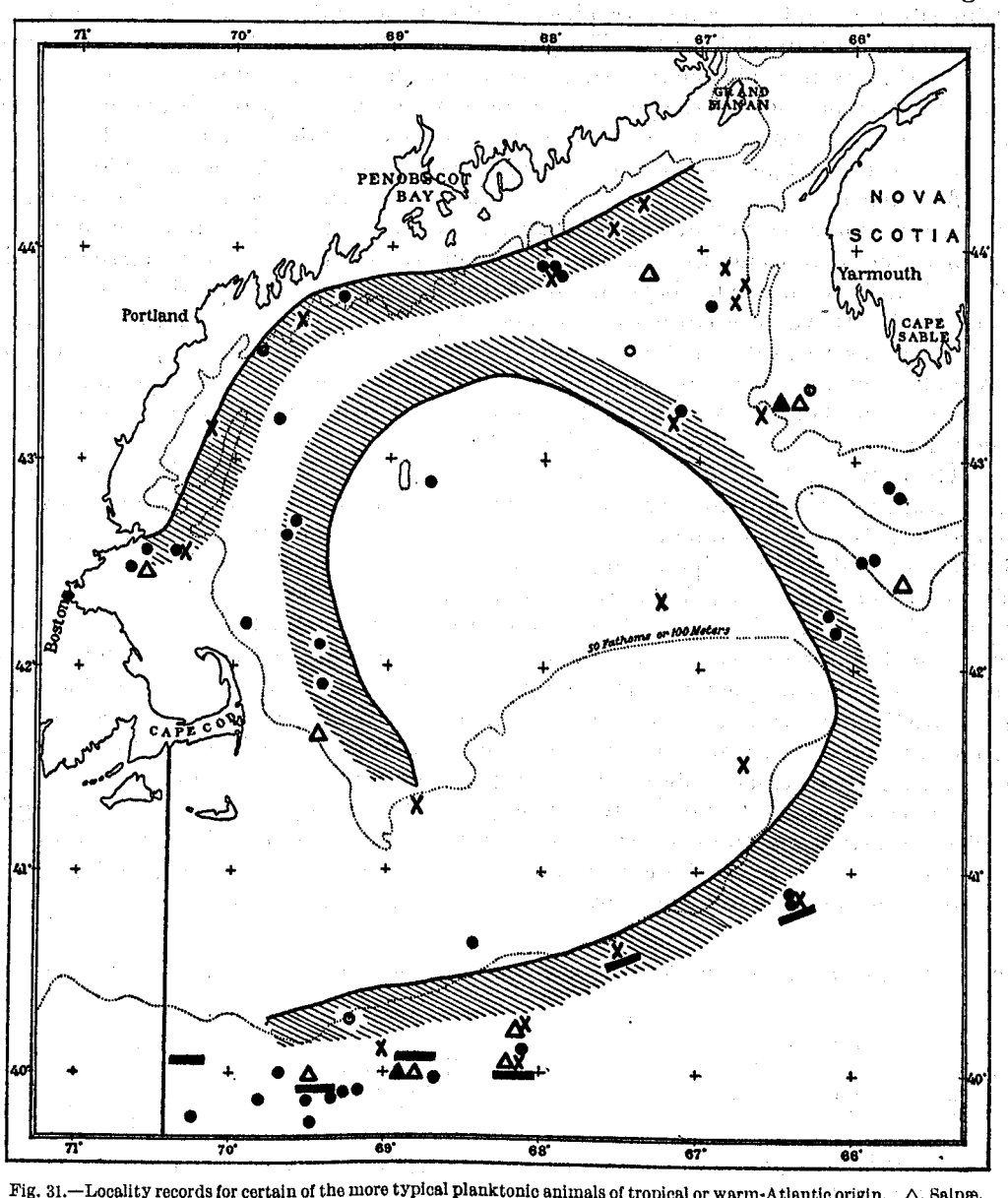


Fig. 31.—Locality records for certain of the more typical planktonic animals of tropical or warm-Atlantic origin. △, Salpæ, ●, *Thysanoessa gregaria*; X, tropical copepods; ○, Portuguese man-o-war (Physalia); ▲ *Physophora hydrostatica*; ⊙, gulf weed (Sargassum); ▬, many tropical species

the continent. Others equally of tropical origin, but which find conditions more favorable for growth (though not for reproduction) in the mixed water, are discussed as belonging to the latter, for it is by that route that they enter the Gulf.

Ever since the early eighties it has been known (from many collecting trips carried on by the vessels of the United States Bureau of Fisheries from the laboratory at Woods Hole) that the inner edge of the tropical water, carrying with it an extraordinarily rich and diversified tropical plankton, lies only a few miles south of the 100-fathom contour off Marthas Vineyard in summer, just as is the case farther west and south. Hence, although actual records of the pelagic fauna and flora at this same relative position farther east have been very scanty up to within the last few years, there was no reason to doubt that a tropical community occupied the same relative position along the slope off Georges Bank; while the deep-sea explorations of the *National* and *Michael Sars*, of the Canadian fisheries expedition of 1915, and of the international ice patrol (Fries, 1922), have shown that the same assemblage of warm-water planktonic animals and plants characterizes the inner (northern) edge of the Gulf Stream to and beyond the southern corner of the Grand Banks of Newfoundland. It was therefore to be expected that any lines we might run seaward as far, say, as the 1,000-meter contour, would bring us into warm water, where our tow nets would yield a tropical plankton instead of the boreal community characteristic of the Gulf of Maine to the north. And so it has proved, as the following brief notes on our offshore hauls will illustrate.

On July 10, 1913, for instance, we saw fragments of gulfweed on the surface near Nantucket Lightship, and the neighborhood of the stream was made evident over the 150-meter contour to the south (station 10061) by "the presence of Salpæ, Phronima, and the amphipod genus Vibilia, though the bulk of the plankton still consisted of *Calanus finmarchicus*, with such other boreal forms as *Euchæta norvegica*, Euthemisto, and *Sagitta elegans*" (Bigelow, 1915, p. 268). We had a similar experience over the 1,000-meter contour, some 70 miles farther east, about a week later in the season the following year (station 10218), when we found the water of the high temperature [27] characteristic of the inner edge of the Gulf Stream, more properly the tropical water (p. 52), with a typically tropical plankton including *Salpa fusiformis* and its relative genus, Doliolum; the tropical amphipod genera, Phronima, Vibilia, and Oxycephalus; the copepods Rhincalanus and Sapphirina; the chætognaths *Sagitta enflata*, *S. hexaptera*, and *Pterosagitta draco;* with the 11 species of tropical pteropods and 19 species of tropical medusæ and siphonophores listed below, and gulfweed (Sargassum) floating on the surface, as I have elsewhere noted (Bigelow, 1917, p. 245).

*Tropical pteropods and cœlenterates taken over the continental slope off Georges Bank, July 21, 1914, station 10218*

| Species | 60–0 meters | 300–0 meters | 400–0 meters |
|---|---|---|---|
| Mollusks: | | | |
| Limacina rangii, d'Orb | | | 1 |
| Creseis conica, Eschscholtz | | | 1 |
| Creseis acicula, Rang | | | 1 |
| Hyalocylis striata, Rang | | | 1 |
| Cuvierina columnella, Rang | | | 2 |
| Diacria trispinosa, Lesueur | | | 1 |
| Cavolina longirostris, Lesueur | | | 1 |
| Cavolina uncinata, Rang | 1 | | |
| Peracle reticulata, d'Orb | | | 1 |
| Corolla calceola, Verrill | 1 | | 1 |
| Firoloida desmarestia, Lesueur | | 1 | |
| Pleurobranchea tarda, Verrill | | 2 | |
| Medusæ: | | | |
| Stomotoca pterophylla | × | × | |
| Toxorchis kellneri | × | × | |
| Laodicea cruciata | × | × | |
| Medusæ—Continued. | | | |
| Rhopalonema funerarium | | × | |
| Rhopalonema velatum | × | × | |
| Liriope scutigera | × | | |
| Liriope tetraphylla | | × | |
| Aglaura hemistoma | × | × | |
| Nausithöe punctata | × | | |
| Siphonophores: | | | |
| Hippopodius hippopus | | × | |
| Diphyes spiralis | × | | |
| Diphyes appendiculata | × | | |
| Diphyes bojani | | × | |
| Diphyopsis dispar | × | × | |
| Diphyopsis mitra | × | × | |
| Agalma elegans | × | × | |
| Anthophysa formosa | × | | |
| Physalia physalis | × | | |

[27] Temperature 17.7° and salinity 36.04 per mille at 40 meters; 20.48° at the surface.

Rather scanty catches at the same relative position on the slope 100 miles farther east on July 22, 1914 (station 10220), likewise included tropical animals (Rhincalanus, a phyllosome crustacean larva, Phronima, Doliolum, and four specimens of the warm-water pteropod *Limacina rangii*) as well as boreal, while the tropical element was similarly represented by Phronima and *Sagitta enflata* in the plankton over the slope off Marthas Vineyard a month later (August 26, stations 10260 and 10261), although the catch was chiefly boreal (Bigelow, 1917, p. 245). In the cold summer of 1916 the tropical water lay farther out from the edge of Georges Bank in July, with the 50-meter temperature ranging from 4.85° to about 8° over the slope between the 175 and 1,000-meter contours on the 23d (stations 10349–10351, and 10352). Corresponding to this, the plankton along this zone was typically boreal (much the same as in on the bank and in the gulf), *Calanus finmarchicus* dominating, with Pseudocalanus, *Metridia lucens*, *Euchæta norvegica*, large *Euthemisto compressa* and *E. bispinosa* abundant (as is usually the case along the slope), *Limacina retroversa*, *Thysanoessa inermis*, *Th. raschii*, and *Sagitta elegans*. Indicative of the zone of mixture between coastal and ocean water was the fact that *Sagitta serratodentata* was about as numerous as *S. elegans* over the 200-meter contour (station 10349) and *Nematoscelis megalops* at the outer station; but the only planktonic animals or plants to which a tropical origin could safely be credited were a few *Salpa fusiformis* at station 10349, many at station 10352, a single *Physophora hydrostatica* (station 10353), a large Pyrosoma (station 10352), and a few fragments of gulfweed (Sargassum, station 10352). This poverty of warm-water forms contrasted strongly with what we had found there in July, 1914, listed above (p. 54).

None of our three lines off Cape Sable (where high temperatures are separated from the slope by a still broader wedge of cold mixed water) has run out far enough to reach Gulf Stream water. Nevertheless we have taken Rhincalanus and *Sagitta enflata* over the 500 to 1,000 fathom contours in summer even there (station 10233), and have seen Physalia (June 24, 1915). No doubt the boreal forms would be left behind altogether a few miles farther out to sea along this line in summer also, to give place to tropical forms on the surface and to typically oceanic plankton in the shadow zone of the mid-depths.

In winter and early spring it is necessary to go considerably beyond the 1,000-meter contour to find surface water as warm even as 10° or tropical pelagic animals in any numbers abreast of the Gulf of Maine. For example, on February 22, 1920, the only representatives of this community in hauls made off the western end of Georges Bank (station 10244) were an occasional copepod (Rhincalanus) and amphipod (Phronima), with Phronima and the medusan genus Rhopalonema at the corresponding location off Cape Sable on March 19 (station 10277). The tow off the southeast face of Georges Bank on March 12 (station 10269) produced no distinctively tropical forms, but by May 17 of that year the Gulf Stream community had again approached so close to the western end of the bank that our nets yielded several Salpæ, subtropical copepods (Eucheirella), amphipods, and medusæ (Rhopalonema) among the boreal organisms of which the bulk of the plankton consisted at the outermost station (20129).

Tropical pelagic animals as conspicuous as Salpa and the Portuguese man-of-war (Physalia), together with others less noticeable, are often carried close in to the coasts of southern New England during the summer, west and south of longitude 70°, by sporadic movements of Gulf Stream water, with the topographic bight west of Nantucket Shoals serving in particular as a trap for them, as the common occurrence of Physalia at Woods Hole and the considerable list of tropical pelagic fishes that have been taken there (H. M. Smith, 1898; Kendall, 1908; Sumner, Osburn, and Cole, 1913) bear witness. Occurrences of this sort are far less frequent east of Cape Cod, however, and when invasions of the inner part of the Gulf of Maine by tropical planktonic animals do take place it is usually in the persons of but few individuals and fewer species.

How slightly this tropical pelagic community encroaches on Georges Bank even in midsummer, when abundantly represented only 15 to 20 miles seaward from its 200-meter (100-fathom) contour, was brought forcibly to our attention in July, 1914, when only occasional warm-water animals or plants (e. g., *Pterotrachea keraudenii*, Doliolum, Phronima, a phyllosome larva, and the tropical pteropod *Cavolina tridentata*) occurred over the southern edge of the bank (station 10219) where the plankton was otherwise boreal, in spite of the rich and varied tropical plankton we have just mentioned (p. 54) as occupying the warmer water over the continental slope only a few miles farther out.

Tropical pelagic animals have been found even more rarely in the inner parts of the Gulf of Maine than along the offshore banks, as might be expected. In fact, the euphausiid shrimp *Thysanoessa gregaria* (p. 142) is the only member of this community occurring regularly there (but see, also, *Sagitta serratodentata*, discussed on p. 320). Except for these, the complete list of tropical planktonic animals so far detected in our catches in the gulf proper is brief. Among copepods the genera Eucalanus, Dwightia, Eucheirella, Pleuromamma, and Rhincalanus may be so classed, because all of them undoubtedly enter the gulf from the inner edge of the Gulf Stream, and, judging from their rarity, are unable to establish themselves in its cool waters, though properly speaking they are oceanic-Atlantic rather than typically tropical. The status of each in the gulf is given in detail in the chapter on copepods. The euphausiid shrimp *Nematoscelis megalops*, often plentiful along the continental slope, appears only as a stray in the interior parts of the gulf (p. 146). Salpæ (perhaps the best tropical indicators of all) have been taken at a number of stations, usually represented, however, by few examples.

This was the case with *Salpa fusiformis* near German Bank and off Lurcher Shoal, August 14, 1912 (stations 10030 and 10031), though other scattered specimens were seen floating on the run from one station to the other. A few *Salpa tilesii* were also taken in the tow near Lurcher Shoal, August 12, 1913 (station 10096). Huntsman (1921) records five *S. fusiformis* found on the beach at Campobello Island (New Brunswick) in the autumn of 1913, and two *S. zonaria* taken in that general region (probably near Grand Manan) in 1910. On September 30, 1912, Capt. John McFarland, of the fishing schooner *Victor*, to whom the Bureau of Fisheries is indebted for other interesting tow-net hauls, made a large catch of *S. mucronata* 25 miles off Chatham, Cape Cod; and fishermen reported great

numbers of large Salpæ (probably *S. tilesii*) in Massachusetts Bay in November and December, 1913, which, so far as I can learn, are the only occasions when Salpæ have been found in such numbers within the gulf, though they are often reported in abundance south and west of Cape Cod. Local swarms, such as this, probably result from their very rapid asexual multiplication (there is no evidence that they can reproduce sexually in cool waters) in summer and early autumn (A. Agassiz, 1866).

The Portuguese man-of-war (Physalia), with its translucent float, is even more apt to attract attention than Salpa, as it drifts on the surface, and it is equally a tropical visitor, though at the mercy of wind as much as of current. We have only one record of Physalia within the gulf, viz, in the eastern basin, June 19, 1915 (Bigelow, 1917, p. 246; a single specimen seen but not captured). In the summer of 1889, however, a year when Physalia was unusually plentiful off the coast of southern New England, many were seen in the Bay of Fundy and several were taken near Grand Manan and submitted to Doctor Fewkes for identification (Fewkes, 1889 and 1890). The only other tropical cœlenterates so far recorded within the gulf are two examples of the siphonophore *Physophora hydrostatica* on German Bank (station 10030) in August, 1912 (Bigelow, 1914, p. 103),[28] while the "Venus girdle" (Cestum), a warm-water ctenophore, is known from off the southeast slope of Georges Bank (Smith and Harger, 1874; Bigelow, 1914b, p. 31).

We have one record for a tropical pteropod (*Limacina inflata*) off Cape Cod on July 19, 1914 (station 10213), while two living specimens of the pteropods *Diacria trispinosa* and Atlanta, genera that are of warm Atlantic if not strictly tropical origin (Meisenheimer, 1905), were taken in a haul near Gloucester on July 8, 1913. The warm-water hyperiid amphipod *Phronima sedentaria* was taken on Browns Bank on June 24, 1915 (station 10296), which, with a fragment of gulfweed near German Bank (September 2 of that year), completes the list.

The geographical locations of these records, the most characteristic of which are shown on the accompanying chart (fig. 31), and their dates prove that occasional planktonic immigrants from the inner edge of the Gulf Stream may be expected anywhere in the Gulf of Maine at any season. Aside from *Thysanoessa gregaria*, however, which may, perhaps, be endemic in small numbers in our waters, or which at least is able to survive there for a long time if it does not reproduce (p. 143), and omitting *Sagitta serratodentata*, which falls in a different category (p. 58), there is a decided preponderance of tropical records in the eastern part of the gulf, though fewer hauls have been made there than in the western, a concentration, that is to say, where the salinity curves locate the chief influx of offshore water. The great majority of the records lie in the peripheral zone corresponding to the anticlockwise oceanic eddy that dominates the circulation of the gulf.

In spite of the considerable tropical list, we have never made anything that could be called a tropical haul in the gulf or encountered a community of animals of warm-water origin there. In fact, most of the records are for single specimens; seldom has the tow net yielded as many as half a dozen at any one station, and, except for certain

[28] Also taken off the southern face of Georges Bank on July 24, 1916, station 10352.

copepods (p. 56), never more than two tropical animal species among the hosts of boreal animals.

This scarcity of planktonic visitors of the tropical category within the Gulf of Maine and even over its shallow southern rim, when so rich a tropical surface fauna inhabits the inner edge of the Gulf Stream along the outer edge of the continental slope only a few miles without the 100-fathom contour, is fundamentally due to their inability to survive or to reproduce in the low temperatures of the coast water. Their sporadic and solitary occurrence there, contrasted with the considerable numbers and even communities of tropical planktonic animals that often drift close inshore west of Cape Cod, is explicable only on the assumption that the surface waters of the Gulf Stream very seldom overflow the barrier formed by Georges Bank, an assumption corroborated by the physical character of the water. Nevertheless, the Gulf of Maine does owe to the tropical water indirectly, if not directly, one common and very characteristic summer visitor, the large chætognath *Sagitta serratodentata*. This species, which is the dominant member of its systematic group in the coastal waters south of New York, occupies a rather peculiar faunal niche in the Gulf of Maine, for while it breeds only in the high temperatures of the Gulf Stream (so far as the area under discussion is concerned), great numbers drift into the cooler mixture zone along the edge of the continental shelf, where they thrive and grow to a much larger size than they do in the warmer waters farther offshore, either because lower salinities and temperatures especially favor their growth (though not their reproduction), or perhaps because of a richer food supply (p. 323, and Huntsman, 1919). As a denizen of this mixed water, *S. serratodentata* is swept in abundance into the Gulf of Maine, where, because of its size and abundance, it is the most prominent of all the exotic immigrants, though it never attains a more permanent status there.

Owing to its peculiar relationship to oceanic temperatures, all the Gulf of Maine records so far obtained for *S. serratodentata* have been for large specimens, the localities of capture indicating considerable longevity for it within the gulf. It is strictly seasonal in its presence there, however, being so rare in winter and early spring that we have taken it only twice between December 1 and May 1, viz, in Massachusetts Bay on December 4, 1912 (station 10048), and again on January 16, 1913 (station 10050). It appears in the eastern side of the gulf as early as the first week in May (p. 320, and Bigelow, 1917, p. 296), and by June it has spread generally over the eastern basin and into the Bay of Fundy as well as over the outer edge of the shelf off Cape Sable, and probably also all along the southern and eastern parts of Georges Bank, where we found it in July, 1914. This species penetrates the inner parts of the gulf so slowly during the early summer that in five years we have found it only once in the western and southwestern parts prior to August 1. Thereafter, however, it spreads so rapidly westward and southward along the coast of Maine that our August and September records for it cover the whole northern half of the gulf from Cape Ann right across to Cape Sable, including Massachusetts Bay, where it occurs regularly in late summer and autumn.

The locations of the stations of capture and the fact that *S. serratodentata* is usually more numerous in the eastern than in the western side of the gulf (p. 322) are

sufficient evidence that its invasion takes place chiefly into the eastern side and from the southwest and south; that is, across the eastern end of Georges Bank and via the Eastern Channel. It is probable (as suggested by Doctor Huntsman in a recent letter) that *S. serratodentata* also comes to the gulf from the east, drifting with recurrent movements of mixed water along the outer edge of the continental shelf off Nova Scotia and entering across Browns Bank or through the Eastern Channel, but there is no reason to suppose that any come by way of the Northern Channel or around Cape Sable across the coastal shallows; in fact, it would be very surprising to find any warm-water species journeying along that route.

Our failure to find *S. serratodentata* off Cape Cod in autumn, although September, October, and November are the months when it is widest spread in the northern parts of the gulf, suggests that the individuals of the species taking part in the successive waves of immigration inward past Nova Scotia seldom survive long enough in the eddy-like circulation of the gulf to journey much beyond Massachusetts Bay in their circuit. The fact that specimens from the outer edge of the continental shelf have been much larger than is usually the case in the Gulf Stream, or in tropical seas generally, corroborates this view, for it indicates a considerable sojourn in the cool band of banks water on the part of *S. serratodentata* before it enters the Gulf of Maine.

## ARCTIC VISITORS

In the Gulf of Maine the Arctic, like the Tropic, immigrants fall in two categories, depending on whether they are able to survive for a considerable period and even to reproduce to some extent there, or whether they find the high temperature of the water so fatal that they soon perish. The latter group—most typically Arctic—has not been represented within the gulf in our midsummer, autumn, winter, or early spring hauls except for an odd Mertensia[29] off Penobscot Bay on June 14, 1915 (p. 371), though this ctenophore and the Arctic medusa *Ptychogena lactea* have previously been recorded in Massachusetts Bay and at Grand Manan in September (A. Agassiz, 1865; Fewkes, 1888); but in early May of 1915 both of these cold-water cœlenterates, with the large shelled pteropod *Limacina helicina* and the appendicularian *Oikopleura vanhöffeni*, which are equally characteristic of a northern origin, were taken in the eastern side of the gulf at localities where temperature and salinity gave clearest evidence of an influx of the cold Nova Scotian water past Cape Sable into the gulf at the time (fig. 32). Since each of these species was represented by several specimens, their capture just then and there can hardly be looked upon as accidental.

As I have pointed out elsewhere (Bigelow, 1917, p. 248), "the appearance of the Arctic Oikopleura in the gulf is especially noteworthy, since it has not been recorded previously on this side of the Atlantic south of Baffins Bay, though known in European waters as far south as the Shetland Islands (Lohmann, 1896 and 1901). Thanks to Lohmann's excellent descriptions and figures (1896, p. 72, Taf. 14, figs. 6, 7, and 10; 1901, p. 15, figs. 16 and 17), it is easily recognized, its chief difference from the closely allied *O. labradoriensis* being the presence of many small dendritic chordal cells. Its very large size (rump length upward of 4 millimeters) is likewise diagnostic, while the red margin of the tail makes it a conspicuous object in the water."

[29] Mertensia occurred over the outer half of the continental shelf off Shelburne, Nova Scotia, on Mar. 19, 1820 (p. 371).

It was for only a brief period, however, that these Arctic animals persisted in the plankton of the gulf during the spring in question, for none of them were captured there during our later cruises (June to October) that year, except for the single Mertensia just mentioned; and although Mertensia, Limacina, and *Oikopleura vanhöffeni* were all present over or outside the continental shelf abreast of Cape Sable as late as June 24, available data suggest that the planktonic species of this category disappear, from west to east, successively, from the coast water between Cape Sable and Halifax with the advance of the summer, as I have noted elsewhere (Bigelow, 1917, p. 249).

Whether the Gulf of Maine is annually invaded by these species is yet to be determined, but what little is known of the seasonal expansion and contraction of the

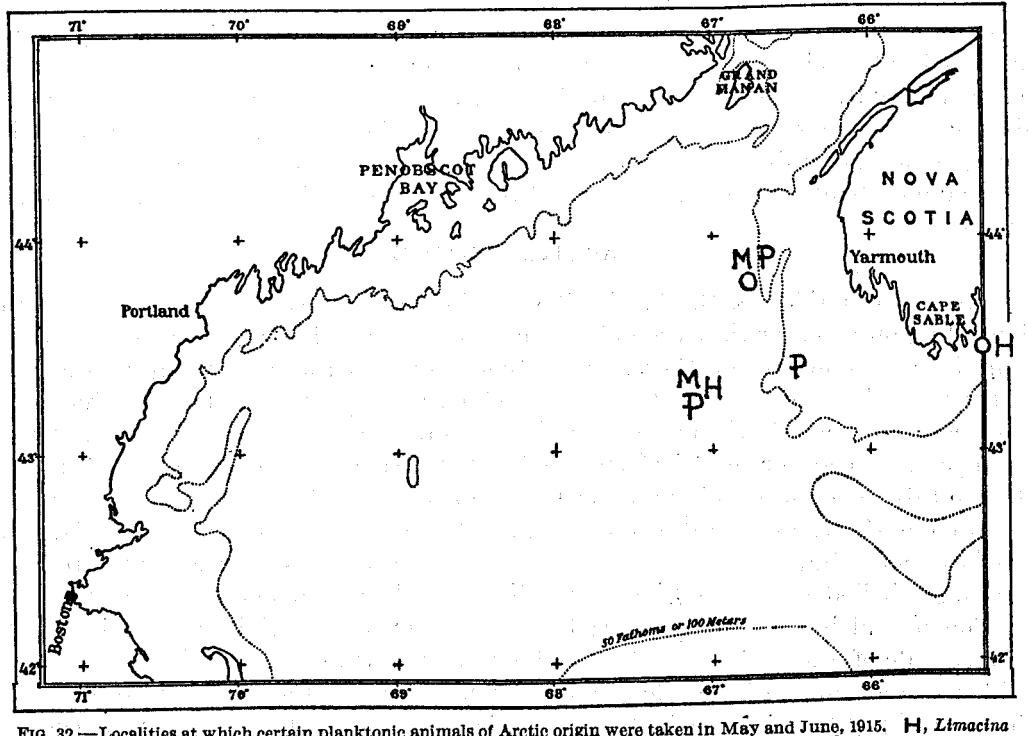


FIG. 32.—Localities at which certain planktonic animals of Arctic origin were taken in May and June, 1915. H, *Limacina helicina*; M, *Mertensia ovum*; O, *Oikopleura vanhöffeni*; P, *Ptychogena lactea*

Nova Scotian current makes this seem probable. Nor does the fact that the more delicate of the Arctic planktonic animals are scarce, if not absent, from the gulf in any given summer mean that no such invasion occurred during the year in question, for Mertensia (A. Agassiz, 1865) is extremely sensitive to water that is too warm. And since, judging from my own experience, this applies equally to *Limacina helicina* and to the Arctic Oikopleura, it is only while a direct and considerable influx of northern water is taking place around Cape Sable into the gulf (distinguished from the increment it contributes to the general inflowing drift) that they are likely to appear in the catches of the tow nets. Consequently, failure to find them in midsummer has no bearing on their presence or absence a month or two earlier in the season.

Judging from our cruise during the spring of 1915, they reach their greatest abundance and their widest dispersal in the gulf some time in May. The localities of capture, with what data are available on the currents at that season, suggest that after they have once passed Cape Sable their general line of drift is westward toward the center of the gulf, not northward along the west coast of Nova Scotia, which is the route followed by most visitors from the south (e. g. by *Sagitta serratodentata*), and that they keep near the surface.

Alexander Agassiz's (1865) discovery of Mertensia and of Ptychogena in Massachusetts Bay in early autumn, of Mertensia in abundance at Eastport, Me., in the early sixties of the past century, and Fewkes's (1888) record of the latter as plentiful there in the summer of 1885 and at Grand Manan in July and August, 1886, are contrary to our experience during the period 1912 to 1915; nor does Doctor McMurrich mention Mertensia at all in his plankton lists for St. Andrews. It is probable that such an abundance of Mertensia and its presence in the inner part of the gulf so late in the season were the visible evidence of a greater influx of northern water past Cape Sable than has taken place at any time during the past decade, and that this inflow turned more northward toward the Bay of Fundy. Unfortunately, however, no record was taken of the temperatures of the gulf during the years in question, and, conversely, no collections were made of the plankton during the abnormally cold summer of 1884.

The group of northern animals that better resist high temperature is represented in our catches with some frequency by the two calanoid copepods *Calanus hyperboreus* and *Metridia longa*, occasionally by a third large copepod, *Gaidius tenuispinis*, and regularly by the naked pteropod *Clione limacina* (p. 125). The status of each of these in the gulf is discussed below. I need only add here, of *Metridia longa*, that while it reaches the gulf chiefly as an immigrant with the Nova Scotian water, it is able to survive there for a considerable period and to thrive "amazingly in their wanderings," says Willey (1921, p. 194), speaking of the species at St. Andrews, in the Bay of Fundy, "if we may judge from their store of oil." Probably, as he suggests, most of them perish eventually in the gulf without leaving descendants, and thus, though the animals concerned are diametrically opposite in faunal origin, the distributional status of this copepod within the gulf is analogous to that of *Sagitta serratodentata*, the specimens that penetrate the gulf as driftage from the north, surviving there long enough to scatter far and wide and to be picked up in the tow net, still flourishing though far from Cape Sable and long after they have passed by it.

*Metridia longa* can not be looked upon as a regular annual visitor to the gulf, for while it has been taken at many stations in some years, in others it has been sought in vain (p. 247). There is some evidence that in the years when it passes west of Cape Sable in greatest number it succeeds in breeding to some extent in the gulf, and the result of its longevity there, coupled with this local reproduction, is that in its years of plenty it becomes so widely distributed that the locality records do not mirror its lines of immigration and of dispersal. For further discussion of this point see page 249.

The copepod *Calanus hyperboreus* affords a second example of an Arctic immigrant that finds an environment in the gulf favorable for the growth of the individual and to some extent for reproduction. Its recorded occurrence in the Gulf of Maine illustrates the care with which such data must be analyzed before general conclusions can be drawn from them, for if its Arctic nature were not well established, the fact that there is a center of abundance for it in the western side of the gulf and a second in the eastern might easily lead one to assume a totally erroneous faunal status for it. In reality it is probable that its comparative abundance off Massachusetts Bay is the result of a certain amount of local reproduction, though replenishment of the stock depends directly on immigration via the Nova Scotian current, as emphasized hereafter (p. 215).

The routes by which *C. hyperboreus* enters the gulf are discussed in the general account of the species. Once past Cape Sable they spread so generally over the gulf that it is impossible to trace their further drift from the actual locality records, probably because the large oily adults, on which most of our records have been based, live long enough to become dispersed far and wide, as well as because of the local production just mentioned.

## OTHER IMMIGRANTS

The indraft of water through the eastern channel and over the neighboring parts of the banks is not only fairly constant in its physical characters but carries with it various planktonic animals as characteristic of this source as those previously discussed are of an Arctic or Tropic origin. They include in their ranks, however, perfectly successful colonists, which, consequently, are also regularly endemic in the gulf (for example, the mammoth copepod Euchæta and the amphipod genus Euthemisto), as well as species that evidently find the gulf a less favorable environment than the salter and heavier mixed water, as evidenced by their comparative scarcity near shore and the smaller size attained there at sexual maturity. Others, too, are included, which are unable to breed at all in the gulf, though they may live there for some time, in which respect they correspond to *S. serratodentata*, of the Tropic group, and to *L. helicina*, of the Arctic category.

The influx of this mixed water into the gulf being more or less continuous throughout the year, either via the two channels, Northern and Eastern, or across Georges Bank, the mechanical agency for replenishing the stock of visitors from this source is always available, their life histories and chiefly their seasons of reproduction determining whether they are in evidence in the gulf at any given season of the year.

As I have pointed out, Tropic and Arctic visitors are brought into the gulf chiefly in the superficial water stratum, but the whole column of water down to the bottom of the deepest trough of the eastern channel serves as a medium for the dispersal of the immigrants entering with the mixed water, the precise "sailing routes" (to borrow a nautical term) followed by its inhabitants depending upon the courses of the inflowing water at the different levels at which they live. For the most instructive animal index to the movements of the surface layers of the mixed water, because the most abundant and conspicuous, we need only refer back to *Sagitta serratodentata* (p. 58); for, although this chætognath primarily originates in the Gulf

Stream, it is not direct overflows or influxes of the latter across the offshore banks that maintain the large stock within the gulf during its season of abundance, but the general indraft of mixed water.

The euphausiid shrimp *Nematoscelis megalops* (p. 146), which is less common than *S. serratodentata* in the inner parts of the gulf but is equally characteristic of the upper strata of water along the continental slope, occupies the same faunal status.

The large and easily recognized chætognath *Eukrohnia hamata* (p. 328) is a characteristic inhabitant of a lower level in the mixed water (say, below 50 meters), though not of the deepest. Its faunal relationship is diametrically opposite to that of its relative, *S. serratodentata*, for while it is widely dispersed over the ocean basins in the mid-depths, it is only in the Arctic or at least in cold seas that it comes to the surface regularly (Apstein, 1911). It enters the Gulf of Maine by the same route followed by *S. serratodentata*, but below it, and is equally unable to breed within the gulf,[30] though in its case this failure is because the temperatures it experiences there are too high instead of too low.

The eastern channel entrance to the gulf is deep enough to include a part of the vertical zone in which this species is most plentiful in the mixed water over the slope, where it appears in considerable numbers between 100 and 300 meters as well as deeper (p. 329, and Huntsman, 1919); hence it is not surprising that it should occur commonly in our deeper hauls in the gulf though seldom on the surface. The varying sizes of the individuals taken there suggest that it is able to "carry on" throughout its natural span of life anywhere in the gulf below, say, 100 meters, though unable to reproduce.

Our records do not show the migration routes for Eukrohnia as clearly as they do for *Sagitta serratodentata*, because the former is a year-round member of the plankton of the gulf. For this reason (coupled, as I believe, with longevity within the gulf), it is to be expected anywhere within our limits below 100 or 150 meters and at any season, though the extreme southwest corner of the deep basin off Cape Cod and also certain isolated sinks to which its access is more or less obstructed, may prove exceptions to this rule. If all our records of Eukrohnia for all seasons are united, however, there is a decided preponderance in the eastern, and particularly the extreme northeastern, parts of the gulf contrasted with its western side, not only in the number of stations at which it has been taken but also in its local abundance, which agrees with the general anticlockwise direction of the inflowing eddy. The distribution of Eukrohnia (p. 328) illustrates how closely its inward route follows the Eastern Channel and the slope of Browns Bank. Although Eukrohnia is a constant constituent of the plankton all along the seaward slope of Georges Bank, the latter must by its shoalness, oppose an absolute barrier to its dispersal, for we have not found a single specimen at any of our stations on the bank at any season. Consequently, none of the Eukrohnia that have passed the mouth of the Eastern Channel as they drift westward can enter the gulf on their farther journey. Finally, I may point out that the regularity with which Eukrohnia appears in the gulf is as good evidence

[30] Although Gulf of Maine specimens are often large, we have found none there with sexual organs developed.

as the salinity and temperatures that its native water is a large if not the major constituent of the inflowing current, for it is not abundant even along the continental slope (p. 333, and Huntsman, 1919).

The cold-water siphonophore *Diphyes arctica*, which occasionally penetrates the Gulf of Maine (p. 379), does so at about the same level as Eukrohnia (about 50 to 150 meters), and it is probable that, like the latter, it journeys with the mixed water, in which we have found it over the slope off Shelburne both in March and in June and off the slope of Georges Bank in July, but not along the Nova Scotian coast. The Eastern Channel is, no doubt, the route by which it enters the gulf, judging from the concentration of the localities of capture along the eastern slope of the gulf basin in March and April, 1920. The ultimate origin of *D. arctica* is not clear as concerns the Gulf of Maine, for while it was formerly supposed to have been one of the most charactersitic of Arctic indicators, captures of it by the *Gauss* in deep hauls off Cape Verde (Moser, 1915) suggest that it may also range widely in the cold mid-layers of more southern seas, just as Eukrohnia does, and thus reach the gulf from the intermediate depths abreast its mouth.

*Sagitta maxima*, the largest of local chætognaths, is perhaps the most useful animal indicator of the deepest stratum of the water entering the gulf via the Eastern Channel, both because its habitat is well known offshore, and because it neither breeds in the gulf nor can long survive there, being unfitted for life in water of low salinity no matter what the temperature (Huntsman, 1919, p. 433). *S. maxima* is so closely confined to depths of 150 meters or deeper, both in the Gulf of Maine and in neighboring parts of the Atlantic Ocean, that its presence anywhere in the inner parts of the gulf is unmistakable evidence of the existence of an inflowing current then, or shortly previous, and close to the bottom of the trough. The locality records for *S. maxima* are concentrated correspondingly in the Eastern Channel, in its immediate debouchement into the general basin of the gulf, and thence northward along its eastern trough as far as the Grand Manan deep, on the one hand, and in the deepest part of the western basin, on the other. As might be expected from its faunistic status, *S. maxima* is no more periodic (seasonally) than Eukrohnia in its occurrence in the gulf; but although specimens drift in more or less constantly throughout the year, it has invariably been so sparsely represented in hauls made within the gulf, contrasted with considerable abundance at 200 to 300 meters along the continental slope to the east and north, that the indraft can tap only the uppermost levels of its natural habitat offshore at any season.

The lines of dispersal followed, respectively, by *Sagitta serratodentata*, Eukrohnia, and *S. maxima* within the gulf correspond closely with the dominant drift of water at as many levels—that is, surface, mid, and deepest—as made evident by the physical data afforded by temperature and salinity and by drift bottles. Thus, while *S. serratodentata* not only spreads widely over the offshore parts of the gulf in its season, it also sweeps right around the coast to Massachusetts Bay (which apparently serves more or less as a cul-de-sac for it, as it has for certain drift bottles released in the Bay of Fundy), and Eukrohnia has much the same distribution except that it lives

so much deeper that it is prevented from entering Massachusetts Bay by the contour of the bottom, and, in fact, hardly encroaches at all on the shallow coastal belt within the 100-meter contour. Furthermore, the two agree in their scarcity in the

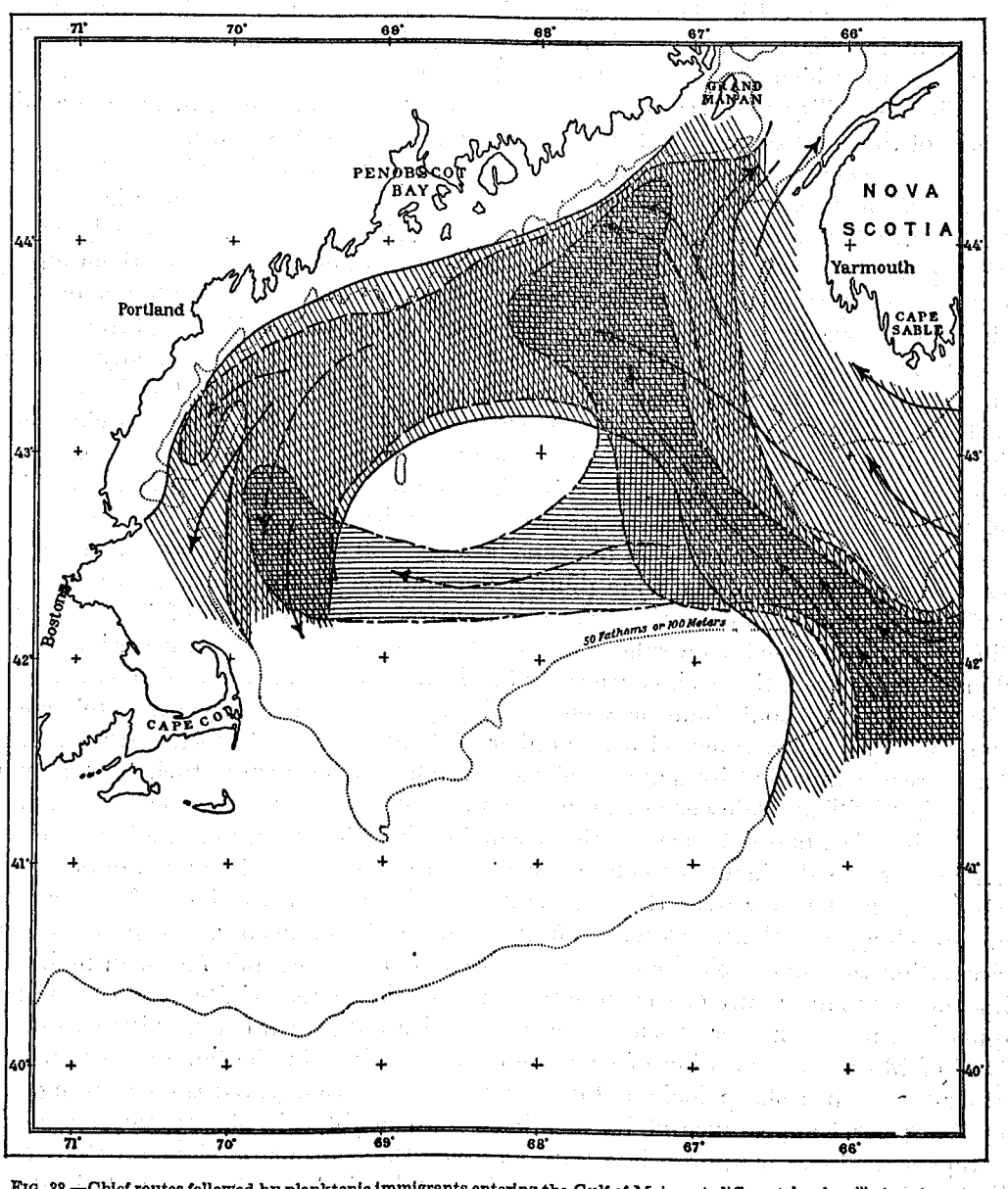


FIG. 38.—Chief routes followed by planktonic immigrants entering the Gulf of Maine at different levels. \\\, immigrants at the surface; |||, immigrants at intermediate levels; ≡, immigrants at the deepest level

southwestern part of the basin of the gulf—that is, just where the physical data, to be discussed elsewhere, locate the "dead water" in the anticlockwise eddy that occupies the gulf. However, *S. maxima*, living in the deepest waters of the basin, must follow

its two diverging troughs, in both of which there is a dominant though perhaps not a constant indraft along the bottom, the result being that while its route parallels those of the two preceding species in the eastern part of the gulf, it crosses below them at a lower level in the western, an interesting phenomenon illustrated in the accompanying chart (fig. 33). No doubt this applies in general to the three bathymetric groups which these three chætognaths typify.

The possibility that visitors may occasionally penetrate the gulf from the mid-depths of the Atlantic basin below, say, 300 meters, deserves a word.

The successive deep-sea expeditions, from the *Challenger* in 1872 to 1876 down to the *Michael Sars* in 1910, have found an abundant and varied pelagic fauna in the Atlantic below the level to which strong sunlight penetrates. Generally speaking, the adults of this community live well below 200 meters (many of them chiefly below 400 to 500 meters) and many of them are characterized by a peculiar coloration. Thus, those dwelling so deep that red light reaches them feebly, if at all, often exhibit a very dense pigmentation (Hjort, 1911 and 1912; Bigelow, 1911a), many fishes of this category being black with phosphorescent organs, decapods dark red, and medusæ either of a beautiful, translucent, deep claret color or opaque chocolate, tints quite unknown among jellyfishes in shallow water. This extreme development of pigment is so characteristic of this whole faunal group that the latter is often referred to as the "black fish-red prawn" community.

At a higher level (that is, in the zone between 150 and 500 meters, but nevertheless below the reach of the wide diurnal fluctuations in illumination to which the surface waters are subject) there exists an entirely distinct series of fishes of quite different aspect, which as a rule are "laterally compressed, with a mirrorlike silvery skin; when colored, the back is generally blackish brown, and the resplendent mirrorlike sides of the body blue or violet. The eyes are large, very often telescopic, and the body is provided with a number of light organs" (Hjort, 1912, p. 628). They are accompanied by sundry medusæ, which parallel them in their pale pigmentation but brilliant iridescence, as I have pointed out elsewhere (Bigelow, 1911a, p. 6).

It is a fortunate chance for the oceanographer that many of the bathypelagic animals are so distinctively colored, because their presence in any numbers anywhere in shoal water over the continental shelf would be the best of evidence of an upwelling of Atlantic water from the mid-depths or deeper, a type of oceanic circulation that has evoked considerable discussion as a possible factor in maintaining the low temperature of the coastal waters off the eastern United States. Consequently, the presence or absence of the black fish-red prawn community within the Gulf of Maine is a question of some moment, and it is in the hope of encouraging others to keep a sharp lookout for it there that I have devoted the preceding lines to the general appearance of its members. No doubt this planktonic community is represented at the appropriate level all along the continental slope off the United States, for it occurs generally over the whole Atlantic basin from high latitudes to low. We encountered it over the 1,500-meter contour off Cape Sable on March 19, 1920 (station 20077), the following being a partial list of its more noticeable representatives in hauls from 500 and 800 meters: Several black lantern-fishes (genus Myctophum); a specimen of the curious deep-sea snipe eel (*Serrivomer beanii*), 45

centimeters long;[32] the wine-red medusa *Periphylla hyacinthina;* 13 specimens of its chocolate-colored relative *Æginura grimaldii;* the iridescent medusæ *Halicreas papillosum* and *Rhopalonema funerarium;* and many red prawns; side by side with the chætognaths Eukrohnia and *Sagitta maxima*, the large copepod *Euchæta norvegica*, and the euphausiids Nematoscelis and Thysanoessa, besides boreal animals such as *S. elegans*, Tomopteris, *Limacina balea*, and Calanus.

Scanty though the catch just listed is, compared with the abundant pelagic fauna that has been encountered by the *National*, the *Valdivia*, and the *Michael Sars* at many stations in the North Atlantic, and by the *Albatross* on many occasions and in localities in widely separated parts of the Pacific, it is the only one in which the black fish-red prawn community has been represented by more than an occasional example even at our outermost stations, though we have towed down to 400 meters or deeper at several other localities off the slope abreast of the Gulf of Maine in February, May, June, July, and August. In fact, to complete our list of captures of this category I have only to add two genera of fishes (Cyclothone and Myctophum) and one red medusa (Atolla) from 750 meters off the southwest face of Georges Bank, February 22, 1920 (station 20044); a few black fish and bathypelagic medusæ (Æginura) from 1,000–0 meters southeast of the bank three weeks later (March 12, 1920, station 20069); a scattering of bathypelagic fish (mostly juvenile Sternoptychids and Myctophids) at our summer stations along the same zone off the bank in June and July, and off Cape Sable.

With bathypelagic animals so scarce in the cool water that washes the continental slope abreast of the Gulf of Maine, and with both the Eastern Channel (the bottleneck through which, alone, the deeper strata of oceanic water flow into the gulf) and the basin into which it debouches considerably shoaler than the levels at which they attain their maximum development offshore, it would be surprising to find any of them in the inner parts of the gulf except as the rarest of stragglers. As a matter of fact, our cruises have yielded only two such records—viz, one *Cyclothone signata* 23 millimeters long on Browns Bank, station 10296, June, 1915, and a mutilated specimen, probably of this same species, taken in an open-net haul from 180 meters in the Fundy Deep on March 22, 1920. Nor have other students been more successful in this respect so far as I can learn. Thus it is evident that members of this community occur only accidentally within the limits of the gulf, for did they enter the latter as often even as the tropical animals discussed above, they would have been sure to attract attention in the tow net by their striking appearance. In short, the plankton of the gulf receives practically nothing from the deeper layers of the Atlantic at any season. Even the most temporary invasion on their part would be so important an event, both faunistically and hydrographically, that sharper and more constant watch should be kept for them in the gulf than their rarity there would warrant otherwise.

The several Tropic and Arctic visitors and immigrants from the continental slope touched on above illustrate the less successful degrees of colonization, ranging from utter failure in the cases of sporadic visits of exotic tropical animals and the equally

[32] For a description of this eel see Goode and Bean, 1896, p. 155, fig. 168. It is not included in the report on the fishes of the Gulf of Maine (Bigelow and Welsh, 1925), because the localities of record lie outside the limits covered therein.

short-lived incursions by the more delicate Arctic forms, to the more successful though equally temporary immigrations by animals that are able to survive under the physical conditions which they encounter in the gulf and even to grow there, but not to breed; such, for example, as *Sagitta serratodentata* and Eukrohnia. The next step toward successful colonization would be the ability to breed in the gulf in small numbers or during especially favorable years, which would still leave the species concerned dependent on immigration from prolific centers elsewhere for the maintenance of the local stock. In the nature of the case instances of this sort are difficult to demonstrate without intensive and long-continued studies of the plankton, but it is evident that the copepods *Calanus hyperboreus* and *Metridia longa* both fall in this class (p. 61); also the curious pelagic worm *Tomopteris catharina*, the continuous and rather common occurrence of which in the gulf and its wide dispersal there depend chiefly on immigrants of northern origin (it is a north-boreal form), for while it breeds in the gulf in some summers it fails to do so in others (p. 338). It is probable, also, that the large naked pteropod *Clione limacina* has this same faunal status, breeding in sufficient numbers for the local production, coupled with individual longevity, to give it a uniform distribution over the gulf and so to obscure the routes followed by the immigrants from colder waters east and north of Cape Sable, on whose visits its continuous presence in the gulf equally depends (p. 127).

The amphipod genus Euthemisto stands a rung higher on the ladder of progressive colonization, for it neither breeds so abundantly (though it does so regularly) in the gulf nor grows to so large a size there as it does over the outer edge of the offshore banks—Georges and Browns (p. 158). Local fluctuations in the abundance of animals of this status throw no direct light on their waves of immigration, being due, as often as not, to local centers of reproduction within the gulf itself and even close up to the land, such as we have occasionally encountered for Euthemisto (p. 160); but greater abundance in the eastern part of the gulf than in the western, especially if coupled with prolific centers of reproduction in the zone of mixed water over the outer part of the continental shelf abreast of it (and this is true of Euthemisto), shows that the stock produced within the gulf receives frequent accessions to its numbers from outside.

No doubt one or other member of the plankton might be found to represent every conceivable intergradation from utter failure to perfect success in colonizing the waters of the Gulf of Maine (for all members of the plankton are colonists in the last analysis) were the known record sufficiently complete. The copepod genus Euchæta, for example, may be taken as representative of animals that breed indifferently and grow equally large along the continental slope, in the Eastern Channel, and in the gulf wherever the depth is sufficient, as proven by the occurrence of sexually adult males, of females with large egg clusters, and of juveniles. For this copepod the gulf basin is simply a diverticulum from its general geographic range. Most successful of all are those that find a more favorable environment in the inner parts of the gulf than in the waters immediately tributary to it, and it is to this group that such members of the local zoöplankton as the copepods *Calanus finmarchicus* and *Pseudocalanus elongatus* and the chætognath *Sagitta elegans* belong. It is true that most, if not all, the animals of this category have equally prolific centers of

abundance elsewhere (chiefly to the eastward and northward), connected with the gulf by a continuous zone of occurrence, but all of them are regularly more abundant in the particular temperatures, salinities, densities, etc., that characterize the Gulf of Maine than immediately outside it, whether to the east or the west or offshore. Indeed, such multitudes of several of these species (Calanus, especially) are produced there that the small accessions which the gulf may receive from the north must be far outnumbered by the emigrants that emerge from it to journey either northward along the inner edge of the continental slope, on the one hand, or around Cape Cod to the westward and southward over the outer part of the continental shelf, on the other. It is probable that the boreal winter plankton of the coast water south of New York draws more from this source than from local production.

## MIGRATIONS OF PELAGIC FISH EGGS AND LARVÆ

One of the most interesting and economically important fields of study to which our Gulf of Maine explorations are introductory is the involuntary migrations of the early stages of fishes, with the effects of such journeyings on the fish population of different parts of the gulf.

Any information obtainable on this subject is instructive from the point of view of the migration of the plankton within the gulf, because every buoyant fish egg floats from spawning until hatching, wherever the current may carry it, rising or falling vertically according to specific gravity of the water only, with the young larvæ equally at the mercy of tide and current until after the yolk sac is absorbed. Even the older pelagic fry of most fishes are hardly less helpless, so far as voluntary horizontal migration is concerned, until they attain considerable size (some species become contranatant—that is, turn to swim against the current—at an early stage), even though they are able and do swim up and down and thus exercise a choice of level at which they live.

Now the water of the open sea never being at rest (no area as large as the gulf lacks some dominant movement, if not a definite current, in one direction or another), it follows that only in the rarest instances does a fish hatched from a buoyant egg ever grow large enough to descend to the bottom in the precise locality where the egg that gave it birth was spawned. The drift during its pelagic life may be only a few miles if spawning occurs in some bay or sound sheltered from the free circulation of the sea by off-lying islands; it may, indeed, be almost *nil* in this case, should the tidal currents in the two directions be of equal strength. Outside the outer headlands, however, the journeyings of floating fish eggs are, generally speaking, so considerable that they are often measured better by degrees of latitude and longitude than by miles. Such, to quote only a couple of the more striking and better known examples, is the case with the cod eggs spawned south and west of Iceland, for most of the fry resulting therefrom drift right around to the north and east coasts of the island before they seek the bottom (Schmidt, 1909). Off Norway, too, cod eggs and fry have long been known to carry out long journeys with the current (Damas 1909a; Hjort, 1914). Indeed, events of this sort are inevitable, given the indicated factors of animals able to swim but weakly, caught up in the set of any current.

Extensive migrations of fish eggs and of young fishes, in fact of all the plankton, are therefore to be expected as characteristic events in the Gulf of Maine with the dominant anticlockwise eddy that governs its circulation—not their occurrence, but their absence would cry for explanation. And so interesting is this question, and so directly does it bear on the practical problems of the fisheries, that it deserves passing notice, even granted that we can not yet outline the travels of so much as a single species of fish in the gulf.

No matter how little related the various species are, it is justifiable to consider as a unit all fishes that are subject to similar influences during their pelagic lives, the precise routes they follow at this early age depending not on themselves but on the locations and times of year where and when their eggs are spawned, in relation to the circulation of water in the gulf, and on the duration of the pelagic stage as governing the length of time during which they drift before they abandon this nomadic life for a more stationary habitat on or near bottom. Several of our gadoid and flat fish are particularly suitable for such a combined survey, because while they do not spawn on precisely the same grounds or at just the same seasons, cod, haddock, silver hake, and such common flounders as plaice, dab, and witch, agree in breeding only in the peripheral belt of the gulf and on the offshore banks, seldom, perhaps never, in its central deeps outside the 200-meter contour. As the composite chart (fig. 34) shows, buoyant gadoid and flatfish eggs of one kind or another have been found all around the coastwise belt of the gulf, likewise widespread on Georges and Browns Bank, the richer clusterings of egg records mirroring the greater number of hauls made at particular localities rather than any demonstrable preponderance of eggs as compared with the intervening stretches. If there were no dominant drift of current in one direction or the other, but only the tide to disperse the eggs in these shoaler parts of the gulf, the distribution of the larvæ would simply parallel that of their parent eggs; but year after year and voyage after voyage we have come to see more and more clearly that such is not the case, but that the young pelagic stages of the cod and flounder families are much less plentiful in the northeastern corner of the gulf than in its southwestern waters in general or in the Massachusetts Bay region (fig. 35) in particular.

The considerable number of towings carried out along the coast of Maine from spring until autumn, in 1915, fairly rule out the possibility that the discrepancy in distribution between eggs and fry is only apparent and results from an imperfect record. To suppose that the same nets would catch young fish in Massachusetts Bay and as consistently miss them off Mount Desert and to the eastward is absurd; nor can the depths of the hauls be made responsible, seeing that we have towed at various levels, surface to bottom, as well as vertically, at many stations along the coast. A difference of this sort between the locations where the eggs are spawned and where the resulting larvæ are to be found is not a novelty, for Petersen (1892) long ago reported a precisely similar phenomenon for Danish waters. In short, I am convinced that the scarcity of larval and post-larval fishes in the one corner of the gulf as contrasted with their abundance in the other is real.

It is, of course, possible that the northeast part of the gulf is so ill fitted for a fish nursery that only a small proportion of the pelagic eggs spawned there ever

hatch or the resultant larvæ survive. The researches carried on during the past few years at the Canadian Biological Laboratory at St. Andrews point unmistakably to the conclusion that few if any floating eggs of any groups of animals hatch success-

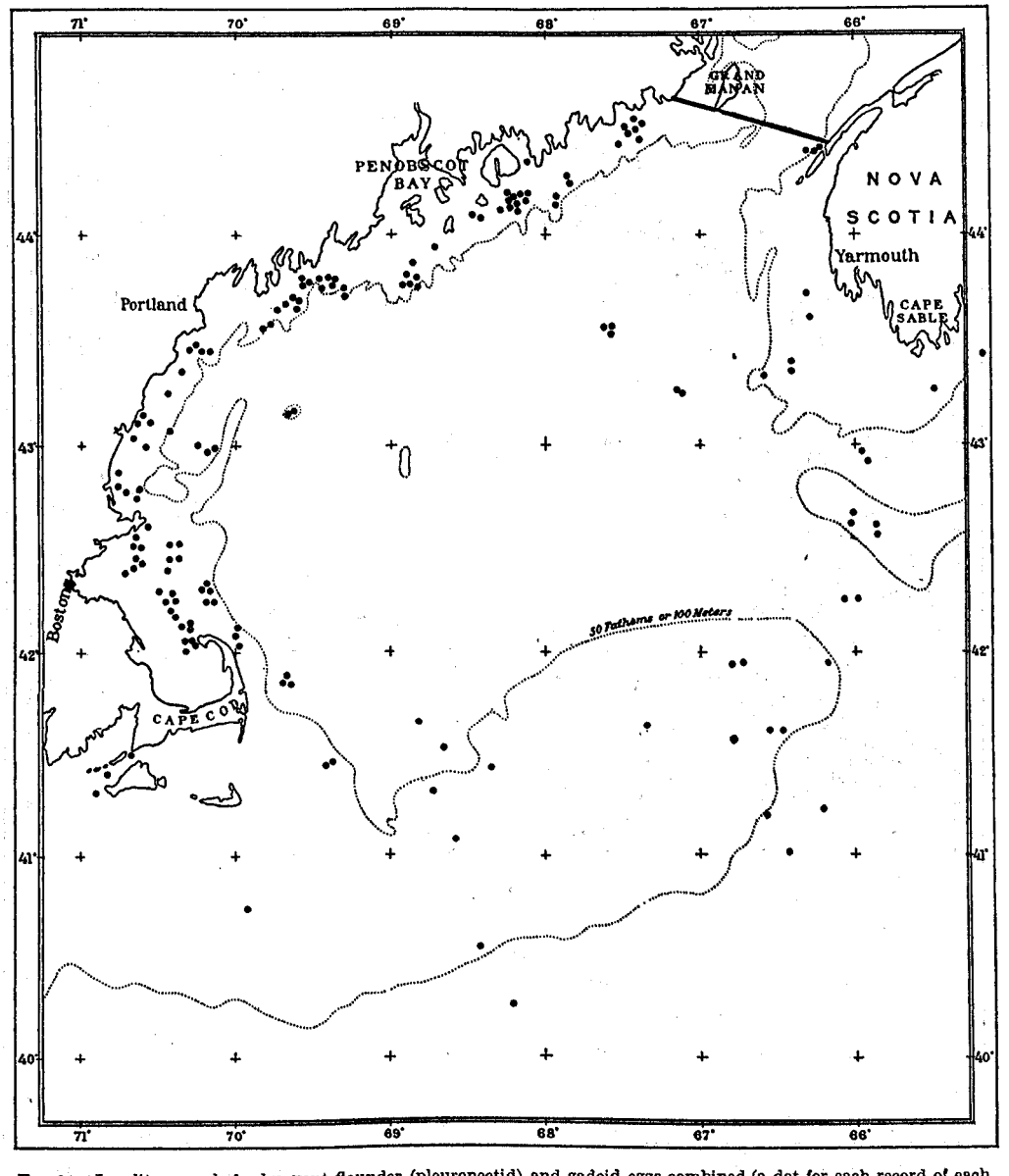


FIG. 34.—Locality records for buoyant flounder (pleuronectid) and gadoid eggs combined (a dot for each record of each species), 1912 to 1922

fully in certain parts of the Bay of Fundy, this being particularly true for chætognaths and fishes (Huntsman, 1922; Huntsman and Reid, 1921). As evidence of the unsuitability of the bay as a breeding ground for fishes with buoyant eggs, Huntsman

(1918, p. 65; 1922) offers the extraordinary rarity of the larvæ, for example, of the plaice (Hippoglossoides), witch (Glyptocephalus), cod, haddock, hake (Urophycis), or pollock (*Pollachius virens*), although the adults of all of these are plentiful there;

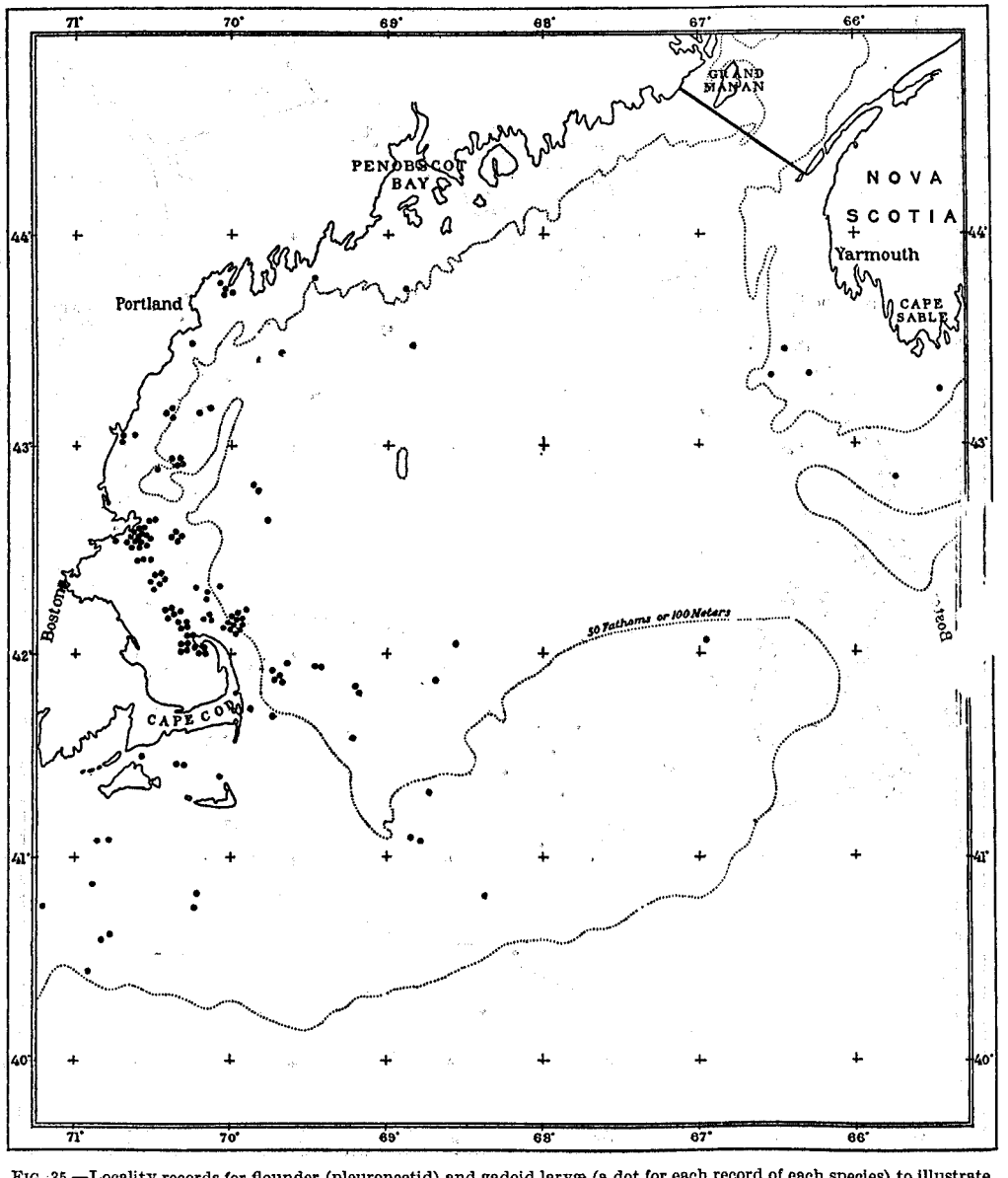


FIG. 35.—Locality records for flounder (pleuronectid) and gadoid larvæ (a dot for each record of each species) to illustrate the probable drift of buoyant fish eggs and larval fishes

all, in fact, spawn in the bay, for cod and plaice eggs have been recognized there in the plankton (Huntsman, 1922), and floating fish eggs of some species were noted by Doctor McMurrich as occurring occasionally during January, February, April, and early May, and regularly thereafter until the end of August at St. Andrews.

Taken by itself, the absence of larvæ, contrasted with the presence of eggs, could as well result from a drift of the latter out of the bay before hatching—such, indeed, as the circulation of water would call for—as from their failure to hatch locally or of the larvæ to survive. But there are two objections to this view, to my mind unanswerable; first, that larvæ and young fry of these several species are fully as rare along the eastern shores of Maine—that is, in just the waters into which the outflow from the bay debouches—as within the latter; second, that the drift into the southern entrance of the bay would naturally bring with it gadoid and flatfish eggs from the shallows off western Nova Scotia. Some of the cunner (Tautogolabrus) larvæ produced in St. Marys Bay, which Huntsman (1922) has found to be an important site of reproduction for this fish, must likewise find their way into the Bay of Fundy either around Brier Island or through the passages; but so few of them survive the conditions they encounter in the Bay of Fundy, that none have been recorded from all the winter and summer towing which has been done from the St. Andrews station.

Most of the common fishes that do succeed in breeding in large numbers in the bay lay demersal eggs; for instance, the several sculpins (Cottidæ), the lumpfish (Cyclopterus), the rock eel (*Pholis gunnellus*), the winter flounder (*Pseudopleuronectes americanus*), and the herring. The rosefish (Sebastes) and the eelpout (Zoarces), which are viviparous, produce young far advanced in development.

The evidence just summarized justifies the hypothesis that while young fish hatched in the bay from demersal eggs, or such as are far developed as to size and at hatching, thrive there, most of the very small and helpless larvæ produced in the bay from pelagic eggs, or which enter it as immigrants from the south, perish. So we may speak of the Bay of Fundy as a deathtrap to buoyant eggs and larvæ drifting northward along the eastern shores of the gulf, and it contributes none of these to the coastal waters to the westward. Even the very abundant stock of young herring produced about the mouth of the bay (notably at Grand Manan) do not spread far to the westward, Huntsman having found that they soon become contranatant and begin to work back against the current, which takes them out of the planktonic category.

An understanding of the causes that prevent successful development in the bay would make it possible to estimate the probable suitability, from east to west, of the waters along the eastern coast of Maine, where eggs are certainly produced in some abundance but where few larvæ have been taken. Huntsman (1918) suggests the violent tidal stirring in the bay as responsible, by preventing vertical stratification of the water. The low surface temperature may also be an effective check to species such as the cunner, which spawn in high temperatures. Neither of these factors, however, would seem likely to interfere with the successful breeding of late autumn, winter, or spring spawners—the American pollock and the haddock, for instance. Further light on this interesting question, to which our own work has contributed nothing, is to be expected from the investigations now being carried out at St. Andrews by the Biological Board of Canada.

From Mount Desert eastward the coastal belt of the gulf more and more closely approximates the Bay of Fundy hydrographically, owing to the increasing strength of the tides and the consequent activity of tidal mixing. Correspondingly,

the general neighborhood of Mount Desert Island is the most easterly location along the northern shores of the gulf where we have found gadoid or flatfish eggs in any numbers.

The rather uniform transition in the state of tidal mixing, with its consequent effect on salinity and temperature, which characterizes the coastal belt from the Bay of Fundy to Casco Bay, indicates an improvement from east to west in conditions for buoyant fish eggs and larvæ; but outside the outer islands [33] salinities and temperatures vary so little from Penobscot Bay westward and southward to Massachusetts Bay, especially during winter and spring when most of the more important gadoid and flatfish species spawn, that there is nothing in the physical state of the water to suggest one part of this zone as notably more suitable for their successful reproduction than another.

With the dominant set of the water tending to drift all fish eggs and larvæ produced along the northern shores of the gulf toward the west and south, and with few or no accessions coming from the east to the coastal zone between Mount Desert and Cape Elizabeth because of the sterility of the Bay of Fundy in this respect, tows there might be expected to take eggs and very young larvæ, but seldom older ones or the post-larval stages. Actually, most of our tow nettings there have yielded eggs alone (fig. 34); but the larvæ hatched from buoyant fish eggs are so small and soft until two weeks or so old that they are apt to be mashed past recognition amongst the mass of other plankton, hence may very well have been overlooked, and by the time they are large and resistant enough to be noticed among the hard-shelled copepods, etc., they may have drifted for a considerable distance.

Mavor's (1920 and 1922) recent experiments with drift bottles give some idea of the actual speed with which the surface water, and consequently the fish eggs and larvæ floating with it, may travel westward and southward around the gulf, indicating that a drift of about 4 nautical miles per day is not unusual in summer and autumn, although more or less intermittent. The rate is probably higher than this during the spring.

On this basis, buoyant eggs spawned off Mount Desert Island and far enough out from the land to be caught up in the general peripheral eddy of the gulf (how far this means is not yet known) might drift well beyond Cape Elizabeth during the two weeks interval that may be set as a fair average incubation period for gadoids and flatfishes in general in Gulf of Maine temperatures. Whether the eggs actually equal the drift bottles in the speed of their journey depends on whether they float at the same level—that is, in the upper two meters or so. Many of them, and perhaps most, taking the year as a whole, do so; but locally, and especially when the surface is at its lightest after the river freshets, many eggs float deeper down where the dominant drift probably is slower, notably those of the haddock, which is spawning actively at that season (Bigelow and Welsh, 1925). During the interval after hatching, when the larvæ are so small that they are seldom recognized in ordinary tow nets, the small proportion of them that survives the vicissitudes of pelagic life very likely drifts another 50 miles or so, so that Mount

[33] Low surface temperature close in along the land between Penobscot Bay and Casco Bay in summer may be a bar to the local breeding of the cunner, though this would not apply up the many estuaries that indent this section of the coast.

Desert fish may well reach Massachusetts Bay in their journey by the time they are 10 to 15 millimeters long, if they remain in the superficial water layers. If they sink to lower levels, as it is practically certain that many of them do, their involuntary migration during this stage probably is not so extensive, there being reason to believe that the general set is more rapid above than below 40 to 50 meters; but whatever depth they seek within the 100-meter contour (which in general limits the offshore dispersal of both eggs and larvæ in this side of the gulf), the majority of them will tend in the same general direction. Similarly, the larvæ hatched from buoyant fish eggs spawned off Machias, where considerable numbers are produced, might well travel as far as Cape Elizabeth before attaining the sizes we have recognized in the tow nettings.

The distribution of the buoyant eggs of the cod and flatfish families in the gulf bears precisely the relationship to that of the older larval stages (fig. 35) which involuntary migration of this sort would produce. In fact, something of the kind might safely have been prophesied from what is known of the circulation of the gulf; and I believe it safe to assert that the great majority of the larval fishes hatched from buoyant eggs spawned in the zone from 10 miles or so outside the outer islands out to the 100 or 150 meter contour, between Cape Elizabeth and the Bay of Fundy, drift a greater or lesser distance around the periphery of the gulf toward the west and southwest (if they survive as long as three weeks or a month), though this drift may be interrupted or even reversed on any given day or over a period of several days. They may tend to hug the coast, as it seems Mavor's (1920) first series of drift bottles did in 1919 (this probably is the usual event in spring), or swing more offshore, and so, if they live pelagic long enough, come around to the northeastern corner of the gulf as other drift bottles released in the summers of 1922 and 1923 have done. The variations in the dominant set are not well understood, but in any case they will tend to follow an anticlockwise and eddying course.

Thus, fish eggs and larvæ, and for that matter every member of the plankton, animal or vegetable, tend to follow the same peripherical migration zone as do the immigrants that enter the eastern side of the gulf in the upper 50 meters (p. 64). Only such buoyant eggs as are spawned among the islands, in bays, or close in along shore (as most of the cunners are) are likely to escape this dominant set.

At the times when the dominant drift of the surface water follows the coast line closest, south toward Cape Ann, Massachusetts Bay probably acts to some extent as a catch basin for all sorts of flotsam from the north, living, of course, as well as dead, as it did for certain of Mavor's drift bottles. The chart (fig. 35) suggests that larvæ that pass Cape Ann tend to be caught up in the back water of the bay, to remain there until they abandon the pelagic life for the bottom. Thus, it is probable that the rich fish fauna of the bay and its adjacent waters is regularly recruited from the north and east.

Similarly, the abundant occurrence of young pollock at Woods Hole in late spring (fry so small that they are evidently the product of the previous winter's spawning) is clear evidence of a migration southward along and around Cape Cod from the very productive spawning grounds at the mouth of Massachusetts Bay,

because no important spawning is known for this fish south of the Massachusetts Bay region (Bigelow and Welsh, 1925).

There is no evidence that the larval stages of the cod or flatfish families acquire a contranatant (that is, up-current swimming) habit, as the herring does. Consequently the extent of their involuntary journeyings depends on the duration of the pelagic stage as much as on the velocity of the drift with which they travel. Very little information has been gathered on this in the Gulf of Maine, but in north European seas both the American pollock (*Pollachius virens*) and the haddock are pelagic for about three months; most of the cod hatched in the Gulf of Maine probably are so for at least two months, if not longer, before they take to the bottom. So far as the elapsed time goes, experience with drift bottles suggests that this may be long enough for some of them to make the entire round of the gulf—that is, from off Mount Desert or Penobscot Bay around to the Bay of Fundy—but whether any of them actually do so is not known. The extent of the actual drifts of different species would be governed largely by the levels in the water at which the larvæ live.

Schmidt's (1909) classic and oft-quoted study of the distribution of cod and American pollock (*Pollachius virens*) eggs and fry around Iceland illustrates how far apart the fry of different species, hatched from eggs spawned in the same general regions, may travel before abandoning their pelagic life, if living at different levels and pelagic for different lengths of time. The two fishes in question spawn at the same season (maximum egg production about April), and both of them mainly, if not exclusively, off the southwest and south coasts of the island, while the fry of both show a tendency to drift thence westward and northward. But while the American pollock mostly descend to the bottom in practically the same waters where spawned, either because their span of pelagic life is short or because living at such a level that they drift slowly, the young cod generally travel right around the island (a trip of something like 500 miles for many of them), and the result is a scarcity of the youngest bottom stages on the south and west but a great predominance of them over those of the pollock off the northeast and east coasts. The Icelandic haddock likewise perform a similar involuntary migration, enduring from May until July.

The great abundance of young pollock only a few inches long along the littoral zone in the Gulf of Maine suggests that the involuntary drift of the pollock is also shorter with us than is that of cod or haddock. Here, again, definite evidence, one way or the other, is lacking for want of systematic towing during January and February.

Very few definite observations have been made on the depths at which the various young fish live while pelagic in the Gulf of Maine, and it is not safe to assume that these will be the same as in the northeastern Atlantic, the vertical distribution of temperature and of salinity being different. It is probable that the young pollock frequent the surface layers more than either cod or haddock (except for such of the latter as live commensal with medusæ), this being the case in European waters; but the involuntary migrations of the Gulf of Maine pollock take place in winter when the circulation of the gulf is believed to be at its minimum. Drift bottles released during the period from January to March would be extremely instructive in this connection. On the whole, the drifts of young cod may be expected to follow

deeper, and of young haddock still deeper currents, but to what extent this differentiates the dispersal of their fry in the gulf from those of the pollock can not be stated until a sounder knowledge of the circulation of the waters of the gulf has been gained.

It has long been known that the larval and post-larval stages of the hakes (genus Urophycis) are apt to be right at the surface in the Gulf of Maine in summer. They might therefore be expected to follow very closely the tracks of the drift bottles released at that season. Silver-hake (Merluccius) larvæ, on the contrary, which are among the most abundant of young fishes in the southwestern part of the gulf in July and August, usually have been taken in hauls from 40 meters or deeper (seldom at the surface), and it would seem that they must therefore travel with the undercurrent. In the case of silver hake it is not improbable that some of the larvæ that journey down past Cape Cod drift on past Nantucket Shoals toward the southwest. Consequently, eggs spawned in the Gulf of Maine may contribute to the fry found west of Nantucket in summer, though most of these are the result of local propagation (Bigelow and Welsh, 1925, p. 395).

It is equally possible that part of the young silver hake circle eastward over the northern part of Georges Bank, and so northward into the gulf again, for drift bottles released on a line running southwest from Cape Cod have shown a division in this respect, many of the outer ones having gone westward and some of the inner ones eastward, but we have found no Merluccius larvæ in any of our July towings over the banks, although they are abundant off Cape Cod during that month.

I have previously (Bigelow, 1917, p. 279) suggested the possibility of a passive migration of cod and haddock from the western part of the gulf out onto Nantucket Shoals and to the western parts of Georges Bank, where we have since found young haddock in some abundance floating commensal with medusæ in July (Bigelow and Welsh, 1925).

The drift of the haddock eggs that are spawned in enormous numbers on the eastern part of Georges Bank in spring (p. 37; and Bigelow and Welsh, 1925, p. 439), and of the resultant larvæ, is a question of great interest. A considerable proportion of these may take to the bottom on more westerly parts of the bank, because the northern part of this spawning ground seems to be affected directly by a set from the northeast during the critical season; but at the time of our March and April visits thither in 1920 the presence of newly spawned eggs in abundance right out to the 1,000-meter contour proved that a drift out to sea was then taking place from the southern point of the bank.

Eggs subject to this drift must suffer one of two fates. Probably they would be caught up in the band of cool mixed water along the continental slope, in which case the eggs and larvæ might again be swept in on the shelf somewhere to the westward by some incurving swirl in the complex interaction of warm and cold waters, or, circling to and fro, come in again on Georges Bank. If they drifted farther offshore, but still not far enough out to reach water of fatally high temperature, they would probably tend to travel to the northeast. Therefore, as Doctor Huntsman suggests in a recent letter, it is possible that the Georges Bank spawning ground, which is

certainly one of the most important off the American coast, may even contribute to the fish stock of the Grand Banks.

Haddock or any other bouyant eggs spawned on Browns Bank, or German Bank to the north of it, would probably tend either northward into the gulf or westward toward Georges Bank, depending upon the precise state of the Nova Scotian current at the time; and it is probable that this was the source of the cod-haddock eggs towed over the eastern side of the basin on May 6, 1915 (station 10270), and on April 17, 1920 (station 20112). Larvæ hatched on Browns and German Banks might be expected to follow the same route during the spring, if living at about 40 to 50 meters, which it is probable that most of them do. Eggs spawned on Browns and German Banks after the rush of water past Cape Sable has slackened, would be more apt to be drifted northward toward the Bay of Fundy, but this would apply mostly after the spawning season of the haddock had passed.

It is obvious that if practically no production of the species of gadoids and flatfishes that lay buoyant eggs takes place in the Bay of Fundy, and if most of those produced along the northern side of the gulf drift away to the southwestward, as the evidence marshalled above seems to prove, there must be as regular an immigration of the older fry back again to maintain the stocks of adult fish. However, this subject does not immediately concern the plankton.

It is interesting to compare the chart of gadoid and flatfish fry (fig. 35) with the corresponding chart for the rosefish (Sebastes), a viviparous species (Bigelow and Welsh, 1925, fig. 120), as an illustration of the degree to which the dispersal of larval fishes depends on the precise locality where they are produced. In the case of the former this happens chiefly inside the 100-meter contour, with the result just described. No doubt, when young rosefish are born in that belt and chance to rise near the surface they follow the same route, journeying with the dominant set. But rosefish also produce their young generally over at least the northern half of the deep basin of the gulf, where the dominant anticlockwise eddy is felt less. It is also probable that in most cases the young Sebastes, like their parents, live rather below the level of the most active currents, hence are less apt to be caught up by them. Further (though less important in its effect than is the location of the breeding grounds in relation to the circulation of the gulf), Sebastes is so comparatively large and strong at birth that its involuntary migrations cover a shorter period than those of most of the fishes that lay floating eggs, and consequently its larvæ are to be found widespread, except close to land, and not concentrated in any one part of the gulf.

## QUANTITATIVE DISTRIBUTION OF THE ZOÖPLANKTON

To give an adequate quantitative picture of the plankton would require a far greater number of vertical hauls than have yet been made in the Gulf of Maine. Not only are the seasonal gaps in the series serious, but hauls should be located closer together than has been feasible for us, even in July and August, unless the plankton is more uniform than our work suggests. However, even a cursory examination of the zooplankton, if extended over a considerable area or through a considerable period of time, is certain to reveal wide fluctuations in abundance as well as in its qualitative

composition, both from season to season and from place to place; and inasmuch as an understanding of the causes of the fluctuations in the numerical strength of any group of marine animals would clarify the interaction of the many physical factors that govern pelagic life in the sea, information along this line is never amiss.

Quantitative data regarding the plankton run the whole gamut from the most casual to the most accurate and precise, depending on the method of collection and enumeration employed, which in turn depends on whether it is the absolute numbers of individuals of any group that is sought or merely their abundance relatively and in a rough way. Perhaps I shall not be taken to task when I add that no wholly satisfactory method has yet been devised for estimating the abundance of the larger and more active members of the zoöplankton.

With immobile objects such as fish eggs, or weak swimmers such as ctenophores and copepods, vertical nets of the more modern patterns yield counts of reasonable accuracy; but when we attempt to deal with animals whose powers of directive swimming are as well developed as those of Sagittæ, euphausiids, young fish, etc., the certainty that some of them—it may be many or it may be few—escape the net introduces an unavoidable source of error and one that is far more serious than the clogging of the meshes, resulting in only partial filtration of the column of water through which the nets fish, and one that must always be reckoned with in quantitative work. For this same reason enumerations of the plankton contained in samples of sea water of known volume, collected by water bottle or by pump, a method that has proved fertile for the study of the phytoplankton (p. 398), are of no value whatever for any animals except the smallest. In short, any absolute census of the total plankton in the open sea will, we think, long remain something of a will-o'-the-wisp. If the goal be no more than a comparative (not an absolute) estimation of the amount of zoöplankton present in the water, these difficulties fade.

If the same type of net is employed for all the hauls and of a mesh calculated for the general size of the plankton elements for which it is intended, and if the length of the column of water fished through is either known accurately or is the same on all occasions, the catches will be fairly comparable one with another, and the net error (that is, failure to filter perfectly) becomes secondary. If the nets are large enough in diameter [34] (say half a meter or more), with filtering surfaces sufficiently extensive in proportion to the mouth area, and of a shape proper for the rapid passage of water, they will certainly capture a majority of the animals in their path up to the size of amphipods, Sagittæ, and euphausiids. In the case of the copepods, which, after all, are the backbone of the zooplankton of the Gulf of Maine, the catch will be sufficiently representative of the actual population for comparative purposes,[35] even if the few individuals that chance to lie near the outer rim of the mouth of the net dodge it and escape. With this end in view we have, since 1914, abandoned vertical nets of the Hensen pattern, with their small mouths, for a vertical net half a meter in diameter, of the *Michael Sars* pattern;[36] and I may add that in making vertical hauls the net has

[34] The larger the better.

[35] A whole literature, from the hands of its sponsors or critics, has arisen about the reliability or the reverse of the vertical net, which has been the classic engine for quantitative plankton studies ever since Hensen (1887) first sponsored it.

[36] For specifications of this pattern see Murray and Hjort, 1912.

invariably been lowered as near to bottom as feasible, so as to sample the whole column of water. As yet we have not attempted a quantitative survey of any particular stratum, though, from the nature of the case, the hauls in the shallow coastal zone have been confined to a thin layer of water.

The results of the vertical hauls are supplemented by the much more numerous horizontal hauls, made with various nets and covering the gulf generally at most seasons of the year. Inasmuch as the quantitative value of horizontal hauls has often been disputed, I must admit at once that they seldom fulfill the basic requirement of fishing through a column of water of known length. Furthermore, while the level at which an ordinary open net works for the major part of the haul can be determined within reasonable limits if it is used at moderate depths, its yield can not be depended upon as an index of the richness of the plankton at that particular depth unless corroborated by other evidence, because it may have passed through a swarm of copepods or what not on its way up or down. Horizontal hauls made in deep water, say of 500 meters or more, have little quantitative value if of short duration, because the horizontal journey made by the net may then be little if any longer than the vertical, which, of course, may be equally true of individual hauls in shallow water under exceptional circumstances. In general, however, it is safe to assume that when the horizontal distance through which the net works exceeds the vertical manyfold, as is the case for shallow hauls of considerable duration (for example, our standard of half an hour at 100 meters or shallower), considerable weight may be given to the average quantitative results of several hauls, the more so the greater the discrepancy between their horizontal and vertical portions, hauls at the surface being entirely satisfactory in this respect. In short, while everyone agrees that it is idle and misleading to expect precise quantitative data from ordinary tow nets used horizontally from a moving vessel, there is no need of going to the other extreme, as some students have done, and discarding a method that is not only so convenient but so often available when rough weather prohibits vertical hauls.[37] As a matter of fact, if they are interpreted with common sense and made at appropriate levels in the water, the catches of the horizontal tow nets often throw much light on the quantitative distribution of the animal plankton, especially in preliminary surveys. At the worst they can be trusted to reveal the existence of areas of markedly rich or of very scanty plankton, for no one can deny that the plankton must be more abundant where tows are uniformly productive than where the same nets as regularly yield little or nothing, especially at times and places when and where the larger animals occur in local shoals, which the vertical net may miss altogether but which a long horizontal tow is almost certain to encounter.

Thus, to quote only one example, Jespersen (1924) was able to demonstrate very wide differences in the abundance of zoöplankton in different parts of the Atlantic, from horizontal hauls of long duration with large nets, especially the general poverty of the so-called "Sargasso Sea."

[37] An excellent example of the light which horizontal hauls may throw on the fluctuating abundance of the plankton is afforded by the long-continued series of tow nettings carried out by the Marine Biological Laboratory at Port Erin, on the Isle of Man, under Professor Herdman's direction.

The choice of a unit and of a method of measurement by which to express the quantitative abundance of the zooplanktonic community as a whole, as distinguished from its several component groups, is a matter of real difficulty. The easiest thing to do is simply to let the whole catch settle in suitable jars or graduates until visible shrinkage ceases and to record the volume of the resulting mass. Unfortunately, however, this does not give a true measure of the actual content of the net, much less (owing to the sources of error just mentioned) of the total column of water fished through, because it likewise includes the gaps between the individual animals composing it, together with any detritus that may have been in suspension in the water. This introduces a serious error, for plankton settles more or less closely according to the shapes of the individual animals composing it, smooth, round, fish eggs, for example, packing far more closely and regularly than do copepods with their long appendages. Nevertheless, even such simple measurements as this yield rough pictures of the abundance of the animal plankton, hence they have been made for all our vertical tows and for many of the horizontal ones. Jespersen (1924) measured the volume of the catch after draining the water from it. The process may be rendered more accurate if after draining a known amount of water is added, when the resultant increase in the volume will correspond to that of the catch plus the small amount of liquid which still adhered to the plankton after the draining. I have employed this method in a few cases where it seemed likely that the direct measurement of volume would be seriously misleading because of the character of the organisms concerned. The use of the centrifuge would be still better, but this has not been attempted for the Gulf of Maine hauls.[38]

Counting is the most instructive method of estimating the catch from most points of view, though it entails much labor and time, and this is the only method by which the actual numerical strength of the several groups of animals composing the zooplankton can be learned. Various types of apparatus have been devised for this purpose, most of them by the Kiel School of Biologists, the process followed for the Gulf of Maine hauls being as follows: The catch of the vertical net (its volume having been measured as above) is first diluted to a volume of 150 cubic centimeters, well mixed, and then, while the plankton is still in suspension, 3 cubic centimeters are taken with a suitable pipette and the copepods, fish eggs, etc., counted. The ordinary pipette, familiar to every biologist, will seldom serve for taking this sample; but it is not necessary to employ the complicated "Stempel" pipette, for one of the shape shown in the accompanying sketch (fig. 36), with large rubber bulb, tube opening about 3 millimeters in diameter, and total volume of

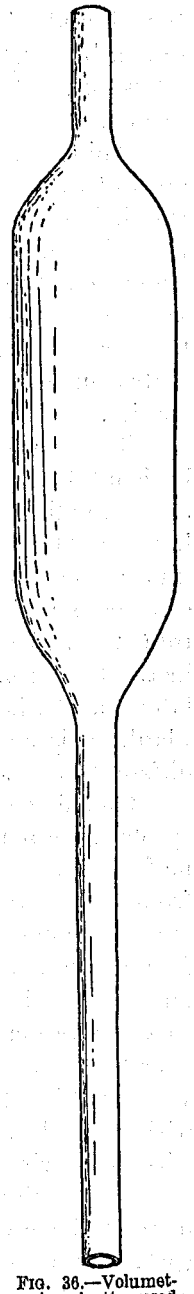

FIG. 36.—Volumetric pipette used for sampling copepods for counting

[38] For an excellent account of these and of other methods of plankton estimation see Johnstone, 1908, p. 129.

about 25 cubic centimeters, graduated as required, serves well for copepods and all smaller animals. The chief difficulty is that it is not always easy to make sure that the diluted plankton is evenly distributed in the fluid while the sample is being taken, because the various animals settle at different rates. Therefore, it is usually advisable to take two or sometimes three samples from each haul and average the results.

Animals as large as amphipods, Sagittæ, and euphausiids are seldom so numerous but that it is easy to count the entire number caught in a vertical haul, and as a rule it is necessary to remove them before taking the sample of copepods, etc., lest they clog the mouth of the pipette. Fish eggs, also, can usually be counted directly from the entire catch, though they sometimes occur in such numbers that it is necessary to take a sample for this purpose. The copepods have been counted for most of the vertical hauls, the results being discussed in the chapter on that group (p. 167). Notes on numerical strength of other animals will be found under the particular species.

The unit of measurement best available for the volume depends upon whether horizontal or vertical nets are used. If the former, calculation of the amount per hour's hauling, as employed by Jespersen (1924), can hardly be bettered; but vertical hauls lend themselves to a somewhat more exact measure, namely, the amount present under some chosen area of the surface of the sea, which is usually expressed in cubic centimeters of plankton per square meter. This would be a sufficient index to the total productivity of any locality at any given time, and hence is often extremely instructive from the biologic viewpoint; but, as I shall have occasion to emphasize later (p. 90), it does not necessarily throw any light on the density with which the plankton is aggregated, since it neglects the possible stratification of the latter at different levels.

On this basis the animal plankton of the gulf as a whole, like the phytoplankton (p. 399), is apparently at its lowest annual ebb late in February and during the first half of March, when it was only in the western basin and over a tongue extending from the Eastern Channel and eastern edge of Georges Bank northward along the axis of the eastern basin to the 100-meter contour off Grand Manan (fig. 37) that we found as much as 75 cubic centimeters per square meter in 1920. Nor did we make any rich hauls then even in these comparatively productive zones, judged by midsummer standards (p. 83). In all other parts of the gulf at the time, both inshore and over the basin, except as just qualified, and on Georges Bank as a whole, the water supported less than 25 cubic centimeters of plankton per square meter of sea surface, with several of the catches too small to measure, while on one occasion (off Cape Elizabeth, March 4, station 20059) the vertical net yielded nothing whatever.

If the minimal catches of February and March, 1920 (less than 25 cubic centimeters), be credited with 15 cubic centimeters of zoöplankton per square meter (probably an excessive estimate), the average for the whole gulf at this season was only about 40 cubic centimeters, contrasted with about 100 cubic centimeters in midsummer, and the distinction between rich and barren was decidedly more sharply marked than we have found it during the more productive seasons of the year.

The few data available suggest that April sees a general augmentation in the amount of animal plankton across the southern half of the gulf from the mouth of Massachusetts Bay to the coastal bank off Cape Sable, including the eastern part of Georges Bank. Over this zone the plankton volumes per square meter averaged about 100 cubic centimeters during the second and third weeks of that month in 1920; but north of a line from Cape Cod to Cape Sable, where diatoms were flowering freely (p. 385), our hauls, horizontal as well as vertical, certainly yielded no larger amounts of animal plankton in April than in March and an unmistakable decrease in the amount of zoöplankton took place from March to April in the northeastern part of the basin coincident with the local flowering of diatoms. However, the swarms of microscopic plants which are then present make quantitative measurements of the larger forms difficult or even impossible, both by clogging the meshes and by overshadowing the copepods, etc., in the catches of the tow nets.

Unfortunately we have not been able to follow the planktonic cycle through the whole of any one spring. But if the May state of 1915 represents the normal sequence to the April state of 1920 (a reasonable working hypothesis unless shown to be false), the zooplankton increases to volumes of 200 to 235 cubic centimeters off Massachusetts Bay and northward toward Cape Elizabeth, on the one hand, and in the eastern basin off German Bank, on the other, during the last half of April and first half of May, as tabulated elsewhere (Bigelow, 1917, p. 312), an increase caused by the tremendous production of copepods which succeeds the vernal flowering of diatoms (p. 41). In fact, it will probably be no exaggeration to set the average volume of zooplankton per square meter by the last of May at 100 or more cubic centimeters for the whole gulf outside the 50-meter contour and north of the Cape Cod-Cape Sable line,[39] with the exception of the coastal zone from Penobscot Bay eastward, where the water still remained extremely barren on May 11 and 12 (volumes of 10 to 20 cubic centimeters at stations 10275 and 10276).

Except for this barren zone, where the catches have been so small as hardly to be measurable, the gulf as a whole probably supports a greater mass of animal plankton during the last week of May and the first part of June than at any other season, though we have few quantitative records for the latter month. The considerable number of vertical hauls made in July and August during the summers of 1912 to 1916 (listed in table on p. 84) make it possible to outline with some confidence the major geographic variations in the amount of zooplankton present in the gulf in midsummer.

During the summer of 1914, which may serve as representative, the animal plankton was most plentiful (volumes of 100 cubic centimeters or more per square meter) in three distinct and separate regions, which I have described elsewhere (Bigelow, 1917, p. 308, fig. 91)—first, over a belt running diagonally across the gulf from the Massachusetts Bay-Cape Cod region to the northeast corner of the basin off the mouth of the Bay of Fundy, as outlined on the accompanying chart (fig. 38); second, over the northeast corner of Georges Bank; and, third, from Cape Sable out across the northern channel to Browns Bank, which, on the evidence of the horizontal hauls, should include German Bank, because of the Pleurobrachia which we

[39] We have no quantitative data for May and June from Georges Bank.

found swarming there in 1912, 1913, and 1914 (p. 19).[40] While 1914 is the only summer for which we have quantitative data from the offshore banks, all the most productive (100+cubic centimeters) of the summer hauls of 1913, 1914, 1915, and 1916[41] were likewise similarly concentrated in the Cape Cod–Bay of Fundy belt just outlined (fig. 38). So uniformly productive has this "rich zone" proved in summer that only 3 of the 25 vertical hauls, which we have made there in June, July, and August, have failed to yield upwards of 100 cubic centimeters of animal plankton per square meter, although the waters both immediately to the north and to the south of it have often proved decidedly barren, as the chart illustrates. The average volume of plankton for all the vertical summer hauls in this rich zone has been nearly 170 cubic centimeters per square meter including those for 1916 (an exceptionally rich year), and more than 150 cubic centimeters if the 1916 hauls are omitted.

*Approximate volume of plankton per square meter of sea surface. July and August hauls, 1912 to 1916*

| Year | Station | Volume in cubic centimeters | Depth |
|---|---|---|---|
| | | | *Meters* |
| 1912 | 10002 | 250 | 119 |
| | 10004 | 50 | 55 |
| | 10007 | 65 | 265 |
| | 10008 | 50 | 41 |
| | 10011 | 20 | 110 |
| | 10015 | 10 | 37 |
| | 10021 | 10 | 110 |
| | 10022 | 30 | 82 |
| | 10025 | 80 | 91 |
| | 10027 | 30 | 165 |
| | 10031 | 30 | 128 |
| | 10035 | Trace. | 73 |
| | 10036 | 30 | 165 |
| | 10038 | 20 | 73 |
| | 10043 | 15 | 165 |
| | | | *Fathoms* |
| 1913 | 10087 | 180 | 128 |
| | 10089 | 80 | 183 |
| | 10090 | 120 | 164 |
| | 10092 | 160 | 219 |
| | 10095 | 60 | 37 |
| | 10096 | 120 | 91 |
| | 10098 | 70 | 55 |
| | 10099 | 30 | 37 |
| | 10100 | 220 | 165 |
| | 10101 | 100 | 73 |
| | 10102 | 90 | 128 |
| | 10103 | 70 | 73 |
| | 10104 | 90 | 146 |
| | 10105 | 55 | 110 |
| 1914 | 10213 | 210 | 110 |
| | 10214 | 120 | 175 |
| | 10215 | 60 | 70 |
| | 10216 | 30 | 70 |
| | 10218 | 50 | 500 |
| | 10223 | 170 | 75 |
| | 10224 | 240 | 55 |
| | 10225 | 30 | 260 |
| | 10226 | 200 | 85 |
| | 10227 | 50 | 220 |
| | 10229 | 170 | 100 |
| | 10230 | 140 | 50 |
| | 10243 | 100 | 55 |
| | 10244 | 15 | 50 |
| | 10245 | 60 | 110 |
| | 10246 | 200 | 190 |
| | 10247 | 10 | 30 |
| | 10248 | 100 | 190 |
| | 10249 | 105 | 220 |
| | 10250 | 350 | 145 |
| | 10253 | 60 | 140 |
| | 10254 | 200 | 260 |
| | 10255 | 70 | 175 |
| 1915 [1] | 10304 | 275 | 200 |
| | 10306 | 110 | 140 |
| | 10307 | 165 | 235 |
| 1916 | 10340 | 125 | 45 |
| | 10341 | 250 | 80 |
| | 10342 | 250 | 55 |
| | 10344 | 225 | 80 |
| | 10345 | 200 | 150 |
| | 10346 | 200 | 62 |

[1] For a list of the hauls for other months of this year see Bigelow, 1917, p. 314.

Contrasting with the rich belt, the entire coastal zone of the gulf, from Cape Ann on the south and west to Grand Manan Island at the mouth of the Bay of Fundy on the east and north, has invariably proved far less productive of zoöplankton in midsummer—never with more than 90 cubic centimeters per square meter, usually

[40] These ctenophores had shrunk in the preservative to only a fraction of their natural bulk before the vertical hauls were measured.

[41] In 1916 the zooplankton was unusually abundant in the waters off Cape Cod and in the southwest corner of the gulf in July, a fact discussed on p. 97.

with less than 70 cubic centimeters, and ranging from this down to traces too small to measure. North of Cape Ann the general rule has been the closer to land in summer the scantier the catch (fig. 38), while the coastal belt as a whole then sup-

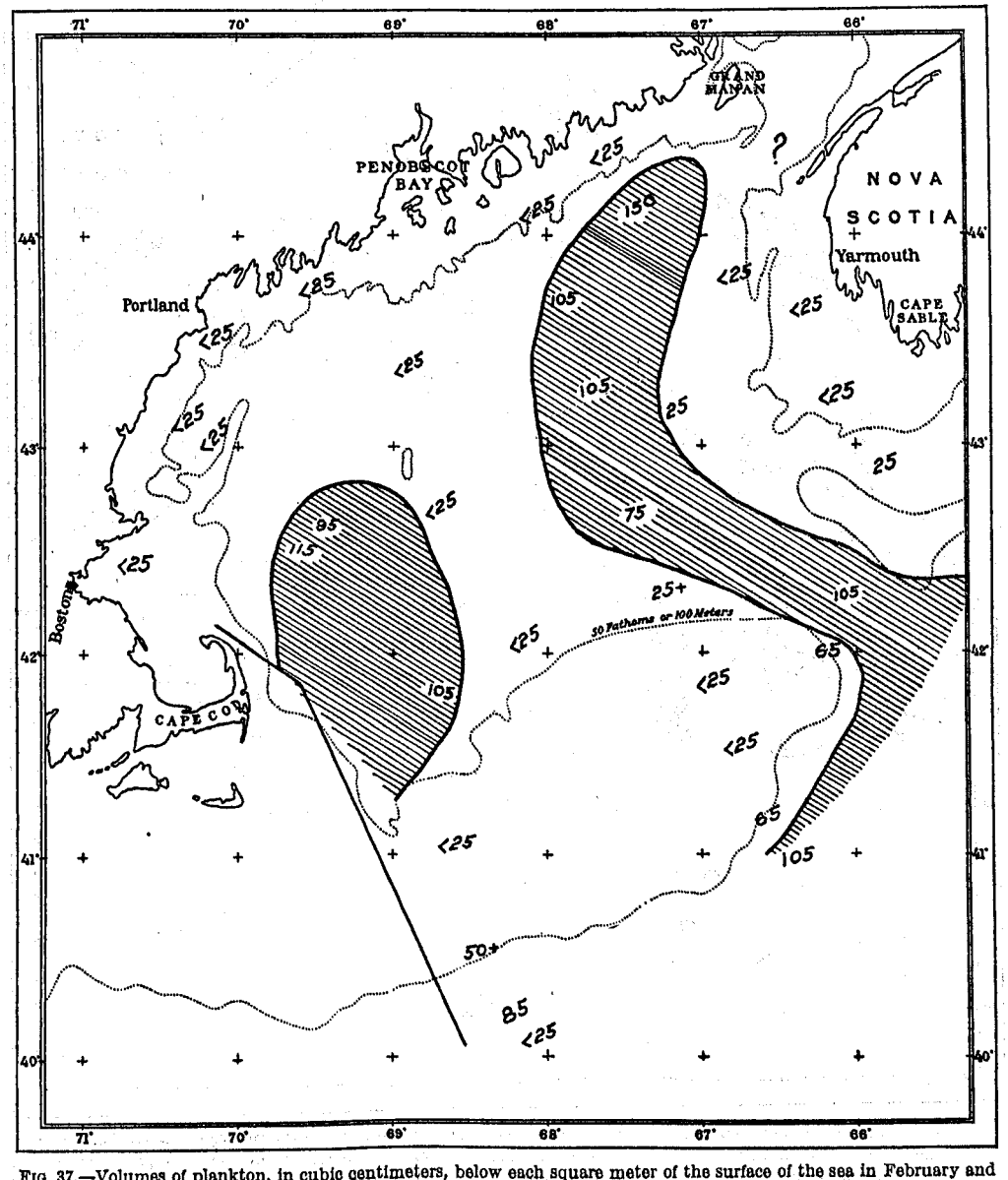


FIG. 37.—Volumes of plankton, in cubic centimeters, below each square meter of the surface of the sea in February and March, 1920, as calculated from the catches made in the vertical hauls. In the shaded area the volumes were uniformly greater than 75 cubic centimeters.

ports less zooplankton to the north and east of Cape Elizabeth than to the south and west, with the Grand Manan Channel the most barren part of the open gulf. We have no quantitative data from the immediate vicinity of the western coast of Nova

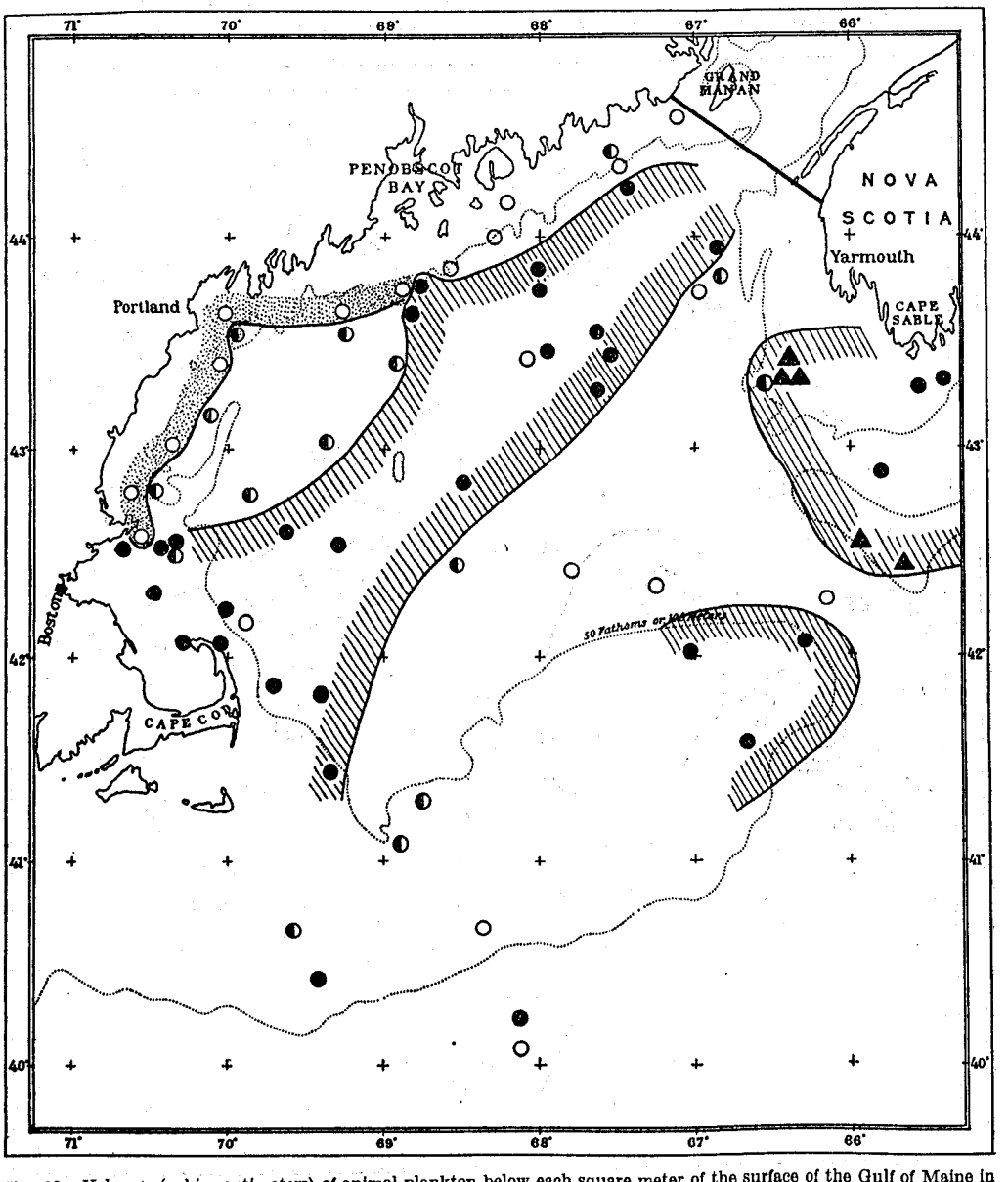


FIG. 38.—Volumes (cubic centimeters) of animal plankton below each square meter of the surface of the Gulf of Maine in summer, as calculated from the vertical hauls made in 1912–1916. ●, 100 cubic centimeters or more per square meter; ◐, 50 to 100 cubic centimeters or more per square meter; ○, 50 cubic centimeters or less per square meter; ▲, stations where horizontal hauls showed an abundant plankton, but where no vertical hauls were made.

The hatched curve includes areas where we have usually found more than 100 cubic centimeters per square meter; the stippled curve where the catches have usually been less than 50 cubic centimeters per square meter.

Scotia, but in 1914 the neighborhood of Lurcher Shoal proved far less productive than the deeper basin near by.

Were all parts of the gulf equally favorable for the existence and multiplication of animal plankton, the catches of the vertical hauls might be expected to vary in direct ratio to the depth—that is, to the amount of water filtered by the net—and, speaking broadly, there usually is more plankton below any given unit of the sea's surface in moderately deep water (say 50 meters or more) than in very shoal water. Notwithstanding the comparative barrenness of the greater part of the coastal zone, however, the regional differences in the abundance of plankton in the Gulf of Maine do not correspond closely to the depth; nor can they be correlated with the distance from the coast, *per se*, because we have repeatedly found the plankton very plentiful in moderate depths both near land, as in Massachusetts Bay, and close in to Cape Sable, and as far offshore as Georges and Browns Banks, while, on the other hand, some of our deep hauls have proved unproductive in spite of the considerable length of the column of water fished through. Such, for example, was the case in the Eastern Channel and the neighboring part of the basin in July, 1914. In fact, the vertical hauls made in the southeastern deep of the gulf in summer (July 23, 1914, station 10225, and June 25, 1915, station 10298), have both proved extremely barren, with only 30 to 70 cubic centimeters per square meter in spite of the considerable depths of the hauls (175 to 260 meters), showing that both in June of 1915 and July of 1914 the rich zone was bounded on the east by much less prolific waters. It is on the strength of these hauls that I have laid down the demarcation between the two zones on the accompanying chart (fig. 38), but the volume of plankton present in the water varies so widely from season to season and from year to year that the lines must not be drawn too finely in plotting its regional variations, and the future alone can show whether it is regularly characteristic of the summer season for such a barren wedge to separate the rich waters to the north from the equally prolific shallows of Georges and Browns Banks.

The presence of more than 200 times as much animal plankton beneath each square meter of the surface of the sea at the mouth of Massachusetts Bay on July 20, 1916, as in water nearly twice as deep in the Grand Manan Channel on August 19, 1912 (only a trace), and the fact that there were 200 cubic centimeters per square meter in 85 meters of water on the northeastern edge of Georges Bank on July 24, 1914, but only 50 cubic centimeters per square meter that same day in the Eastern Channel, 15 miles distant, where the depth was 220 meters, illustrate the contrast between productive and barren waters.

Vertical hauls in the Massachusetts Bay region, the only part of the gulf where our data warrant even a tentative account of the quantitative fluctuations that take place during late summer and autumn, suggest a diminution in the volume of zooplankton during the late summer followed by an autumnal increase, which was so considerable in 1915 that there was over twice as much plankton per square meter in water only 80 meters deep by the end of October as we had found at a neighboring station in 140 meters depth two months previous.

*Zoöplankton volumes, mouth of Massachusetts Bay*

| Date | Station | Depth of haul in meters | Approximate volume, cubic centimeters per square meter | Date | Station | Depth of haul in meters | Approximate volume, cubic centimeters per square meter |
|---|---|---|---|---|---|---|---|
| July 10, 1912 | 10002 | 119–0 | 250 | Aug. 31, 1915 | 10306 | 140–0 | 110 |
| July 19, 1916 | 10340 | 45–0 | 125 | Oct. 1, 1915 | 10324 | 140–0 | 150 |
| Do | 10341 | 80–0 | 250 | Oct. 27, 1915 | 10338 | 80–0 | 250 |
| Do | 10342 | 55–0 | 250 | Mar. 1, 1920 | 20050 | 150–0 | ±25 |
| Aug. 9, 1913 | 10087 | 128–0 | 180 | Apr. 9, 1920 | 20090 | 120–0 | 10 |
| Aug. 22, 1914 | 10253 | 140–0 | 60 | May 4, 1915 | 10266 | 125–0 | 270 |

Evidence that a similar augmentation spread generally throughout the coastal waters west of Penobscot Bay in 1915 is afforded by volumes as great as 100 to 150 cubic centimeters per square meter off Penobscot Bay, off Cape Elizabeth, and near the Isles of Shoals during that October. However, we have yet to learn whether this increase is an annual event, nor does our experience suggest that it extends east of Penobscot Bay, because vertical hauls yielded only 30 cubic centimeters per square meter off Mount Desert Island and 20 cubic centimeters off Machias on October 9 (stations 10328 and 10327).

We have made no quantitative hauls in the gulf during the period between October and late February, but the comparative scantiness of the yields of the horizontal nets in Massachusetts Bay during the cold months of 1913 (Bigelow, 1914a) and at all our inshore stations from Cape Cod to Yarmouth, Nova Scotia, in December, 1920, and January, 1921, points to an ebbing zoöplankton as characteristic of the coastal belt in late autumn and early winter, leading progressively to the extremely barren state of the water typical of the first weeks of spring (p. 82). Hauls made near Mount Desert Island and in the northeast corner of the gulf from January 1 to 5, 1921 (stations 10497, 10500, and 10502) were equally unproductive,[42] but I hesitate to conclude from this that the water was actually so barren there, because horizontal hauls were hardly more productive in that general region in March, 1920, although the vertical nets yielded large catches, a fact suggesting that the former missed the level at which the plankton was most concentrated. However this may be, it seems that in winter and early spring the zoöplankton is far more plentiful in the western side of the basin than near shore, because we made a rich horizontal catch there on December 29, 1920 (station 10490), a rich vertical haul (though a rather scanty horizontal) on February 23, 1920 (station 20049), and a rich horizontal and a comparatively rich vertical on March 24 of that year (station 20087).

The results of both vertical and horizontal hauls point to the Massachusetts Bay region and the neighboring part of the basin, on the one hand, and to the deeps off Lurcher Shoal and the eastern part of Georges Bank, on the other, as the parts of the gulf uniformly most productive of zoöplankton; while the deep water in the

[42] Yield of half an hour's haul with a ½-meter net was only about 100 to 150 cubic centimeters in each case at 50–0, 75–0, and 150–0 meters.

southeastern corner of the gulf, where vertical hauls have yielded only 25 to 65 cubic centimeters per square meter on four visits (March 11, 1920, station 20064; April 17, 1920, station 20112; June 25, 1915, station 10298; and July 23, 1914, station 10225), although made in depths of from 200 to 340 meters, and the coastal zone east of Penobscot Bay would seem to be the least productive.

Recapitulating for the Massachusetts Bay region, the zooplankton is at its scantiest some time in March, earlier or later according to the forwardness of the season; it increases very rapidly in amount during May, reaches its annual maximum of abundance late in May or early in June, when there may be from 10 to 20 times as much animal life in the water (200 to 300 cubic centimeters per square meter) as in March, and wanes in August. A second well-marked pulse is noticeable in September, culminating in October, after which the plankton diminishes once more. Our experience during the cold months of 1912 and 1913 (Bigelow, 1914a) was that a moderate amount of zooplankton is to be found in the bay throughout the winter, but that it suddenly declines almost to the vanishing point late in February or early in March.

The plankton passes through a corresponding quantitative cycle throughout the entire coastal zone from Massachusetts Bay to the mouth of the Bay of Fundy; but although the waters east of Cape Elizabeth are as barren as the region from the Isles of Shoals to Cape Cod in early spring, they are never as productive of zoöplankton as is the latter in late spring and early summer, and, consequently, the difference between the seasons of maximum and of minimum abundance of plankton is not as great.

The fact that the northern corner of the eastern basin proved extremely barren on April 20, 1920 (station 20100), whereas we have found an abundant animal plankton there in summer, suggests that this region, like Massachusetts Bay, is the site of a wide seasonal fluctuation, with a brief period of barrenness in spring coincident with the vernal flowerings of diatoms. This applies likewise to the shallows off Cape Sable and over the eastern part of Georges Bank, where the zooplankton is extremely plentiful in midsummer but sparse in March.

So far as our experience goes, the seasonal fluctuation in the amount of plankton present is widest in the neighborhood of the Isles of Shoals, with a range of from practically *nil* to upwards of 300 cubic centimeters per square meter. The coastal belt along the outer islands east of Penobscot Bay illustrates the opposite extreme. Here the catches of the vertical nets may be but little larger (25 to 30 cubic centimeters per square meter) in summer (the richest season) than in spring, and we have only once made a reasonably productive vertical haul in this zone (70 cubic centimeters per square meter at station 10098).

The quantitative fluctuations are also comparatively narrow from season to season, or at least no pronounced impoverishment takes place in spring, in the deep waters of the western basin, so that the plankton of that part of the gulf is classed as "rich," not "scanty," the year around, as shown by the following table.

*Volumes of plankton per square meter, western basin*

| Date | Cubic centimeters of zooplankton per square meter | Date | Cubic centimeters of zooplankton per square meter |
|---|---|---|---|
| Feb. 23, 1920 | 175 | June 26, 1915 | 250 |
| Mar. 24, 1920 | 95 | July 15, 1912 | 65 |
| Apr. 18, 1920 | 150± | Aug. 22, 1914 | 200 |
| May 5, 1915 | 250 | Aug. 31, 1915 | 165 |

There is, likewise, less fluctuation with the seasons on the western part of Georges Bank than on the eastern. The largest volume of plankton per square meter yet recorded for the Gulf of Maine was 425 cubic centimeters in the eastern side of the basin on September 1, 1915 (station 10309), while the smallest was a bare trace. In fact, the animal population may be so sparse locally that a vertical haul may catch nothing at all, as has been our experience at several stations along the coast of Maine and in the Grand Manan Channel (p. 84); but even then, a half hour's tow with the horizontal net has invariably yielded a few copepods or other animals, proving that although the planktonic community may fall to a very low ebb, indeed, at its season of scarcity, it never vanishes wholly from any part of the gulf at any time of the year.

## DENSITY OF ASSOCIATION OF THE ZOÖPLANKTON

A statement of the volume of zooplankton existing in the total column of water below any chosen unit of sea area—e. g., each square meter—serves to illustrate the total regional and seasonal production of the gulf; but unless the water in question be very shallow, it throws little light on the density in which the animals concerned are congregated, because the catch of the vertical haul may be distributed generally over a column so long that even a considerable volume of plankton might mean only a sparse population. To meet this need, another unit of measurement is required, the one usually employed in other seas, and of which I have made use in previous reports (Bigelow, 1915 and 1917), being the volume of plankton present in each cubic meter of water. This, of course, is simply the product of the volume per square meter of sea surface divided by the depth (in meters) covered by the haul in question.

Were the zooplankton of the gulf uniformly distributed from the surface down to bottom, this simple calculation would not only "establish the relative richness of different regions in plankton, and hence in food for the pelagic fishes" (Bigelow, 1915, p. 327), a question naturally of much importance in the economy of the gulf, but go far to explain many biologic problems even more far reaching. Unfortunately for the statistician, however, such is not the case, all our experience tending to show that the zooplankton is often more or less stratified and that the degree of stratification varies widely from place to place with the time of day and with the change of the seasons. Consequently, the results always require analysis in the light of any information bearing on the vertical distribution of the planktonic communities represented in the catches in question. Otherwise one is apt to be led to conclusions so widely astray as to be worse than none.

On the whole, it is in late winter and early spring, when the physical characters of the sea water are most uniform vertically and when its vertical stability is least, that the zooplankton of the Gulf of Maine and of other boreal seas most nearly approaches vertical uniformity of distribution. At this season, as illustrated by the March cruise of 1920, the volumes of zooplankton present in the water are so small in all parts of the gulf, and the depth of water through which it was distributed at the more productive localities is so considerable, that the volume per cubic meter (by direct calculation) was only 0.7 to 1 cubic centimeter even where the plankton was densest—for instance, in the eastern and northeastern troughs of the basin, in the Eastern Channel, and over the northeastern and southeastern parts of Georges Bank. It ranged down from this to a minimum of practically nothing in the deep water in the southeastern corner of the gulf, the average for all stations being about 0.4 cubic centimeters, which is something less than half the summer average by the lowest possible estimate. Nor is it likely that this calculation seriously understates the density of aggregation of the zooplankton for any large portion of the gulf in March, because there was little evidence of vertical stratification during that month.

*Zooplankton volumes per cubic meter, March, 1920*

| Locality | Date | Station | Cubic centimeters per cubic meter | Locality | Date | Station | Cubic centimeters per cubic meters |
|---|---|---|---|---|---|---|---|
| Western Basin | Feb. 23 | 20049 | 0.6 | Georges Bank: | | | |
| Off Gloucester | Mar. 1 | 20050 | .1 | Northeast part | Mar. 11 | 20065 | 0.3 |
| Near Cashes Ledge | Mar. 2 | 20052 | .1 | Eastern part | do | 20066 | .3 |
| Central Deep | Mar. 3 | 20053 | .3 | Southeast part | Mar. 12 | 20067 | .5 |
| Eastern Basin | do | 20054 | .4 | Southeast slope | do | 20068 | .7 |
| Off Mount Desert Rock | do | 20055 | .5 | Northeast part | Mar. 13 | 20070 | 1.0 |
| Off Mount Desert Island | do | 20056 | .2 | Eastern Channel | do | 20071 | .7 |
| Off Matinicus Island | Mar. 4 | 20057 | .2 | Fundy Deep | Mar. 22 | 20079 | .1 |
| Off Seguin Island | do | 20058 | .5 | Off Machias (Me.) | do | 20080 | .4 |
| Near Isles of Shoals | do | 20060 | .2 | Northeast trough | do | 20081 | .7 |
| Off Isles of Shoals | Mar. 5 | 20061 | .1 | Off Yarmouth, Nova Scotia | Mar. 23 | 20083 | .4 |
| Off Boston | do | 20062 | .5 | Off German Bank | do | 20086 | .5 |
| North of Georges Bank | Mar. 11 | 20063 | .1 | Western Basin | Mar. 24 | 20087 | .4 |
| Southeast Deep | do | 20064 | .0 | Off Boston | Apr. 6 | 20089 | .4 |

With the advance of the spring the concentration of the plankton is augmented both by the increase in the total amount present in the gulf, just remarked, and by its stratification at one level or another. Not only does the first of these factors raise the volume per cubic meter to 2 to 4 cubic centimeters at the very least by midsummer in such prolific though rather shallow regions as the waters off Cape Cod, the neighborhood of Cape Sable, and the eastern part of Georges Bank,[43] but stratification may result in a far denser concentration of the plankton at some particular level while rendering other strata of water far more barren than the ostensible volumes per cubic meter (as derived from the usual calculation) would call for. We have encountered this phenomenon in its most extreme form in the deeper parts of the gulf, but experience has shown that a greater or less tendency on the part of the zooplankton, as a whole, to congregate at some particular level is to be expected anywhere in the gulf in summer, leaving the shoaler as well as the deeper

[43] Plankton volumes per cubic meter, calculated from our summer and autumn hauls, have been published already; those for the year 1913 in Bigelow, 1915, p. 326; for 1914 and 1915 in Bigelow, 1917, pp. 310 and 314; and for 1916 in Bigelow, 1922, p. 136.

layers of water practically deserted except in regions where active vertical currents keep the water thoroughly mixed. Therefore, it is usually safe to assume that the plankton is far more densely aggregated at some level, though perhaps only through a very narrow vertical zone, than the calculation of volume per cubic meter would indicate; but since we have occasionally found it rather uniformly distributed from the surface downward, even in the more stagnant parts of the gulf, no hard and fast rule can be laid down in this respect.

Vertical stratification may result from a definite vertical migration of various animals toward the surface during the hours of darkness and downward again at sunrise, but quite apart from this phototropic phenomenon, which has often been described in other seas and which I have touched on above (p. 24), the tendency frequently shown by animals of different systematic groups (one of which may be and often is far more plentiful than the others) to segregate at different levels during the warm half of the year—copepods, for instance, at one depth and Sagittæ at another—often causes a very uneven quantitative distribution of the plankton vertically in summer and early autumn.

In July and August, 1913, for instance, it was invariably the shoaler subsurface haul that yielded the largest catch at stations where two such were made with the horizontal nets at different levels, even after making allowance for the use of nets of different types, although the reverse might have been expected because of the greater volume of water strained by the deeper hauls.[44] Evidently, then, the zooplankton was usually densest in the upper strata of water during that particular summer, say from 20 meters down to 50 at the localities of record, which were generally distributed over the offshore parts of the northern half of the gulf, and it was decidedly less abundant below 75 meters on the one hand or in the surface stratum on the other. This rule did not hold during the summer of 1914, however, when it was sometimes the deeper haul (stations 10215, 10246, 10248, and 10254), sometimes the shallower (stations 10214 and 10249), that yielded the largest catches, but usually one was much more productive than the other, as illustrated by the following table:

*Comparative catches of horizontal hauls of half an hour's duration (reduced to a column 1 square meter in cross section) during July and August, 1914*

[The depth is the level at which the major part of the haul was made [a]]

| Locality | Station | Date | Depth in meters | Volume in cubic centimeters |
|---|---|---|---|---|
| Southwest Basin | 10214 | July 19 | 30 | 3,550 |
| | | | 150 | 250 |
| Georges Bank, northwest part | 10215 | July 20 | 30 | 150 |
| | | | 60 | 375 |
| Southeast Deep | 10225 | July 23 | 60 | 150 |
| | | | 240 | 125 |
| Eastern Basin | 10249 | Aug. 13 | 50 | 2,180 |
| | | | 175 | 500 |
| Northeast Deep | 10246 | Aug. 12 | 50 | 150 |
| | | | 150 | 1,000 |
| Off Mount Desert Rock | 10248 | Aug. 13 | 50 | 150 |
| | | | 150 | 1,250 |
| Western Basin | 10254 | Aug. 22 | 75 | 150 |
| | | | 225 | 625 |

[a] Assumed to have fished through three quarters of a mile.

[44] For discussion of these hauls, with necessary corrections, and for the tabulated results, see Bigelow, 1915, p. 327.

Although it was often the deeper haul that yielded the larger amount of plankton, all the very rich tow-net catches (2,000 cubic centimeters or more) made in the gulf during that summer (six in number; see Bigelow, 1917, p. 312) were from depths of 100 meters or less, with the average volume (about 900 cubic centimeters) of all the subsurface catches made shoaler than 100 meters, almost three times that of the deeper hauls (about 350 cubic centimeters), although the latter fished through a longer column of water on their journey down and up. Thus, it seems that the gulf is usually richer in zooplankton above than below 100 meters depth during the summer season, and very rich catches were made in vertical hauls shoaler than that at the few stations which the *Grampus* occupied in the gulf during July, 1916 (p. 92; Bigelow, 1922, p. 136).

With the plankton often concentrated at some one level, it becomes more or less a matter of chance whether a net fishing horizontally hits or misses the richest zone. Consequently, the yields of the two sorts of hauls, horizontal and vertical, are often far from parallel. When there is a wide discrepancy between the two it has usually been in favor of the horizontal net (especially in deep water), for we have usually made at least one horizontal tow in the productive stratum between 40 and 100 meters at each station, whereas the vertical catch mirrors the plankton content of the barren strata combined with that of the rich. Occasionally, however, the tables are turned, as was the case on July 23, 1914, on the eastern part of Georges Bank (station 10223), where the volume per cubic meter taken by the vertical haul was more than seven times as great (2.2 cubic centimeters) as that taken by the horizontal haul (about 0.3 cubic centimeter) although the depth of water—that is, the length of the column fished through—in the case of the former was only 82 meters, whereas the latter worked for about three-quarters of a mile. Thus, the vertical net must have passed through water much more productive than the level at which the horizontal net was fishing. In 1913 and 1914, too, the richest catches with horizontal nets were not at the stations where the volumes per square meter or per cubic meter were largest, as calculated from the vertical hauls.

It follows from these facts that while the ostensible volumes per cubic meter may be a satisfactory index to the density of the planktonic population of the Gulf of Maine in winter or early spring, and in summer at stations where no stratification is apparent from the yields of the horizontal hauls, and while this calculation may approximate the truth in very shallow waters generally at most times of year, as a rule it greatly understates the actual maximum density of aggregation of the plankton in deep water, making such regions appear much less prolific as feeding grounds for pelagic fishes than their richer layers actually are, while crediting far too high a plankton content to their more barren strata, as I have pointed out elsewhere (Bigelow, 1917).

Owing to the tendency of the zooplanktonic community as a whole to congregate in the upper 100 meters of water during the warm months, but at the same time to keep some few meters down (p. 24), the seasonal difference between the volumes of plankton per cubic meter present in March, on the one hand, and in July and August, on the other, is actually much greater than the ratio arrived at by any calculation which fails to take account of its vertical stratification. A more

nearly correct picture of the summer state results from the assumption that the entire catch of zooplankton in the vertical net at that season was taken below 10 meters at each station, but that it was only one-third as dense as the ostensible volume per cubic meter below 100 meters, and correspondingly concentrated above that level. The results of such a calculation for 1914 are given in the following table:

*Volumes of plankton per cubic meter (in cubic centimeters) between the depths of 10 and 100 meters, July to August, 1914*[1]

| Locality | Date | Station | Total depth in meters | Volume per cubic meter if calculated as above, in cubic centimeters | Volume per cubic meter if uniformly distributed, in cubic centimeters |
|---|---|---|---|---|---|
| Off Cape Cod | July 19 | 10213 | 110 | 2.2 | 1.90 |
| Southwest Basin | do | 10214 | 175 | 1 | .68 |
| Georges Bank: | | | | | |
| Northwestern part | July 20 | 10215 | 70 | 1 | .85 |
| Southwestern part | do | 10216 | 70 | .5 | .43 |
| Eastern part | July 23 | 10223 | 75 | 2.6 | 2.40 |
| Northeastern part | do | 10224 | 55 | 5.3 | 4.30 |
| Northeastern part | July 24 | 10226 | 85 | 2.6 | 2.30 |
| Southeast Deep | July 23 | 10225 | 260 | .2 | .12 |
| Eastern Channel | July 24 | 10227 | 220 | .4 | .23 |
| North Channel | July 25 | 10229 | 100 | 1.9 | 1.70 |
| Near Cape Sable | do | 10230 | 50 | 3.5 | 2.80 |
| Do | Aug. 11 | 10243 | 55 | 2.2 | 1.80 |
| German Bank | Aug. 12 | 10244 | 50 | .4 | .30 |
| Northeast trough | do | 10246 | 190 | 1.7 | 1. |
| Off Machias, Me | do | 10247 | 30 | .5 | .33 |
| Off Mount Desert Rock | Aug. 13 | 10248 | 190 | .7 | .52 |
| Eastern Basin | do | 10249 | 220 | .8 | .48 |
| Off Penobscot Bay | Aug. 14 | 10250 | 145 | 3.3 | 2.40 |
| Off Cape Ann | Aug. 22 | 10253 | 140 | .6 | .42 |
| Western Basin | do | 10254 | 260 | 1.4 | .77 |
| Center of gulf near Cashes Ledge | Aug. 23 | 10255 | 175 | .6 | .40 |

[1] For tables of the volume per cubic meter for July and August, 1913, and for May to October, 1915, see Bigelow, 1915, p. 328, and 1917, p. 314.

The most instructive feature of this table is its demonstration that, although the total amount of plankton present below any given unit of the sea's surface rules larger in the deeper parts of the gulf than in the shallower water, as a rule it is most densely aggregated in the coastal belt within the 150-meter contour and in the shallows of Georges Bank, no matter which calculation be employed. This was true, also, in the summer of 1913. In fact, the northeastern part of the deep basin, where the water has proved very productive on several occasions in summer and early autumn, as well as in late spring, has been the only exception to this rule for any time of year.

Enough hauls have now been made to show that the zooplankton (especially the Crustacea) is usually most densely congregated, summer after summer, in four rather definite areas—(1) over the eastern end of Georges Bank, (2) in the shoal water south of Cape Sable, (3) in the deep northeastern basin, and (4) off Massachusetts Bay out to the 100-meter contour (fig. 39). At the other extreme the western and southern parts of the deep basin and the coastal belt inside the 100-meter contour east of Penobscot Bay have never yielded as much as 2 cubic centimeters of plankton to the cubic meter of water at any season by either mode of calculation, nor has the water over the coast bank west of Nova Scotia proved productive except for the Pleurobrachia swarms so characteristic of that locality (p. 19).

The most abundant concentrations of plankton which we have yet encountered in the Gulf of Maine have been off Cape Cod on May 26, 1915 (station 10279, nearly 4 cubic centimeters per cubic meter); on the eastern part of Georges Bank on July

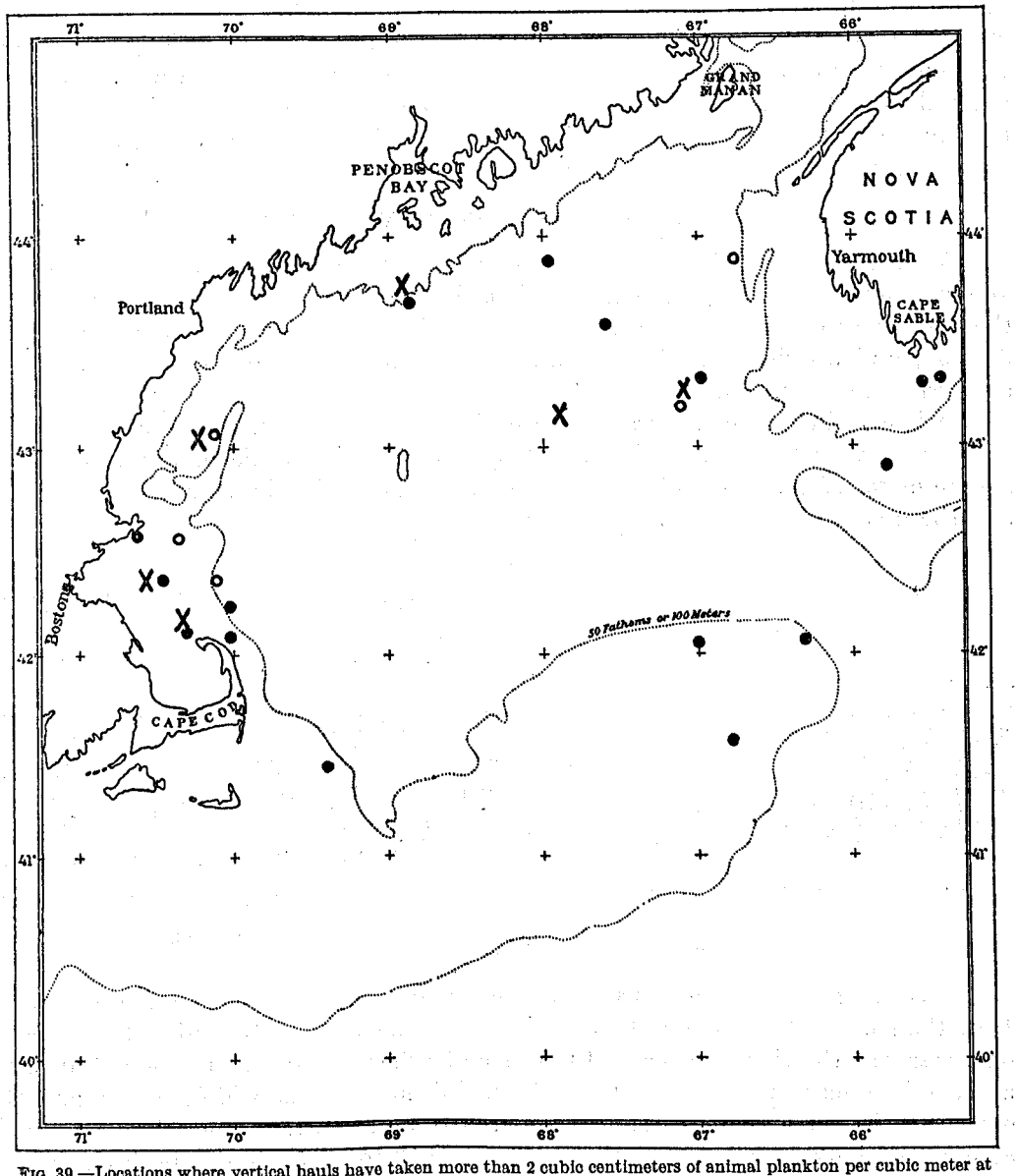


FIG. 39.—Locations where vertical hauls have taken more than 2 cubic centimeters of animal plankton per cubic meter at different seasons, calculated by the method described on page 94. X, September to November; O, May; ●, July to August 15

23, 1914 (station 10224, about 5 cubic centimeters per cubic meter); in the eastern basin on September 1, 1915 (station 10309, approximately 3.5 cubic centimeters per cubic meter, assuming some stratification); and at the mouth of Massachusetts Bay

in July, 1916 (station 10342, at least 4.5 cubic centimeters per cubic meter); but occasionally it is much more dense than this at one level or other, the volumes just listed being the minima possible. For example, a horizontal haul of 15 minutes' duration at 40 meters depth, with a net 1 meter in diameter, off Cape Cod on July 22, 1916 (station 10344), yielded over 6 liters, mostly copepods, which is equivalent to about 12 cubic centimeters per cubic meter for the water fished through (the tow covered about one-third of a mile). In fact, it was the richest tow-net catch we have ever made in the gulf, although the vertical haul indicated only about 2.8 cubic centimeters of plankton per cubic meter.

## ANNUAL VARIATIONS IN ABUNDANCE

Annual variations in the amount of zooplankton living in the waters of the gulf will mirror the long-time fluctuations in its physical state—may, indeed, be the best clue to such—and exert an important influence on the growth, local reproduction, and distribution of the adults of such important plankton-feeding fishes as herring, mackerel, and pollock.

It is certain that considerable fluctuations of this sort in the plankton do take place from year to year, as illustrated by the following table of the volumes per square meter of sea surface for corresponding localities in the summers of 1913–14 and the first week of September, 1915.[45]

| Locality | Stations | | | | Plankton, in cubic centimeters per square meter | | | |
|---|---|---|---|---|---|---|---|---|
| | 1912 | 1913 | 1914 | 1915 | 1912 | 1913 | 1914 | 1915 |
| Off Cape Ann | [1] 10002 | 10087 | 10253 | 10306 | 250 | 180 | 60 | 110 |
| Western Basin | [1] 10007 | 10089 | 10254 | 10307 | 65 | 80 | 200 | 165 |
| Near Cashes Ledge | ------- | 10090 | 10255 | ------- | ------- | 120 | 70 | ------- |
| East Basin, west side | 10028 | 10092 | 10249 | 10309 | 30 | 160 | 105 | 425 |
| German Bank | ------- | 10095 | 10244 | 10311 | ------- | 60 | 15 | 45 |
| Off Lurcher Shoal | 10031 | 10096 | 10245 | 10315 | 30 | 120 | 60 | 50 |
| Northeast corner of basin | 10036 | ------- | 10246 | ------- | 30 | ------- | 200 | ------- |
| Off Petit Manan Island | 10033 | 10098 | 10247 | 10316 | [2] 25 | 70 | 10 | 12.5 |
| Off Mount Desert Rock | ------- | 10100 | 10248 | ------- | ------- | 220 | 100 | ------- |
| Off Penobscot Bay | 10038 | 10101 | 10250 | [3] 10318 | 20 | 100 | 350 | 25 |
| Average | ------- | ------- | ------- | ------- | 74 | 123 | 117 | 117 |

[1] July hauls.
[2] From horizontal hauls.
[3] A few miles west of the corresponding stations, 1912 to 1914.

According to these measurements the volume of the plankton was greater in 1913 than in 1914 at all but two stations. As between 1913 and 1915, however, one year was the richer at some, the other at other localities. However, since the average is practically the same (or at least did not differ as widely as the probable error) for the three years, there was apparently no important general change in the amount of plankton existent in the gulf from 1913 to 1915, though both these years were apparently decidedly more productive, on the whole, than was 1912 during the corresponding months (Bigelow, 1915, p. 337). During the summer of 1916 (a year of low temperatures) the waters off Massachusetts Bay proved more produc-

[45] Although different types of nets were used during these years, the results, reduced to the common standard, will allow a rough and ready comparison.

tive than we have previously found them at that season, thanks to the abundance of large Calanus, with volumes of plankton per square meter for six stations along the shore from Cape Ann to southern Cape Cod (July 19, 1922) ranging from 135 to 250 cubic centimeters (average 208 cubic centimeters), and it was then that we made the exceptionally rich horizontal net haul already mentioned (p. 96).

Notes on the yearly numerical fluctuations in the local stock of the commoner copepods will be found under the discussions of the several species.

## PLANKTON AS FOOD FOR WHALES AND FISHES

We might, figuratively, conceive of the swimming and floating life of the sea as a pyramid, with the microscopic plants as its base and the large sharks and whales as its apex, the latter few in numbers but each enormously destructive of the smaller organisms on which it preys. The general thesis that the smaller plankton, animal and vegetable, is practically the sole food supply for young marine fishes no longer requires further proof or argument. It likewise so serves for many species of fish when adult, especially for the schooling fishes, such as herrings, menhaden, mackerel, shad, and the like. The large adult gadoids, too, feed on plankton to a greater extent than is generally appreciated. The great basking shark (*Cetorhinus maximus*), which is still an occasional visitor to the gulf, is exclusively a plankton feeder throughout its life, and most of the northern whalebone whales have long been known to subsist largely on the smaller pelagic animals—several of them exclusively so—a fact widely heralded in zoological textbooks.

The literature dealing with the dependence of the larger marine animals on the plankton has grown to formidable dimensions in the last half century, but very few first-hand observations have yet been made on the relationships between fish and plankton in the Gulf of Maine. So far as these go, however, they show that what is true of north European seas in this respect applies equally to American waters, as, indeed, might have been prophesied, allowing for the differences between the composition of the planktonic communities of the two sides of the north Atlantic Ocean.

In the Gulf of Maine the groups of Crustacea that are of chief importance in the diets of adult fishes and whales are the copepods and the euphausiids. Examination of stomach contents at European whaling stations has proved that instead of subsisting indiscriminately on all sorts of plankton, large and small (as has sometimes been taken for granted), or on pteropods (as the Arctic right whale often does), the planktonic part of the diet of the other species of whalebone whales common in boreal seas consists almost exclusively of these two groups of Crustacea. While there is ample ground for the choice of a crustacean rather than a molluscan diet in the greater abundance of the former than of the latter on both sides of the north Atlantic, it is possible that the whales in question may voluntarily prefer the harder and more oily shrimps and copepods.

The finback (*Balænoptera physalus* Linné), commonest whale in the Gulf of Maine to-day, eats a mixed diet of plankton and fish, devouring the latter, particularly the herring, in great numbers, but probably depending more on the smaller pelagic animals in the long run. A considerable number of finback stomachs have

now been examined by various observers, and in every case (apart from fish) they have been packed with euphausiids and with euphausiids alone. Thus G. M. Allen (1916, p. 200) writes that "on the Newfoundland coast stomachs of several finbacks which I examined contained enormous quantities of the small shrimplike schizopod *Thysanoessa inermis.*" Lillie (1910), too, found the stomach contents of several finbacks taken off Ireland in July and August to consist altogether of euphausiids (in this case Meganyctiphanes) and of fish; and in more than 150 finbacks killed at the Belmullet whaling station on the west coast of Ireland, Burfield (1913) and Hamilton (1915 and 1916) found nothing but immense numbers of these same pelagic shrimps (Meganyctiphanes), with occasional fragments of fish. Nor have I been able to find any definite evidence that this whale ever succeeds in capturing copepods, or any of the smaller plankton for that matter, though, according to Murie (1865), the stomach of one captured near Gravesend, England, contained fragments of medusæ as well as of Crustacea. In short, euphausiids, and these alone, are its support, apart from fish.

The Atlantic humpback (*Megaptera nodosa*), which is not uncommon off the New England coast, though never so plentiful there as the Atlantic right whale once was or as the finback now is, subsists on much the same diet as the latter—viz, fish and pelagic shrimps (euphausiids)—while Andrews (1909) found its close ally, the Pacific humpback, feeding on the latter alone; smaller planktonic animals have never been found in humpback stomachs so far as I am aware.

The blue whale, or sulphur bottom (*Balænoptera musculus*), which is not uncommon along the coasts of the Gulf of Maine and is numerous in Newfoundland waters, is even more dependent on euphausiids than are the two whales previously mentioned, for it is not known to eat fish at all, on the one hand, or copepods, on the other. All the sulphur-bottom stomachs recently examined (a considerable number in the total) have been packed with euphausiids alone—Thysanoessa in whales from Newfoundland (G. M. Allen, 1916), Meganyctiphanes in others taken off the west of Ireland (Lillie, 1910; Burfield, 1913; Hamilton, 1915 and 1916), and Euphausia in the Antarctic (Liouville, 1913). The destructiveness of these huge mammals is illustrated by Collett's (1877, p. 161) statements that sulphur-bottom stomachs frequently contain 300 to 400 liters of shrimps, and that occasionally one is taken crammed with up to 1,200 liters of Thysanoessa. Andrews (1916), too, writes that this whale feeds exclusively on euphausiids; Millais (1906), however, credits it with a copepod diet.

The North Atlantic right whale (*Eubalæna glacialis*), once common in New England waters though now unhappily nearly extinct there (and with it the glories of the New England coastwise whale fishery), subsists largely on euphausiids, notably on Thysanoessa (Kükenthal, 1900). Collett (1909), indeed, found nothing else in right whales taken off the Hebrides and off Iceland. The only eyewitness's account of its feeding habits in New England waters, for which we must turn back nearly 200 years (Dudley, 1734, quoted by G. M. Allen, 1916) tells of "this whale, in still weather, skimming on the surface of the water to take in a sort of reddish spawn or brett, as some call it, that at some times will lie on the top of the water for a mile together." From its geographic situation and mode of occurrence this

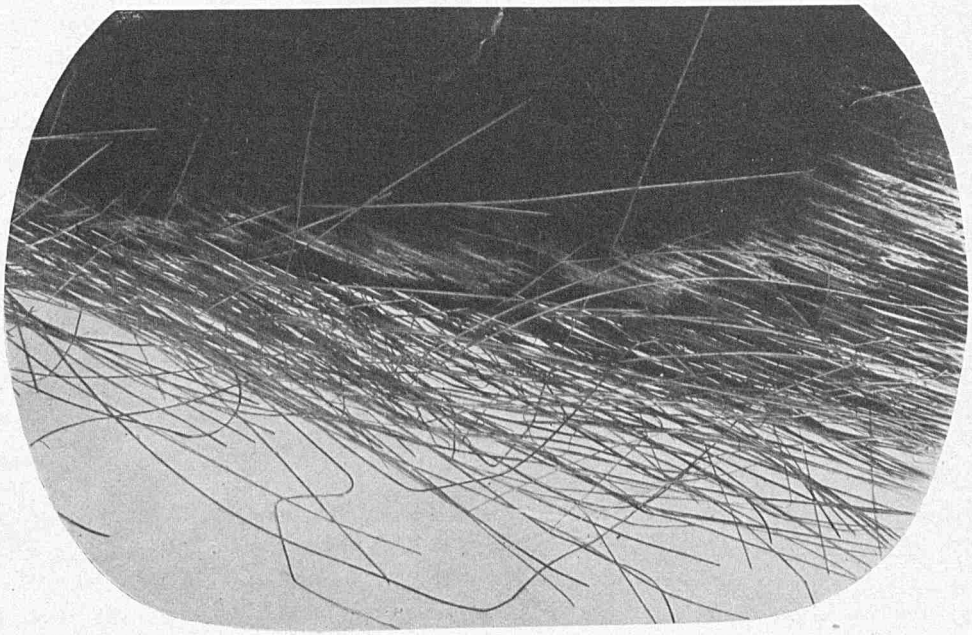

FIG. 40.—Marginal fringe on one of the whalebone plates of a finback whale (*Balænoptera physalus*) from the Gulf of St. Lawrence. Natural size

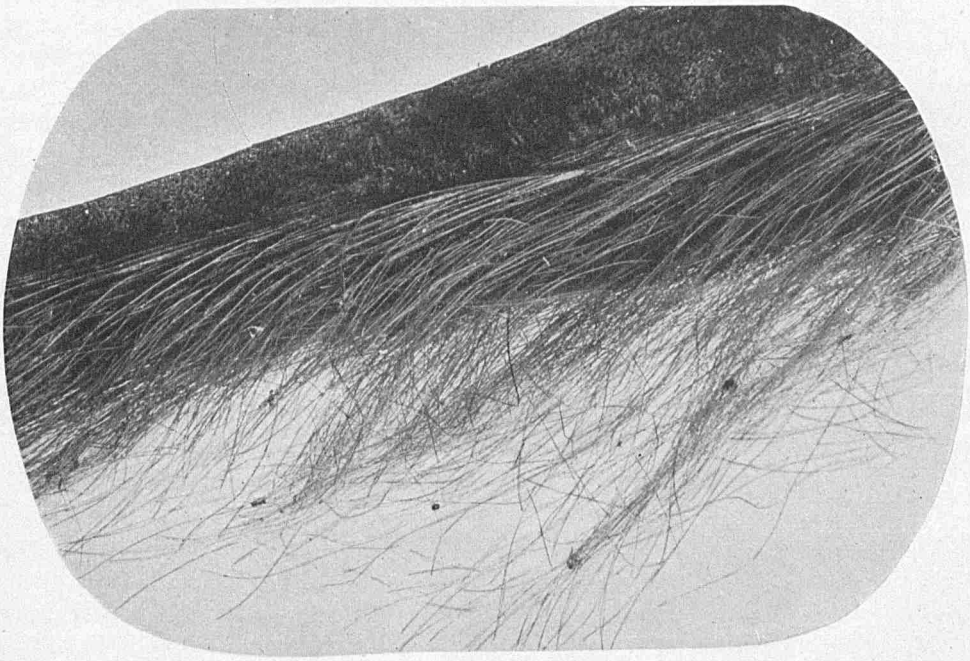

FIG. 41.—Marginal fringe on one of the whalebone plates of a pollock whale (*Balænoptera borealis*) from the Gulf of Maine. Natural size

was probably Calanus or other copepods. Unfortunately, little is known of the habits of the Atlantic right whale, but it is well established that the pollock whale (*Balænoptera borealis*) feeds chiefly on copepods at certain times and places, for Collett (1886, p. 26) found the stomachs of several, killed off East Finmark in July, "filled with a fine gritty mass, which consisted entirely of *Calanus finmarchicus*," with the Calanus occurring "in great numbers and in a tolerable state of preservation" among the hairs of the baleen plates; and since he gives excellent figures of these copepods, their specific identification is assured. In West Finmark, however, this same whale has been reported as subsisting chiefly on euphausiids (Collett, 1886). Kükenthal (1900) likewise states that it feeds on these shrimps, and Andrews (1916) writes that most of the specimens which he opened in Japanese waters contained euphausiids only, while a few had eaten fish. G. M. Allen (1916) and Millais (1906) are therefore fully justified in crediting it with a mixed copepod (Calanus and Temora) and euphausiid diet.

The fact that only two of the species of whalebone whales known to occur in the Gulf of Maine eat copepods, while all feed on euphausiids, seems not to have been appreciated, though established past cavil by the analyses of stomach contents just mentioned.

It is, I think, impossible to explain this preference for shrimps on the ground of voluntary selection, for while it is not unreasonable to suppose that whales follow the schools of Crustacea rather than the soft-bodied Sagittæ, cœlenterates, or mollusks, copepods (and particularly Calanus) usually abound in northern seas wherever euphausiids are plentiful, and finback, pollock whale, and right whale must gather them all, the large with the small, into their open and expectant mouths as they swim. With whales, however, just as with tow nets of different mesh, the fineness of the straining apparatus determines what part of the total planktonic population is retained to serve as food. If the whalebone be coarse or comblike, as it is in the finback whale (fig. 40), the blue whale, and the humpback, objects as small as copepods are driven out through the sieve with the outrush of water when the mouth is closed, while the much larger euphausiids are retained. The pollock whale, however, possesses, in the "unusually fine and curly, almost wooly bristles" on the inner side of the baleen plates (fig. 41), so well described by Collett (1886, p. 263), a straining apparatus so much more efficient as to sift out the copepods as well as the larger crustaceans. This is true also of the right whale, with its silky-fine baleen (Collett, 1909, p. 95) and ability to strain large volumes of water with little effort.[46] However, the finer the strainer and the better adapted for the capture of the smaller animals, the less effective it is for capturing fish, as witness the dependence of the pollock whale on plankton contrasted with the piscivorous habit of the finback.

The fertility of the gulf as a feeding ground for whales depends, then, not only on the total amount and local concentration of the plankton or on its nature—whether or not crustacean—but equally on the size of the units of which it is composed. Thus, the abundance of Calanus in Massachusetts Bay and off northern Cape Cod

[46] For a general account of its feeding habits see Beddard, 1900.

provided an ideal pasture for the Atlantic right whale, of which it once fully availed itself, as early records show, but not for the finback, for which the bay is a desert except when herring or other fish are schooling there or during the brief local swarmings of euphausiids. It is common knowledge among fishermen that finbacks seldom appear in any numbers anywhere in the gulf except when in pursuit of fish. It is also probable that the volumetric preponderance of copepods over euphausiids in most parts of the gulf explains the comparative rarity there of the shrimp-eating blue whale with its very coarse whalebone.

Before leaving this subject I should emphasize that the large, easily recognized, pelagic amphipod Euthemisto, locally and temporarily so abundant, has never been recognized in the stomachs of any of the whalebone whales. Is it not eaten? And if not, why not?

It is probable that copepods are the main dependence of the basking shark (*Cetorhinus maximus*), whose gillrakers perform the same service in filtering its crustacean food from the water taken into the mouth as do the baleen plates of the whalebone whales. I need merely point out that the alimentary canal of a specimen taken at West Hampton Beach, Long Island, on June 29, 1915, contained a large quantity of minute Crustacea, "whose reddish bodies lent color to the entire mass" (Hussakof, 1915, p. 26).

When we turn to the dependence of the smaller fishes on crustacean plankton, we are confronted by a published record so embarrassing for its wealth (mostly, however, based on experiences in European seas) that I shall lay only a few of the more typical examples before the reader, and those most applicable to the Gulf of Maine.

The unicellular plants have been described repeatedly in zoological literature as the chief food supply of the youngest larval fishes, and a long list of diatom and peridinean species has, at one time or another, been recorded as having been eaten by them; but recent studies of the stomach contents of large series of various common fishes in the English Channel (Lebour, 1919, 1920, 1924) have proved that although many fish do take more or less diatoms, peridinians, etc., few depend on these unicellular forms to the extent that has been generally supposed, even during their earliest larval stage (cf. also Hjort, 1914, p. 205), but begin to take larval copepods and other microscopic animals by the time the yolk sac is absorbed, if not sooner. However, Lebour found the young European flounder (*Pleuronectes flesus*) subsisting chiefly on the green flagellate genus Phæocystis up to the time of its metamorphosis, with other flatfish taking a considerable proportion of peridinians and diatoms, and this proved true of young herring less than 10 millimeters long, which also take Halosphæra.

Outside of the littoral zone, where the mummichogs (*Fundulus heteroclitus*) consume diatoms as well as other small organisms indiscriminately, the menhaden is the only important Gulf of Maine fish that continues throughout life to subsist chiefly on diatoms and peridinians, with the most minute of Crustacea and other animals. These it is enabled to sift out of the water by its fine branchial sieve, as Peck (1894) long ago described.[47]

[47] On the feeding habits of the menhaden see also Bigelow and Welsh, 1925, p. 123.

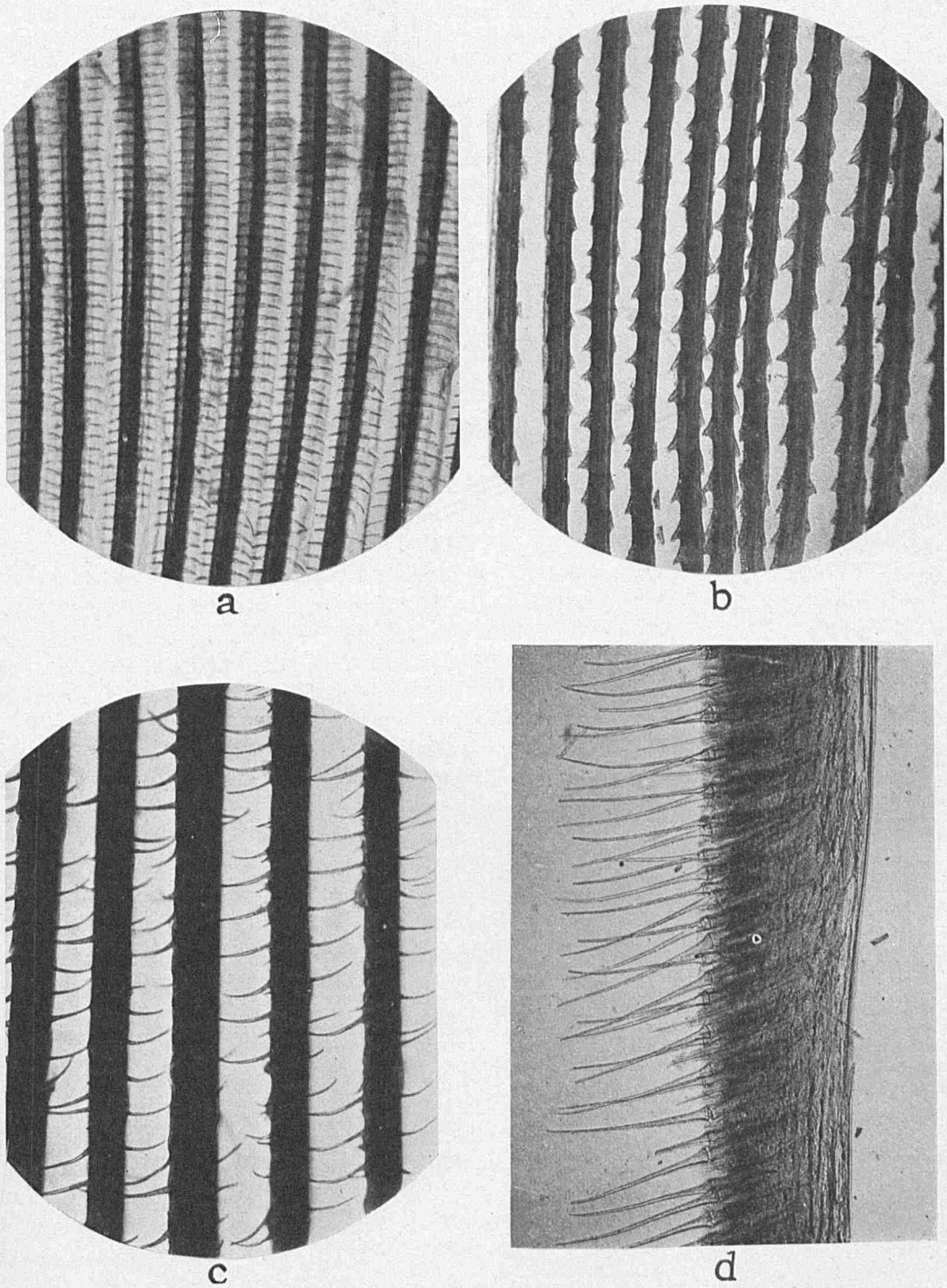


FIG. 42.—Segments of the branchial sieves of three common fishes that feed on plankton. **a**, Menhaden, *Brevoortia tyrannus;* **b,** herring, *Clupea harengus;* **c**, mackerel, *Scomber scombrus;* **d**, mackerel, side view of gill raker, with gill spines. × 25

The menhaden has no rival among the fishes of the gulf in its utilization of this pelagic vegetable pasture (indeed, Peck (1894) so noted); nor is any other local species possessed of a filtering apparatus comparable to that of the menhaden (fig. 42a) for fineness and efficiency, though in European waters its relative, the sardine (*Clupea pilchardus*), feeds equally on microscopic plankton as well as on copepods. The Pacific anchovy also feeds on diatoms and peridinians as well as on zoöplankton (W. E. Allen, 1921, p. 54).[48]

Among clupeoids, as among whalebone whales, a direct relationship obtains between the fineness of the sieve through which the water taken in through the mouth is strained—in this case the gillrakers—and the minimum size of the organisms that can be retained and utilized; everything smaller passes through. Even the menhaden (though most of its food is microscopic) is unable to capture the very smallest organisms, such as coccolithophorids and infusoria; and the herring and alewife, with coarser sieves (fig. 42b), subsist chiefly on organisms with a longest dimension of at least 0.5 millimeter (copepods or larger animals), which they select individually and not by swimming open-mouthed, as the menhaden does [49] (Bigelow and Welsh, 1925, p. 103).

Experience with the tow net shows that if diatoms are plentiful enough they will be picked up by a coarse mesh, and the mackerel, which carries broadly spaced spines on the long rakers on the foremost gill arch (figs. 42c and 42d) consumes more or less pelagic plants, and especially the diatom genera Lauderia and Chætoceros, in British waters in winter when the fish are in deep water (Bullen, 1908 and 1912). I know of no direct evidence, however, that mackerel ever feed on diatoms or peridinians in the Gulf of Maine unless taken accidentally along with other plankton.

Pelagic Crustacea of one kind or another form the major part of the diet of the adults of all plankton-feeding fishes other than the menhaden in the Gulf of Maine and in northern seas generally, and of the fry of all Gulf of Maine fishes, the sundry crustacean members of the plankton appearing in the lists of stomach contents with monotonous regularity. For most species of fish, indeed, this is true from the earlier larval stages onward, as just noted. In fact, Lebour (1920 and 1924) found that herring, and others as well, devour larval mollusks, small Crustacea, etc., even before the yolk sac is absorbed. Thereafter the diet of all the species of fish which she studied consisted chiefly of the latter, most frequently of copepods, adult and larval, and of Cladocera, with decapod and other larvæ playing a secondary rôle and microscopic plants taken only vicariously, except that some larval herring had fed to some extent on unicellular organisms.

Perhaps the most interesting result of Lebour's work, apart from her general conclusion (1920, p. 262) that copepods, other Entomostraca, and molluscan larvæ are the chief food of nearly all young sea fish, is that "usually each species of fish selects its own favorite food, to which it keeps, indiscriminate feeding seldom or never taking place."

It would not be safe to postulate the precise larval food of any of the Gulf of Maine flounders from that of their European congeners, so widely do the latter

[48] Mullets also subsist largely on unicellular plants, but they are only accidental visitors to the cool waters of the Gulf of Maine.
[49] It is easy to watch them doing so in the aquarium.

differ among themselves in their choice of diet,[50] nor were any of the gadoids common to American and North European waters studied by Lebour. However, several North Sea members of the family were feeding on small copepods—mainly Pseudocalanus—and Calanus was taken freely as the larval fishes grew in size. Dannevig, too, writes that numbers of newly-hatched cod placed under observation at the hatchery at Flödevigen, Norway, took no food until the yolk sac had been absorbed, and thereafter fed from the first on such animals as mollusk larvæ, nauplii, etc., "seeming to despise the innumerable diatom forms which are likewise present in the water" (Dannevig, 1919, p. 48). Evidently this applies to the American cod as well, because young fish 12 to 20 millimeters long have been observed to feed exclusively on copepods at Woods Hole (Bumpus, 1898), and according to Mead (1898) copepods are likewise the favorite diet there for young sculpins and sand launce (Ammodytes).

Judging from the general similarity between the planktonic communities of the two sides of the North Atlantic, there is every reason to assume that the dietary lists which Lebour gives for very young herring and mackerel would apply as well (in a general way) to the Gulf of Maine as to the North Sea. For the former species this diet consisted chiefly of larval gastropods, with copepods, particularly Pseudocalanus, next in importance, barnacle (Balanus) and bivalve larvæ in smaller amounts, and with unicellular forms, as just noted (curiously enough, out of about 1,000 specimens 8 to 15 millimeters in length over 700 contained no food); while the young mackerel had eaten copepod nauplii (chiefly Calanus and Temora) and crustacean (probably copepod) eggs, with a few ostracods, euphausiid larvæ, and even young fish.

In Norwegian waters, according to Nordgaard (1907), the older herring feed chiefly on euphausiids and copepods, especially the genera Calanus and Temora, with ostracods, tintinnids, larval barnacles, Halosphæra, and other small members of the plankton consumed in smaller amounts. Copepods and euphausiids together constitute almost the entire diet of the herring in the Gulf of Maine, with fish smaller than about 4 inches long taking chiefly the former and larger ones taking both at localities where they are available (Moore, 1898; Bigelow and Welsh, 1925, p. 103). Young herring, taken while feeding on the surface at Woods Hole, have been found full of copepods of several species. What is known of the feeding habits of the alewife (*Pomolobus pseudoharengus*), and blueback (*Pomolobus æstivalis*), is to the effect that they also subsist chiefly on these two groups of Crustacea during the part of the year when they are in salt water, and that shad (*Alosa sapidissima*) subsist on copepods and mysid shrimps. Mackerel, in the Gulf of Maine, have also long been known to feed greedily on calanoid copepods (the "red feed" or "cayenne" of which fishermen often describe the fish as crammed full). I have found fish, taken off Cape Elizabeth, August 12, 1912, packed with *Calanus finmarchicus* and *Pseudocalanus elongatus;* Goode (1884a) found the stomachs of mackerel, taken off Portland in 1874, full of large copepods and euphausiids. The schools of mackerel frequenting the Bay of Fundy have also been reported as following and preying upon the shoals of

[50] So far as I can learn there is no record of the stomach contents of the larval witch (Glyptocephalus) or American plaice (Hippoglossoides).

shrimp (Meganyctiphanes and Thysanoessa), which so often appear on the surface there (S. I. Smith, 1879). Richard Rathbun (1889) reports some of the mackerel that he examined from the southern fishery (off the coasts of Virginia and Maryland in latitudes 37° 48′ N. and 38° 01′ N.; longitudes 74° 13′ and 74° 21′ W.) in 1887, as full of copepods and others of euphausiids. Dr. W. C. Kendall found the mackerel on the northern part of Georges Bank feeding on Calanus (probably also Pseudocalanus) and on small brown copepods (probably Temora), as well as on other planktonic animals (Bigelow and Welsh, 1925, p. 201); and many more instances might be mentioned where copepods, euphausiids, or both, have been reported as mackerel food in American waters as well as in European. The larger copepods also enter to some extent into the dietary of the American pollock (*Pollachius virens*) in the Gulf of Maine—witness Willey's (1921) record of a fish taken near Campobello Island with many *Euchæta norvegica* in its stomach and some *Calanus finmarchicus* and *C. hyperboreus*.

Euphausiid shrimps offer as important a food supply for this large and active gadoid as do small fish. Thus, Moore (1898) describes pollock at Eastport as feeding chiefly on them and following them in their appearances and disappearances. Willey (1921) also found pollock feeding on euphausiids at Campobello. Welsh saw great numbers of pollock schooling in pursuit of shrimps and greedily feeding on them in the neighborhood of the Isles of Shoals in spring, as I have described elsewhere (Bigelow and Welsh, 1925, p. 401).

In the North Sea region medium-sized specimens of this gadoid (there called the "coalfish" or "green cod") eat considerable amounts of small pelagic Crustacea, such as Calanus, Temora, Centropages, Pseudocalanus, cirriped larvæ, ostracods (Evadne), as well as euphausiids, in addition to the small fish and to the bottom-dwelling worms and Crustacea that form their staple food.

It is probable that when euphausiids descend toward the bottom in the Gulf of Maine they become food for the hakes (genus Urophycis), which, in the main, are shrimp eaters (Bigelow and Welsh, 1925, p. 450), and which are known to gorge on euphausiids along the outer part of the continental shelf (Hansen, 1915, p. 94). So, too, the deep-water fish Macrourus (Bigelow and Welsh, 1925, p. 470); and even as typical a bottom and fish feeder as the cod is known to adopt a pelagic life and to feed on euphausiids off the north and east coasts of Iceland (Paulsen, 1909, p. 39; Schmidt, 1904). The common skate (*Raja erinacea*) also feeds on copepods on occasion (Linton, 1901, p. 279), though this is quite exceptional for it.

In North European waters the hyperiid amphipods are a major food for herring (Brook and Calderwood, 1886), but although the genus Euthemisto is widespread and at times locally abundant in the Gulf of Maine, I have found no record of herring feeding on it there, and have recognized none in the stomachs of the Gulf of Maine herring I have opened. Probably this is due to the mutual geographic distribution of the two animals, Euthemisto being most plentiful offshore and herring along the coast. These amphipods may be expected to form an important item in the diet of herring on Georges Bank. This is certainly true of the mackerel there, for Dr. W. C. Kendall found the latter feeding on Euthemisto on the northern part of the Bank in August, 1896 (Bigelow and Welsh, 1925, p. 201). Mackerel taken

near Woods Hole in summer have also contained Euthemisto (Rathbun, 1896), and Rathbun (1889) found mackerel feeding largely on amphipods off Virginia and Maryland in the spring. European mackerel also feed on Euthemisto, and, generally speaking, the latter are no doubt more important as a source of fish food over the outer part of the shelf and along the continental edge (where they are constantly abundant) than in the inner part of the Gulf of Maine; but no evidence is at hand that any Gulf of Maine fishes depend on them to the extent to which the long-finned albacore (*Germo alalunga*) does off the French coast (Le Danois, 1921).

Whenever and wherever the larvæ of decapods are plentiful, all plankton-eating fishes feed on them greedily. In the Gulf of Maine the "megalops" stages of crabs are of considerable economic importance in this respect. Linton (1901 and 1901a), for example, found many young herring at Woods Hole full of them, and Doctor Kendall in his field notes records some of the fish in certain schools of Georges Bank mackerel as packed with them, almost to the exclusion of other plankton. Larval shrimps, prawns, and lobsters also enter regularly into the dietary of many fishes in European seas, notably the various clupeoids. In Swedish waters the young stages of bottom-dwelling shrimps are regularly consumed by mackerel (Nilsson, 1914); no doubt also in the Gulf of Maine, though definite information so far available on this point is scanty. Adult decapods hardly enter into the plankton of the Gulf of Maine, except for the large deep-water prawn Pasiphæa, which may be expected to prove a staple food for hake (genus Urophycis).

Sagittæ are eaten in considerable quantity by mackerel. Rathbun (1889), for example, found them in fish taken in the southern fishery off the Middle Atlantic States, and Doctor Kendall, in his notes, records some of the mackerel taken on the northern part of Georges Bank during the last week of August, 1896, as full of them. Sagittæ probably will be found to enter largely into the dietary of the mackerel in Massachusetts Bay in early summer; in fact, whenever they are plentiful (p. 18). They are also eaten by herring in Scottish waters (Brook and Calderwood, 1886), and probably this will also prove to be the case to greater or less extent in the Gulf of Maine. In the Adriatic Sagittæ are also the chief dependence of the young goosefish (*Lophius piscatorius*) while it lives pelagic (Stiasny, 1911), which probably applies equally to the Gulf of Maine goosefish (Bigelow and Welsh, 1925, p. 526). The American pollock also consumes Sagittæ in the Gulf of Maine (Willey, 1921).

The shell-bearing pteropods, represented locally by *Limacina retroversa*, are seldom plentiful enough in the Gulf of Maine to be of much importance as a possible food supply for the schooling fishes there, but when these mollusks do swarm mackerel would no doubt feast on them, for they are an important food for this fish off the west coast of Ireland (Massy, 1909). According to Rathbun (1889), mackerel eat *L. retroversa* off the Middle Atlantic States, and mackerel taken off No Mans Land (an islet near Marthas Vineyard) have been recorded as full of them. In Norwegian waters, according to Nordgaard (1907), this pteropod also enters into the dietary of the herring, but as Limacina seems not to have been recorded as herring food elsewhere in north European seas it probably does not so serve to any great extent in the Gulf of Maine. Lebour's (1920) observation that young fish of various species not only had not eaten Limacina, although the latter were plentiful in the tow, but

refused them when offered in the aquarium is interesting as suggesting that the mackerel is rather an exception in feeding on this pteropod. Naked pteropods are never plentiful enough in the Gulf of Maine to be of any importance as food for larger animals.

Probably all the fishes that eat plankton consume buoyant fish eggs to some extent, the amount taken depending chiefly on the local supply conveniently available. Thus Brook and Calderwood (1886) found fish ova more or less prominent in the diet of Scottish herring, according to the varying abundance of the eggs in the plankton, and although fish eggs have not actually been recorded from the stomachs of Gulf of Maine herring there is no reason to doubt that the latter consume them whenever they offer, as is also the case in the English Channel, according to Lebour's (1924a) recent studies.

Mackerel also are known to take eggs of their own as well as of other species. Fish eggs have been found in small mackerel from the Woods Hole region, to quote a local instance, and in European seas medium-sized specimens of the American pollock (*Pollachius virens*) eat considerable amounts of fish eggs among other plankton.

The only groups of planktonic animals sufficiently plentiful in the Gulf of Maine to be of any importance in its natural economy, but which are not regularly consumed by its fishes in as large quantities as the supply allows, are the medusæ, siphonophoræ, and ctenophores. E. J. Allen (1908) and Goode (1884 and 1884a) record medusæ and siphonophores from mackerel stomachs; but this is exceptional, and although they may bite out pieces of large medusæ this is probably for the sake of the amphipods (Hyperia) living within the cavities of the latter (Nilsson, 1914). It would not be surprising to find mackerel gorging on Pleurobrachia in the Gulf of Maine at the places and times when this ctenophore swarms, for Andrew Scott (1924) reports mackerel in the Irish Sea full of them during one of their incursions.

The spiny dogfish (*Squalus acanthias*) feeds to some extent on ctenophores (Pleurobrachia) in spring, the fish often containing them when they first appear at Woods Hole in May; and in north European waters this troublesome little shark sometimes devours ctenophores in such quantity that their stomachs are full of them (Mortensen, 1912, p. 72, *fide* Dr. C. G. J. Petersen). The lumpfish likewise feeds regularly on medusæ and ctenophores in European waters, hence probably in the Gulf of Maine, and the sunfish (*Mola mola*), which is only an accidental visitor to the gulf, subsists chiefly on these watery organisms (Bigelow and Welsh, 1925, p. 303); but so far as is known neither the herring tribe nor any of the gadoids ever eat them—in fact, no Gulf of Maine fishes other than those just mentioned.

With the young fry of the whole fish population of northern seas dependent for their existence on the supply of plankton, it is but natural that many attempts should have been made to correlate the movements and migrations of the more important food fishes with local and temporal fluctations in the supply, either of the plankton as a whole or of such members of it as serve as the chief diet of the particular species in question, as well as with the far-reaching physical phenomena that may be looked on as the ultimate causes of such fluctuations. Thus, to mention only a couple of examples, Bullen (1908) has established at least a plausible causal

relationship between the fluctuations in the amount of zooplankton present in the sea and in the seasonal and yearly catch of mackerel, corroborated by experience for herring, also, in the Irish Sea (A. Scott, 1924); and E. J. Allen (1908) aroused an interesting discussion by his tentative hypothesis that the abundance of mackerel at any given locality depends on the amount of sunshine during the previous months, sunny weather favoring the multiplication of diatoms and thus affording a rich pasture for copepods, an abundant stock of which attracts mackerel. Dr. C. B. Wilson, in a letter, suggests that the diurnal migrations of copepods upward toward the surface at night and downward by day may be the reason why mackerel and herring most often school at the surface at night, following the daily migrations of their prey.

To attempt to connect the fluctuations in the stock or the movements of the fish population of the gulf, even of such typical plankton feeders as the herring, with variations in the supply of plankton is as yet out of the question, neither digested statistics of the catch of the former nor sufficiently definite information as to the latter having been gathered. However, it is evident that a correlation between the two must exist, and, as Dr. C. B. Wilson writes, "anything that contributes to a detailed knowledge of the presence and movements of the copepods throughout the year will give us information as to the movements and distribution of the fish," and is therefore of as direct interest to the fisherman as to the scientist.

## FOOD OF THE PLANKTON

The study of the stomach contents of the smaller pelagic animals, which together make up the zooplankton, is, as Steuer (1910, p. 622) points out, beset by many obstacles, principal among which is the rapidity with which the various organic substances are digested after being eaten, leaving as recognizable in the masticated or half-digested state only such objects as are provided with spines, bristles, etc., or with calcareous or silicious shells of characteristic outline. Then, too, it is a common experience to find whole series of animals, even of the larger species, perfectly empty.

In spite of these difficulties, however, so considerable a body of observations has been accumulated that the general diet of most of the important planktonic groups can now be stated with some confidence, and although little attention has yet been paid to the diets of the plankton of the Gulf of Maine, there is no reason to suppose that the feeding habits of its various members differ essentially from those of their north European representatives.

Among the zooplankton, as among the pelagic fishes, some species or groups are carnivorous while others depend for subsistence on the unicellular vegetable life of the high seas, but within the various groups the smaller planktonic animals are decidedly uniform in their feeding habits. Perhaps as striking an illustration of the carnivorous habit as any is afforded by naked pteropods such as *Clione limacina*, which, so far as known, live exclusively on other pelagic animals and most often on their own shell-bearing relatives (for instance, on Limacina), which they devour by thrusting the protrusible proboscis into the shell and tearing the inmate to pieces in spite of its futile efforts to escape by contracting into the smallest possible compass, as Schiemenz (1906, p. 29) has so graphically described.

Equally voracious, and far more destructive to smaller animals in the Gulf of Maine because of its greater abundance there, is the pelagic amphipod Euthemisto. The few Euthemisto stomachs which I have examined all contained copepods, often so nearly intact as to show that they had been swallowed whole and were not torn to pieces by their captor's mandibles. In seven Euthemisto upwards of 20 millimeters long, from several localities (stations 10294, 10296, and 10307), the stomachs were packed with copepods (mostly Calanus, but occasionally Temora), with more or less other crustacean débris, parts of legs, antennæ, etc., and in one instance a fish egg. The presence of an entire young Euthemisto in the stomach of one adult shows that this amphipod, like so many other marine animals, is cannibalistic when opportunity offers. Euthemisto is so large and so active that wherever it is abundant it must wreak havoc among the Calanus hordes among which it swims. Probably it materially decimates the stock of copepods existing all along the outer edge of the continental shelf (p. 165), and it may also be a serious enemy to them locally and temporarily within the gulf. Small individuals of Euthemisto feed on unicellular organisms as well as on Crustacea, specimens about 10 millimeters long[51] from the western basin, August 31, 1915 (station 10307), containing more radiolarians (Acanthometron) than copepods.

Decapod larvæ, so abundant at times in shallows and in coastwise waters, are also, as a rule, carnivorous in their later stages (*vide* Steuer's (1910, p. 631) account of zoëas devouring young fish, smaller Crustacea, etc.). Lobster larvæ also feed greedily on other young decapods of smaller size (Weldon and Fowler 1890), their cannibalistic habit being the bane of the fish-culturist. Lebour (1922), however, describes crab zoëas as also eating green plant cells, Phæocystis, and diatoms, most often Coscinodiscus among the latter. The young lobster also consumes diatoms in large amount, likewise fragments of algæ during its pelagic life (Herrick, 1896), and this is probably true of most other decapods, if not of all Crustacean larvæ, at least when they are newly hatched and until they are large enough to capture and subdue more active organisms.

Sagittæ are strictly carnivorous and so active, fierce, and well-armed that it is no wonder they are recorded as feeding on things as far apart as tintinnids, crustaceans, other Sagittæ, and young fish. Among the Gulf of Maine species, *S. maxima* is notable in this respect, for while the commoner *S. elegans* and *Eukrohnia hamata* are usually empty or contain, at most, oil globules or unrecognizable débris, I have on several occasions found *S. maxima* that had perished in the preservative while in the act of devouring animals as large as Euchæta and Tomopteris, as well as their own kind, or containing in their guts newly-swallowed copepods or smaller Sagittæ of other species. Lebour (1922 and 1923) speaks of the larval herring as frequently falling victim to Sagittæ, which may be serious enemies when as plentiful as they often are in the Gulf of Maine.

It is probable that the comparative scarcity of copepods, often remarked at the precise levels, localities, or times when Sagittæ abound, is direct evidence of the extent to which the latter may reduce the stock of their prey. But of all the members of the plankton, the most destructive to smaller or weaker animals are the

[51] Euthemisto as small as this can contain but one or two large copepods at the most.

several cœlenterates, and especially the ctenophore genus Pleurobrachia, a pirate to which no living creature small enough for it to capture and swallow comes amiss. Small Crustacea of all kinds, other cœlenterates, Sagittæ, fish eggs, and even fish of considerable size all are devoured, and so clean does it sweep the water with its trailing tentacles that wherever these ctenophores abound practically all of the smaller animals are soon exterminated.

The larger ctenophore Beroë is even more voracious, though, fortunately for the productivity of our seas, it is less numerous than Pleurobrachia. As Chun (1880) long ago observed and graphically described, Beroë feeds on its own relatives, even on other ctenophores many times as large as itself, as well as on whatever else it can capture. Lebour (1922 and 1923) found it dieting chiefly on Pleurobrachia, also to some extent on other ctenophores and diatoms, while we ourselves have often found Calanus and other copepods in its gastric cavity.

Mertensia is no less voracious, for I have seen one individual of this genus which "had entirely engulfed a young sculpin (*Acanthocottus grœnlandicus* Fabricius) no less than 21 millimeters long, the victim being doubled up so as to fit into the digestive cavity of its captor" (Bigelow, 1909a, p. 317). The various species of medusæ, large and small, all belong to the piratical category, and the total destruction they wreak on euphausiids, copepods, appendicularians, the various larval forms, etc., is beyond any estimation. Even animals as active and themselves as voracious as Sagittæ may fall victims to medusæ (Obelia) far smaller, as Steuer (1910, p. 631) describes. The siphonophores, too, of which our waters support one species in abundance (p. 377), destroy countless copepods, etc.

The common boreal euphausiids, important in the faunal community of the Gulf of Maine, may typify the planktonic animals that feed chiefly on pelagic vegetables, but which also consume animal food in less amount. Thus Lebour (1922) found bits of green weed, diatoms, and fragments of mollusks in *Nyctiphanes couchii.* Paulsen (1909, p. 48) records *Thysanoessa inermis* from Icelandic waters stuffed with the diatoms Asterionella, Chætoceras, and Coscinodiscus, and describes Meganyctiphanes as full of these same diatoms, with tintinnids (Cyttarocylis), peridinians (Dinophysis, Ceratium, and Peridinium), and Globigerina in addition; but his discovery of crustacean débris (Calanus antennæ recognizable among it) in the stomachs of both these species of pelagic shrimps proved that they had also eaten smaller Crustacea—some of the specimens examined had, indeed, partaken of a purely animal diet. Holt and Tattersall (1905, p. 103) likewise found some examples of Meganyctiphanes with the leg basket more or less stuffed with prey, including copepods, schizopods, and decapod larvæ, Limacina and other animal débris, and one with the tail of a young fish actually in its mouth. Lebour (1924a) reports Meganyctiphanes feeding on Sagittæ, Crustacea, and dead specimens of its own kind in the aquarium. We can substantiate these observations in part, having recognized algal filaments and diatom débris among the mass of finely comminuted particles (themselves, to judge from their brownish green color, probably vegetable in nature) with which the alimentary tracts of numerous specimens of Meganyctiphanes from various parts of the gulf are packed, and we have often found specimens of this shrimp carrying loads of small crustaceans. For example, one taken off Cape

Cod on December 29, 1920 (station 10491), had a dozen or more Metridia and as many Pseudocalanus, five or six large Calanus, the siphon and part of the stem of a Stephanomia, besides a considerable mass of diatoms (Rhizosolenia) and some unrecognizable animal débris clasped between its thoracic legs. Several others taken at random from a large catch of these shrimps, made in the northeastern corner of the gulf on June 10, 1915 (station 10283), carried packs consisting chiefly of Calanus, occasionally a Euchæta, and Pseudocalanus, matted together with unrecognizable vegetable débris. One had a starfish larva and two eggs, probably of its own species, with the young nauplius almost ready to hatch out. Lest the reader think this omnivorous diet is at all seasonal, I may add that most of the Meganyctiphanes taken in the eastern basin on August 7 of that year carried loads of Calanus, Metridia, and Temora, with the cladoceran genus Evadne in great numbers, besides algal filaments and débris, the origin of which I could not determine. At Eastport, too, I have seen Meganyctiphanes clasping bits of herring refuse from the sardine factories.

Up to very recently the method by which euphausiids gather their food had not been actually observed in life, but since the preceding lines were written, Lebour (1924a, p. 405) has described the food as "brought to the thoracic limbs by a current from behind, set up by the movement of the abdominal limbs, the thoracic limbs forming a sort of basket-like receptacle for the accumulated food." Thus with the bristly armature of their legs they sweep the water for their prey just as barnacles do, gathering whatever copepods, Cladocera, diatoms, peridinians, or indeed small animals or plants of any sort, come within their reach as they dart to and fro in the water.

The nourishment of the marine copepods remained a riddle until Dakin (1908) found that the alimentary canals of hundreds of Calanus, Pseudocalanus, Centropages, and other genera of copepods from the North Sea contained chiefly diatoms. He counted up to 200 diatom shells in the stomach of a single copepod, with peridinians and a green substance (previously noted by other students), apparently the remains of shell-less unicellular plants. Esterly (1916) has similarly described the contents of the guts of several hundred copepods (mostly Calanus) from San Diego, Calif., as consisting chiefly of Coscinodiscus and other diatoms, silicoflagellates, Dinophysis, Peridinium and other peridinians, and of coccolithophorids. Lebour (1922) also found diatoms of various species, Phæocystis, coccoliths, and peridinians in Calanus; diatoms and green remains in Pseudocalanus; diatoms and flagellates in Temora; and Phæocystis in Anomalocera.

Murphy (1923, p. 450) writes that the copepod *Oithona nana* ate kelp and diatoms in the aquarium, and we have recognized remnants of Thalassiosira in sundry specimens of Calanus, and Thalassiosira, Chætoceros, and Biddulphia in Metridia from Massachusetts Bay at the time of the vernal diatom flowering. Diatom fragments have also been detected repeatedly in the excreta of copepods, which are familiar objects in the catches of tow nets, but Esterly's (1916) discovery of an occasional nauplius and copepod fragment in copepod stomachs proved that they are not exclusively vegetarian. Lebour (1922) has more recently found that the large blue copepod Anomalocera may feed largely on micro-Crustacea, while

smaller copepods form a considerable item in the diet of Temora. Calanus, however, she found chiefly vegetarian, and Pseudocalanus perhaps exclusively so. Marshall's (1924) more recent study of the gut contents of large numbers of Calanus taken throughout the year in the English Channel corroborates this, diatoms proving the chief article of diet in spring and autumn with peridinians (curiously enough, however, no Ceratium) in summer. Silicoflagellates were also eaten in small quantities, while a few of the Calanus had eaten other copepods, molluscan larvæ, and tintinnids.

All the Tomopteris I have examined have been empty, which has been the experience of most students, but it is probable that they are vegetable feeders chiefly, Lebour (1922 and 1923) having found diatoms their principal diet, with some green flagellates. Tomopteris, however, sometimes turns carnivorous, for she watched one swallow a Sagitta whole and saw another that contained a larval herring. All the shell-bearing pteropods (*Limacina retroversa*, for example) are also vegetarian, dieting chiefly on diatoms. The Salpæ likewise feed on diatoms, peridinians, and other small organisms, animal as well as plant, their gut contents and fœcal masses having long been a treasure house to the student of the microscopic plankton. For example, the "guts" of large *S. tilesii* collected south of Nantucket Lightship in July, 1913 (station 10061), contained a varied assortment of diatoms, Peridinium, and Ceratium, besides an occasional newly-hatched Euthemisto; but the most successful captors of the unicellular pelagic plants are the appendicularians, which, thanks to their very fine-meshed straining apparatus, are able to utilize gymnodinids, rhizopods, naked flagellates, coccolithophids,[52] etc., forms so tiny that for the most part they pass through the finest tow nets. Appendicularians likewise devour the larger protozoans and unicellular plants. For example, a large *Oikopleura vanhöffeni* from the neighborhood of Lurcher Shoal (May 10, 1915, station 10272) was packed with the horns and other fragments of Ceratium, besides small Peridinium of several species, tintinnids, and silicoflagellates (Distephanus).

None of the pelagic tunicates are plentiful enough in the Gulf of Maine to make serious inroads on the phytoplankton. In the Gulf Stream to the south Salpæ sometimes occur in hordes, and on such occasions strain the water bare (Bigelow, 1909).

Among the unicellular planktonic animals the infusorians are proverbially rapacious. The tintinnid genus Cyttarocylis has been found to contain a great variety of microsocopic organisms—e. g., Peridinium, Dinophysis, Goniaulax, and diatoms (Lebour, 1922)—and even the Infusoria, which are provided with chromatophores, are known to take solid food (Steuer, 1910, p. 627). Radiolarians engulf diatoms, tintinnids, and other Infusoria; hence, when Acanthometron swarms in the gulf (p. 460) it must locally take heavy toll of other microscopic animals and of planktonic plants. Foraminifera are also rapacious animals, but have never been found plentiful enough in the plankton of the Gulf of Maine to be of any great importance in the economy of its planktonic communities.

On the border line between plant and animal, so far as their mode of nourishment is concerned, stand the peridinians, for while the shelled forms are typical producers

[52] For an account of the food of appendicularians see Lohmann (1903, p. 23, pl. 4) and Johnstone (1908, p. 139).

the naked peridinians have repeatedly been found to contain other peridinians, Phæocystis, and occasionally a diatom.[53]

It is a question of moment in the economy of the sea, and of practical bearing on the fisheries problems of the gulf, to what extent the sundry carnivorous members of its plankton menace the survival of the stocks of larval fishes that are produced there.

The preceding pages contain sundry instances of planktonic animals eating young fish, which could be multiplied manyfold from published reports, were this worth while. In the Gulf of Maine it is probable that the most deadly enemies of newly-hatched fishes are the medusæ, ctenophores, and Sagittæ. The rapacity of Mertensia and Pleurobrachia in this respect has been mentioned; when and where the latter are abundant (as is so often the case on German Bank) it is hard to see how any larval fishes can escape their constant fishing. Pleurobrachia is also known to devour buoyant fish eggs of various species. In view of its local abundance, this ctenophore must be a serious enemy to the propagation of cod and haddock over the banks to the south and west of Cape Sable. Lebour (1925) has also reported Bolinopsis, another ctenophore plentiful in the gulf (p. 372), as devouring larval goosefish (Lophius) in the aquarium; no doubt it accepts a fish diet equally in nature.

The two medusæ which are most abundant in the open waters of the gulf—Aurelia and Phialidum—are also proven fish eaters, as are others plentiful in the coastal zone,[54] and the swarms of both of these which we have frequently encountered (pp. 350, 362) must take heavy toll of the little fishes that cross their paths.

With *Sagitta elegans* so plentiful and so widespread in the gulf, it, too, must destroy great numbers of young fish; must, then, be as serious a menace to the stock of herring, etc., in the Gulf of Maine as Lebour (1923) has found it in the English Channel. It may, perhaps, be named the most effective check among all the planktonic category to the local propagation of such fishes as pass through a prolonged planktonic stage, and this incudes most of the important food-species of the gulf. I have found no published record and have seen no actual instance of the amphipod genus Euthemisto eating fish; but in view of its known rapacity it is likely to do so when occasion offers. Decapod larvæ certainly do (p. 107), and these are abundant locally near shore at certain seasons. Euphausiids also eat fish to some extent, though probably it is a minor article in their dietary (p. 108).

It is fortunate, indeed, that the copepod species which so usually dominates the plankton of the gulf (*Calanus finmarchicus*) is not a fish eater (at least, it is not known to eat fish). Were the blue copepod Anomalocera as plentiful as Calanus, hardly a young fish could survive. As it is, few can "run the gauntlet" of the medusæ, ctenophores, Sagittæ, and crustaceans that prey upon them; and so many species (and these plentiful in the gulf) of these groups are now known to prey on fish larvæ that they are almost certainly the most effective check on the survival of the countless myriads of young fish that are yearly produced in the gulf. There is good reason, then, to believe that the fluctuations known to occur from year to year

[53] Lebour (1922) has recently given a considerable diet list for Amphidinium and Gymnodinium.

[54] Lebour (1923, 1924) found Aurelia, Phialidium, Aequorea, Obelia, Laodicea, Rathkea, and Bougainvillea feeding on young fish; likewise several other medusæ and Pleurobrachia.

in the stocks of herring, mackerel, haddock, etc., which are reared in the gulf, depend more on the abundance of the rapacious members of the planktonic community (and especially on the abundance of Sagittæ, medusæ, Pleurobrachia, and Euthemisto) than on any other one factor. If plankton studies need any defense from the standpoint of the fisheries we need look no further.

## THE MORE IMPORTANT GROUPS OF PLANKTONIC ANIMALS

### MOLLUSKS

In coastal and estuarine waters generally the larval stages of mollusks are abundant in the plankton, but in the open gulf they hardly figure in the catches, leaving the pteropods as the only molluscan group that is a regular factor in the planktonic community. The cephalopods are also considered briefly because of their importance in the natural economy of the sea, although so large and such active swimmers that they are not properly "plankton."

#### CEPHALOPODS

Only two of the considerable list of cephalopods recorded at one time or another from the coasts of New England (for a complete list see Johnson, 1915) play a rôle of any importance in the pelagic life of the Gulf of Maine, but these two—*Loligo pealii* Lesueur and *Illex illecebrosa* (Lesueur)—are extremely abundant locally in their proper season, when they form one of the principal sources of bait for fishermen. While, on the one hand, their young provide an important element in the diet of various larger fishes, the adult squids devour innumerable fish fry.

So active are these cephalopods and so easily do they avoid small or slow-moving gear that we have never taken a single specimen in our tow nets. Indeed, I can, from my own experience, verify Verrill's (1882, p. 306) statement that it is hard to capture them with a dip net, even when confined in a fish pond or weir. Hence I can offer the reader only a brief summary of accounts published previously, with such notes as have been gleaned from personal observation on the beaches, and from accounts given me by fishermen and other observers.

Loligo is the common squid south of Cape Cod, Illex north of Cape Ann, with the ranges of the two overlapping in Massachusetts Bay. Illex also occurs, if less commonly, as far south and west as the Woods Hole region (Sumner, Osburn, and Cole, 1913a). Loligo, on the other hand, has long been known occasionally as far north as Penobscot Bay, and Dr. A. G. Huntsman and Dr. A. H. Leim write me that it has recently been found to be quite common in summer in various estuaries of the Bay of Fundy; for instance, Passamaquoddy Bay, Scotsman Bay, and Cobequid Bay.

Since more is known of the life history of Loligo than of Illex, it may be considered first. Loligo is common in the Woods Hole region from April or May until November but disappears during the winter. During the 10-year period, 1900 to 1909, the earliest captures ranged from April 16 to May 7 (Sumner, Osburn, and Cole, 1913a), which probably applies to Massachusetts Bay, though, taking one year with another, this squid appears there later in spring and disappears earlier in autumn than it does along the southern coast of New England. During the late

spring, summer, and early autumn Loligo is extremely common both south and north of Cape Cod, passing part of the time on or near the bottom, but often seen swimming in shoals near the surface, and it is taken in great numbers in fish traps and weirs and even in eelpots. Many specimens have likewise been dredged. Along the shores of southern New England it breeds from May until September, or later. I am informed by W. F. Clapp that he has frequently found its eggs in Duxbury and Plymouth Bays from June until October, and in the Bay of Fundy its eggs and larvæ are reported by Doctor Leim in August and September. Since Verrill (1882) notes the capture of considerable numbers in breeding condition near Cape Ann as early as May in 1878, it is safe to credit it with a breeding season enduring throughout the warmer half of the year over the major part of its range. The eggs, which adhere together in bunches of hundreds of gelatinous capsules, attached to some fixed object, are laid chiefly (perhaps not exclusively) in depths varying from just below tide mark down to 50 meters or so and have been trawled in large numbers on every sort of bottom south of Cape Cod (Verrill, 1882; Sumner, Osburn, and Cole, 1913a). It has been estimated that individuals of the European representatives of this genus may lay as many as 40,000 eggs.

According to Verrill, hatching takes place from June until October south of Cape Cod; probably during these same months along the shores of Massachusetts Bay, according to Mr. Clapp's observations. We owe to Verrill (1882) an extensive series of measurements of the young squids at various seasons, and though he found it difficult to follow their rate of growth, owing to the protracted period over which spawning endures, his general conclusion was that June-hatched squids attain a mantle length of 60 to 85 millimeters by November; that the smallest have grown to about 150 to 180 millimeters when they reappear the next May; that the later-hatched summer broods are about 60 to 80 millimeters long in the following spring; and that the largest adult breeding squids are probably from 2 to 4 years old. The young squids, from less than 6 up to 25 or more millimeters in length, often swim near the surface, where they have been taken in immense quantities with the tow net. Mr. Leim informs me that he towed young Loligo 2 to 4 millimeters long in Cobequid Bay, Bay of Fundy, in September, 1921. Nevertheless, although young Loligo must be produced in myriads on their main breeding grounds, the larval stages are so closely confined to the coastal or inclosed waters of their nativity during their first summer that we have never taken them even in Massachusetts Bay (though they spawn abundantly in its tributaries) or anywhere in the open Gulf.

It is not known whether this squid moves offshore as the water chills in autumn or whether it passes the cold season inshore on the bottom. There is, however, some slight presumption in favor of the latter alternative, for it seems to be strictly a coastal form, which, so far as I can learn, has never been reported from the offshore banks in summer or from deep water.

North of Cape Ann Loligo is always far outnumbered, and, except for the small Bay of Fundy colony, is practically replaced east of Penobscot Bay by *Illex illecebrosa*,[55] a squid much resembling it in appearance but easily distinguished (indeed it

[55] This squid has often been referred to the genus Ommastrephes. Recent students of the cephalopods, however, unite in referring it to Illex, a genus founded by Steenstrup for the reception of its European relative, *I. coindeti*. For a recent discussion of Illex see Pfeffer (1908 and 1912).

belongs to a different family) by its perforated eyelid as well as by its shorter fins. It has long been known that this beautiful animal is very abundant from Massachusetts Bay northward to the shores of Newfoundland and Labrador, and my own observations lead me to believe that its numbers increase from southwest to northeast around the coasts of the Gulf of Maine. However, though its economic value has been fully appreciated by fishermen for over a century, and while it has often been referred to in scientific literature, practically nothing is known of its life history.

Illex appears along the shores of the gulf in late spring or early summer (I have been unable to find any record of the exact date of its vernal arrival), is found very plentifully there throughout the summer and early autumn, and vanishes from the coast some time in October or November. According to reports by fishermen it is present offshore in winter, though not to be found in the coastal zone at that season, a phenomenon to which I shall have occasion to recur. During its season Illex occurs even more abundantly than does Loligo farther south, the vast schools in which it visits the coast having been described long ago by Verrill. Owing to a habit of stranding, the presence of this squid is very evident, as it oftens comes ashore in large numbers on the beaches from Cape Cod to the Bay of Fundy. On the islands near the mouth of the latter, in particular, I have found them, as did Verrill, in windrows on the flats in August and September, stranded squids being a familiar sight there to everyone. At low tide shoals of squid may often be seen darting to and fro over the sand or struggling in the shallows. For some inscrutable reason the squid, once aground, seems forced by instinct to drive farther and farther ashore—throw it out ever so often into deeper water, and it shoots, arrowlike, back on the beach, to perish there as the tide ebbs. This fatal habit causes the destruction of multitudes of squid, as long ago recounted by Verrill and by Smith and Harger (in Verrill, 1882, p. 307), who tell us that when in pursuit of young mackerel many of the "squids became stranded and perished by hundreds, for when they once touch the shore they begin to pump water from their siphons with great energy, and this usually forces them farther and farther up the beach." "It is probable, from various observations," says Verrill (1882, p. 307), "that this and other species of squids are mainly nocturnal in their habits, or at least are much more active in the night than in the day." Certainly it is at night that they most often enter the weirs and pounds. During the dark hours in summer and autumn the presence of shoals of squid is often disclosed by their phosphorescent wakes, Hjort (1912, p. 649) describing the common Norwegian squid, of the genus Ommastrephes, as "moving in the surface waters like luminous bubbles, resembling large milky white electric lamps being constantly lit and extinguished." The Gulf of Maine Illex, however, is often seen swimming near the surface during the daytime as well.

Whenever and wherever found, these squids are extremely voracious, and the schools that run ashore often do so in pursuit of fish fry. At the mouth of the Bay of Fundy, both in summer and in early autumn, I have seen them eagerly following the schools of young herring, which in their turn are feeding upon shrimps (euphausiids), often so common in the surface waters there (p. 135). I can corroborate Verrill's observation that squid stomachs are then often distended, both with shrimp and

with fragments of herring, having found this to be the case in dozens of specimens. Young mackerel, too, suffer from their attacks, and we owe to Smith and Harger (quoted by Verrill, 1882, p. 306) a graphic account of their pursuit of the latter among the wharves of Provincetown Harbor during the month of July. Particularly interesting is their activity at such times, the ferocity of the attack, and the deadly nature of the single bite. The cannibalistic habits of Illex have likewise been commented upon, its own young being a common article of diet. This squid, like so many of the pelagic fishes, is very erratic in its appearance, being here to-day in hordes and gone to-morrow, perhaps to reappear in a few days.

Illex provides a valuable source of bait for the offshore fishermen. It has been estimated that at one time squid formed fully half the bait supply of the vessels resorting to the Grand Banks (Goode, 1884), and we have record of 30,000 to 40,000 taken in one Newfoundland harbor in a single day. Probably Illex never occurs in the Gulf of Maine (which is the southern outpost of its regular range) in such abundance as this, but as long ago as 1897 the squid fishery of Massachusetts Bay alone (no doubt this and the preceding species combined) yielded over a thousand barrels of bait, and in 1902 the catch of squid in Massachusetts was upward of 5,000,000 pounds. At one time or another large numbers are taken by various methods all along the coasts of the Gulf as well as on the offshore banks. So voracious and active an animal, and one at the same time so numerous, must take a heavy toll of the young fish, not to mention the various planktonic animals.

Illex is probably to be classed as an oceanic animal, for it occurs commonly on the Grand Banks far from land and is often plentiful on Georges Bank as well. Probably its vernal appearance and continued presence off the coasts of the gulf of Maine throughout the summer are to be explained as a feeding migration (certainly this has nothing to do with its spawning), while its disappearance from the coast in autumn is part of a general offshore movement. Mr. Clapp's capture of several large specimens on Georges Bank (taken in otter trawl) during the last week of November in 1911 harmonizes with this suggestion. The fact that a whale (species unknown) that stranded on the south shore of Cape Cod on January 29, 1869, contained in its stomach thousands of Illex beaks [56] belonging to squids of about 12 to 15 inches body length throws no light on this point, for it may have eaten them many miles away from where it came ashore. We have no other winter records for Illex from the Gulf of Maine.

Nothing is known of the breeding habits of this squid; its eggs have never been found, nor have its newly hatched young been recorded.[57] However, it is safe to say that it does not spawn along the coast of the Gulf of Maine at any season, for all the adult squids examined by Verrill and all that I have seen have been sexually inactive. Neither did McMurrich find its young at any season in his tows at St. Andrews. Indeed, the smallest Gulf of Maine specimens of which we can learn are one of about 10 centimeters, reported by Capt. H. E. Calder near Campobello, at

[56] Some hundreds of these are preserved in the collection of the Museum of Comparative Zoology. Their identity has been established by Mr. Clapp by comparison with the beak dissected from an Illex from Georges Bank, which measured about 14 inches in length from the edge of the mantle to tip of tail.

[57] One with a mantle measuring only 33 millimeters in length is recorded by Pfeffer (1912).

the mouth of the Bay of Fundy (date unknown), and others of 16 to 19 centimeters, taken off Shelburne, Nova Scotia, in July, 1921.[58] Very likely its eggs are pelagic, as are those of some of its relatives, but it is certain that they do not occur regularly among the plankton of the Gulf of Maine, pelagic squid eggs (at least such as I have seen in the West Indies) being very easily recognized at all but the very earliest stages by the characteristic embryo.

In European waters *Illex illecebrosa* is replaced by the form *I. coindeti*, so closely allied that Pfeffer (1912) regards the difference between them as no more than subspecific. *I. coindeti* ranges from Scottish waters to the Mediterranean.

No squids other than Loligo and Illex have ever been found in any numbers in the Gulf of Maine, nor is it likely that any other species are ever numerically important in its pelagic fauna, with the possible exception of the boreal-arctic *Gonatus fabricii*. There is only one actual record of this species from the Gulf, a single specimen taken from the stomach of a cod near Seal Island, off Cape Sable (Johnson, 1915); but since its larvæ have been taken at several localities between Newfoundland and Ireland, once, even, close to the southern edge of the Grand Banks (Hjort, 1912), the adult (which resembles Illex so closely that it might well be overlooked among the shoals of the latter) may be more common along the coasts of Nova Scotia and even in the Gulf of Maine than the paucity of actual records suggests. Finally, we may note that no "giant squids" seem ever to have been found in the Gulf of Maine.

## Pteropods

### Limacina retroversa Fleming[59]

This shelled pteropod, a boreal form known from latitude about 50° to northern Norway, off the European coast, and from latitude about 34° to the southern part of Davis Strait, in the western Atlantic, is one of the most characteristic of the permanent pelagic inhabitants of the Gulf of Maine, where its numbers depend on local reproduction and not on immigration from elsewhere. It is the only pteropod of which this can confidently be asserted. Although it has now been taken in all parts of the gulf at one season or another, it is, as I have previously pointed out (p. 45; Bigelow, 1917, p. 299), far less regular in its occurrence in the gulf than certain of the calanoid copepods, the amphipod genus Euthemisto, or *Sagitta elegans*. It has commonly been our experience to find it comparatively plentiful at one station but rare or absent at another hard by. Similarly, waters where the nets yield an abundance of Limacina on one visit may prove quite barren of it a few weeks later, as was the case in the spring of 1920 on the eastern part of Georges Bank, where large Limacina were plentiful on March 11 (station 20065), but were sought in vain on April 17 (station 20111). Limacina was present on one cruise and absent on the next, or vice versa, at several localities during the season of 1915, notably off Monhegan and Matinicus Islands and in the northeast corner of the basin of the gulf.

[58] Information supplied by Doctor Huntsman.

[59] I follow Meisenheimer (1905) in uniting under this name the *L. retroversa* and *L. balea* of the early malacologists. Bonnevie (1912), it is true, has separated the two once more, basing the distinction partly on the shape of the shell (in which character, however, her specimens intergraded) and partly on the structure of the radula; but W. F. Clapp writes that "a careful examination of the quantities of Limacina from the Gulf of Maine has shown that it is impossible to consider the material as belonging to more than one species."

As appears from the accompanying charts (figs. 43 and 44), this pteropod has been taken over all the offshore waters of the gulf, on Georges Bank, and over the continental shelf off Nantucket. During our summer cruises (the season for which

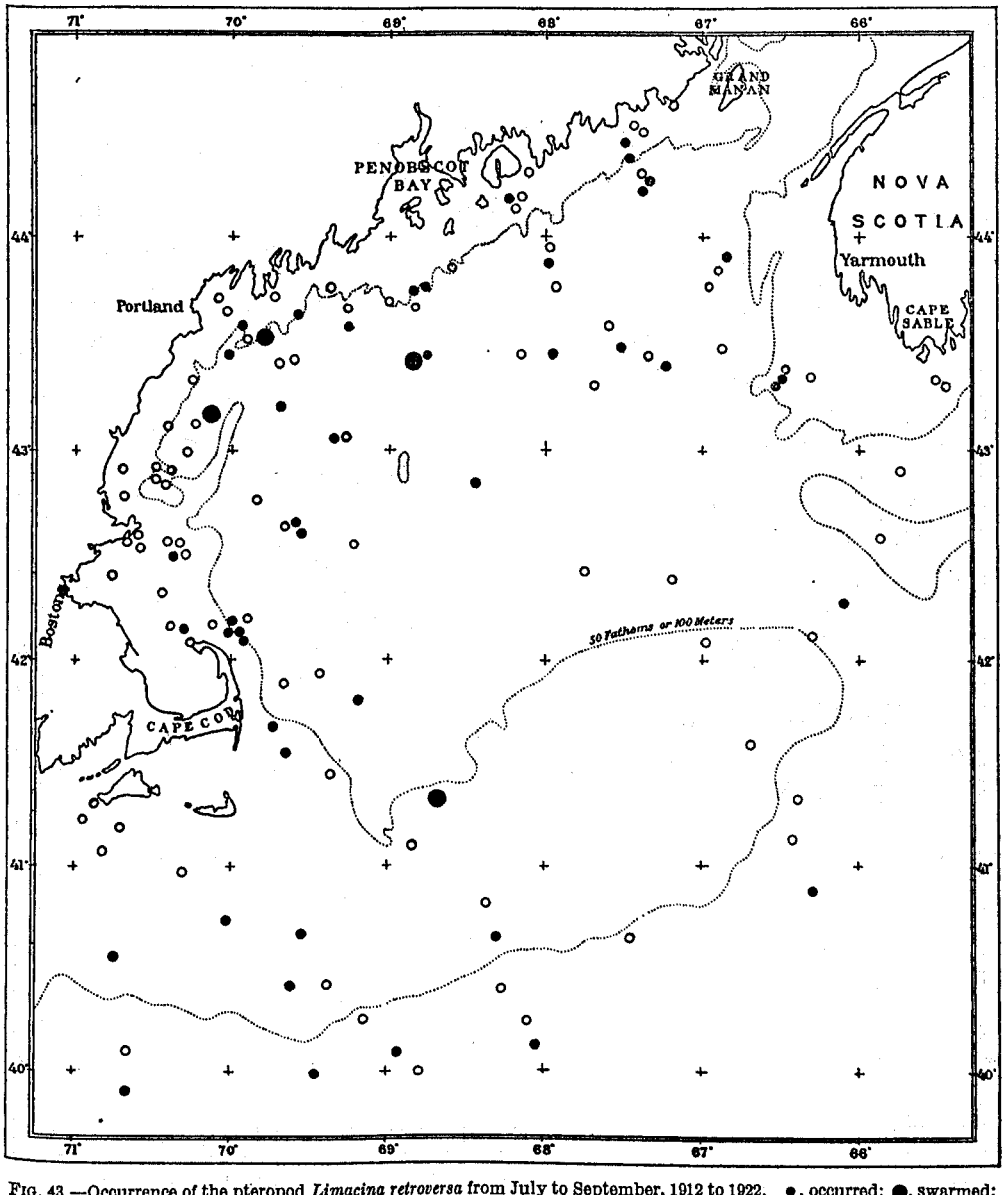


FIG. 43.—Occurrence of the pteropod *Limacina retroversa* from July to September, 1912 to 1922. ●, occurred; ●, swarmed; ○, not taken

our records are most extensive) it has appeared at rather more than half of all the stations, but the regularity of its distribution differs from summer to summer. For example, it was practically universal over the deeper parts of the gulf in August,

1913 (Bigelow, 1915, p. 302), whereas in July and August, 1912, we found it only in the northwest part of the gulf, on the one hand, and over German Bank, on the other (Bigelow, 1914, p. 120). At the same season in 1914 we found no Limacina

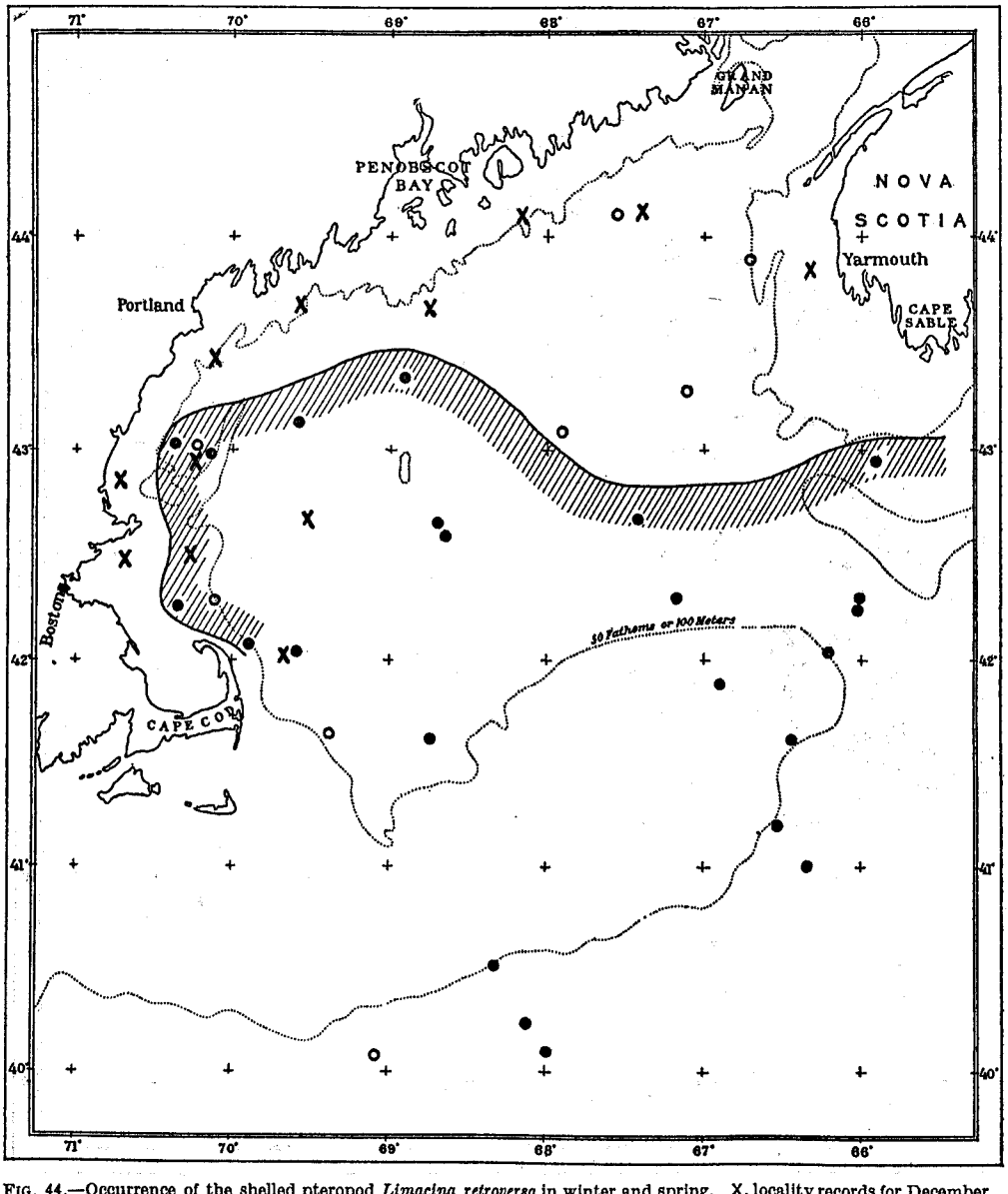


FIG. 44.—Occurrence of the shelled pteropod *Limacina retroversa* in winter and spring. X, locality records for December, 1920–January, 1921; ●, February to April, 1920; ○, May of 1915 and 1920. The hatched curve incloses its area of occurrence in early spring up to May

off Penobscot Bay, where it had been plentiful during the two summers preceding, but towed numbers of them in the northeastern corner of the gulf (stations 10246 and 10247) not far distant, and likewise in the Eastern Channel, over the northwest

part of Georges Bank, and off Cape Cod (Bigelow, 1917, pp. 298 and 299). We have not taken Limacina on Browns Bank either in spring or in summer, but since it has appeared at several of our stations over the shelf farther east, as well as on German Bank, in June, July, and August, and in the eastern basin of the gulf in March and April, it is more likely that our failure to find it on Browns Bank was accidental than that this pteropod does not occur there.

Our most productive summer catches of *Limacina retroversa* have been as follows: On July 29, 1912, we encountered a swarm of juveniles off Casco Bay (station 10019); in 1913 great numbers were taken off Nantucket on June 21 (by Capt. John McFarland, lat. 40° 45′ N., long. 70° W.); off Penobscot Bay, August 11 (station 10091); and near Cape Elizabeth, August 15 (station 10104); while the largest haul of all, yielding about 125 cubic centimeters of Limacina (besides other plankton), was made over the northeast edge of Georges Bank on July 20, 1914 (station 10215). Thus, the few rich stations just mentioned (fig. 43) show no definite grouping in any one part of the gulf, but are spread far and wide. We did not find Limacina in numbers at any time during the spring, summer, or autumn of 1915, though it was taken at about 50 per cent of our stations for that year; nor was it more plentiful in the gulf at our few stations for July and August of 1916, though odd specimens were detected at about half of them.

In spite of the erratic way in which Limacina appears and disappears (or at least vanishes from observation) in the Gulf of Maine, the records for the five years 1912 to 1916 show that in summer this pteropod is much less plentiful in the coastal zone and out to the 100-meter contour, from Massachusetts Bay northward and eastward as far as Mount Desert Island, than it is farther offshore. Limacina has appeared in less than 10 per cent of the June-August stations in this inshore zone, to which we have paid particular attention, but seldom in any of the hauls at that season in the inner part of Massachusetts Bay or in any of the other indentations of the coast west of Mount Desert. Close proximity to the coast and shoalness of the water do not necessarily imply a scarcity of Limacina in summer, however, for this, it seems, is its period of maximum abundance at St. Andrews, where Doctor McMurrich found it at almost every station from mid-June until September in 1916. Limacina is likewise a regular summer inhabitant of the coastal waters along the outer shores of Cape Cod and of the shallows over German and Georges Banks, and south of Nantucket. Furthermore, it may occasionally appear in great numbers in Massachusetts Bay in summer, when it is usually rare or absent there, for Alexander Agassiz (1866) found it swarming at Nahant (some 12 miles from Boston) during the summer of 1863.

A considerable number of records of Limacina for September, October, and November show that this pteropod, like Euthemisto, tends to work inshore in the western side of the gulf in autumn. Thus, in 1915[60] it occurred at four out of six late October and early November stations in Massachusetts Bay, whereas we have only once found it inside a line from Cape Cod to Cape Ann in July or August of recent years (station 10342, July 19, 1916). Similarly, no Limacina were taken in the hauls along the Maine coast inside the 100-meter contour in 1915 until Sep-

[60] See Bigelow, 1917, p. 299, for records of Limacina in 1914 and 1915.

tember, though in other years it has appeared in numbers off Casco Bay in summer, as just noted (p. 119). Apparently it partially withdraws from the Bay of Fundy in autumn, for McMurrich found only occasional examples at St. Andrews from the first week of October until the new year.

It is not yet possible to plot the distribution of Limacina over the gulf as a whole for winter, our December–January cruise having been confined to the northern and western parts; but there, at least, Limacina is as widespread during early winter as it is in summer; and if the season of 1920–1921 be representative, it is even more regularly distributed, for it occurred at 10 out of 14 tow-net stations, both in Massachusetts and Ipswich Bays near land, and from Cape Cod to Nova Scotia offshore (stations 10488 to 10491, 10493, 10495, 10496, 10497, and 10500 to 10502). Similarly, Stimpson (1854) described it as present in Massachusetts Bay from February until April, more than half a century ago, though the fact that it appeared in the tow near Gloucester late in November, 1912, and again in February, 1913, but neither in December nor in January of that winter, shows that it is as subject to sporadic fluctuations in abundance there during the cold season as during the warm.

Failure to find Limacina in the Fundy Deep on January 4, 1921, with McMurrich's record of it as only occasional at St. Andrews during the half-year from December to May,[61] suggests that it occurs less regularly and is much less plentiful in the Bay of Fundy in winter than in summer, which is just the reverse of its seasonal history in Massachusetts Bay.

If the season of 1920 can be taken as representative, Limacina withdraws from the whole northern and eastern part of the gulf and likewise from the immediate coastal zone in the western side during the last few weeks of winter or first days of spring, for we did not take a single specimen anywhere in the gulf during that March or April north or west of the undulating curve laid down on the accompanying chart (fig. 44); although Limacina in various stages in growth then occurred irregularly along Cape Cod, in the western, southern, and southeastern parts of the basin, and over and off the slope of Georges Bank.

Our records point to the months of March and April as the season when the geographical range of Limacina in the Gulf of Maine is least extensive, and to the area just outlined as the only part of the gulf where this pteropod is regularly present the year round. With the advance of spring it once more spreads over the northern corner of the gulf, occurring at four stations in the eastern side of the basin in May, 1915; but while a considerable augmentation in its numbers takes place in the St. Andrews region (which probably mirrors conditions in the Bay of Fundy generally) by late June, as reflected by the frequency of captures listed by Doctor McMurrich, this does not happen in the coastal zone of the gulf west and south of Mount Desert until three months later, as just noted.

In this connection it is interesting that Limacina is present all the year round off the west and south coasts of Ireland, just as it is in the offshore waters of the Gulf of Maine, but is seasonal along the Irish shores, with its maximum in spring

[61] From his plankton lists for 1915 and 1916.

and summer (Massy, 1909), and that it is as erratic in its occurrence in the North Sea as it is in the Gulf of Maine.

Limacina has been taken at about 50 per cent of our stations over the continental slope between the longitudes of New York and Cape Sable in late winter, spring, summer, and early autumn, though never in great numbers. Only one specimen was taken at our most oceanic station (10218, July, 1914), where the plankton as a whole was tropical, nor did we find it associated with the warm-water pteropods at our outermost stations south of New York in 1913.

Being typically boreal in its affinity to temperature, it is not to be expected in the warm waters of the so-called Gulf Stream off the American littoral except as an accidental and probably short-lived straggler from the cooler coastal zone, but in more northern seas Limacina occurs chiefly in what is generally known to European oceanographers as the "Atlantic" water. This, for example, is the case south of Iceland, where it appears in great shoals, and it is with the general drift of this water (which is warm in contrast to the polar currents) that Limacina penetrates the Norwegian sea (Paulsen, 1910), for it is not at home in the icy cold Arctic water of comparatively low salinity.

Most of the records of Limacina in the gulf have been from subsurface hauls, for which the precise depths can not be stated because made with open nets; but most of them have apparently come from comparatively shoal levels, for when two hauls have been made at different depths below the surface the shallower has usually taken the most Limacina. On the whole, the most prolific depth zone may be stated as from 20 to 25 meters down to about 80, which corroborates Paulsen's (1910) generalization that Limacina lives chiefly shoaler than 50 meters in north European seas, though it has occasionally been taken much deeper.

In summer we have never detected Limacina on the surface during the hours of bright sunlight. In August, 1913, for example, "it was only once taken on the surface (station 10103), although a surface haul was made at every station, usually with a net of the same mesh as the one in which Limacina was taken in the depths" (Bigelow, 1915, p. 303), that one occasion being at 7 p. m. On several occasions during August, 1914, however, and the summer and autumn of 1915 (stations 10247, 10264, 10294, 10295, 10308, 10329, and 10333), surface tows between sunset and sunrise have yielded it in some numbers. This suggests that Limacina, like many other planktonic animals, performs a more or less regular diurnal migration in summer, rising toward the surface during the dark hours, to sink again at sunrise. The fact that the surface captures of Limacina (10 stations) [62] on our March and April cruises of 1920 were made invariably either in the dark or during the twilight hours between sunset and sunrise shows that this also takes place in spring, but perhaps not in autumn and early winter, when the sun is at its lowest.[63] This habit certainly is not so characteristic of Limacina in the more northern seas, where the sunlight is

[62] *Limacina retroversa* was taken at the following stations during the spring of 1920: 20044, 20045, 20046, 20048, 20053, 20057, 20060, 20061, 20064, 20065, 20067, 20068, 20070, 20071, 20088, 20091, 20094, 20105, 20107, 20110, 20114, 20116, 20119, 20120, 20126, 20129; and at the following in the winter and early spring of 1920–21: 10488, 10490, 10491, 10493, 10495, 10496, 10497, 10501, 10502, 10505, 10509, 10510, 10511. For earlier Gulf of Maine records of this pteropod see Bigelow, 1914, 1915, 1917, and 1922.

[63] We lack direct information on this point, our surface hauls for that season having been made with small, fine-meshed nets, through which so little water filters that the apparent absence of Limacina may not be significant.

weaker. In fact, it may not be followed at all there, for this pteropod is occasionally met with in great shoals on the surface off Iceland in daytime, though usually not when the sun is high.

The presence of *Limacina retroversa* in the Gulf of Maine throughout the year, together with its very general distribution there, proves that its local presence or absence is not governed by small variations in temperature or salinity. On the contrary, Limacina (both large and small) has been taken at one season or another in water varying in temperature from 2° to about 16.6°—that is, over practically the entire range proper to the gulf except for the very coldest and the very warmest. Probably its habit of coming up to the surface at night brings it into the latter also, on occasion. But the great majority of the Gulf of Maine records for this pteropod have certainly been from temperatures lower than 15° at all seasons, and since it has never been found regularly or abundantly in water warmer than this in any part of the ocean, 15° may be set arbitrarily as the upper temperature limit to its continued presence and prosperous existence. Thus, in our latitudes it is probably the high temperature of the oceanic water that is the offshore barrier to it, confining it to the continental edge and shelf off the coast of the United States.

On the other hand, although Limacina occurs in temperatures as low as 2 to 3° in the gulf in winter, it does not tend to congregate in the very coldest water at that season, but rather the reverse, for it was either absent altogether or at least very rare during the spring of 1920 (one or two only at stations 20055 to 20061) wherever the major part of the column of water was colder than 2°, although it was present in the neighboring parts of the gulf at the time. We have found it equally lacking or very rare in early spring in the icy cold water over the whole breadth of the shelf abreast of southern Nova Scotia, and certainly it is very scarce, if it occurs at all, in the coldest water along that coast in summer. Furthermore, Doctor McMurrich's notes show that there is a very close agreement between winter chilling and scarcity, vernal warming and regular presence of Limacina at St. Andrews, where it practically disappears when the temperature falls below about 3°, not to reappear regularly in the tows until the water warms to 8 or 9° the following spring. Although the evidence is not so clear, it seems that the presence or absence of Limacina may be correlated similarly with temperature in Massachusetts Bay, whence it appears to vanish when the water chills below, say, 2 to 3°, as happened in February and March of 1920; whereas in warmer winters, as that of 1912–1913, when the temperature of the water did not fall much below 3°, Limacina may occur sporadically and in small numbers right through from autumn until February (p. 120). These facts obviously suggest that it is the local cooling of the water that drives this pteropod from the coastal waters of the gulf, and from its northeastern corner generally, in late winter and early spring.

Temperature may also determine the bathymetric occurrence of Limacina. For example, we found it comparatively abundant on the surface over the outer part of the shelf abreast of Cape Sable early in the summer of 1915 (station 10294, June 23), when the superficial water had warmed to 9° to 10°, but with temperatures as low as 2° to 3° only 40 meters down it was certainly scarce at deeper levels. In

fact, it may not have occurred at all, for the few specimens brought in by the deep hauls may have been picked up by the nets close to the surface on their journey down or up; and the scarcity, if not absence, of this species in the coldest water along Nova Scotia is sufficient evidence that it is not an immigrant to the Gulf of Maine by that route. The general thesis that it is not at home in water of Arctic temperatures is further corroborated by Doctor Huntsman, who informs me that *Limacina retroversa* is scarce, if not wanting, in the Gulf of St. Lawrence, where, by contrast, its larger Arctic relative (*L. helicina*) is very plentiful.

I have pointed out elsewhere (Bigelow, 1917, p. 299) that *L. retroversa* occurs in numbers in waters of widely varying salinity in the Gulf of Maine, which agrees with experience in European seas; but in spite of its tolerance for variations in salinity it is clearly characteristic of the salter rather than of the fresher waters of the gulf. Thus, it has been detected at only five stations out of 55, where the upper 10 meters or so have been fresher than 31.5 per mille; never in any numbers except where the underlying layers were much salter (e. g., station 10294, surface 31.06, 80 meters, 32.79 per mille). While such evidence is perhaps not conclusive for an organism so sporadic in its local appearances and disappearances, at least it justifies the working hypothesis that *L. retroversa* is seldom to be expected in water fresher than, say, 31.5 per mille, and not likely to persist in much lower salinities. About 31.06 per mille is the lowest salinity in which it has certainly been taken within the limits of the gulf, and Paulsen (1910) has already suggested the probability that when this pteropod chances to stray into water much fresher than 30 to 31 per mille it perishes.

The dependence of *L. retroversa* on comparatively high salinity may have as much to do with making Massachusetts Bay and the coastal belt of the gulf generally unfavorable for it in spring as has its avoidance of very low temperatures.

Until the seasonal cycle of these two sets of phenomena—biologic and hydrographic—has been followed more closely, the dependence of the former on the latter can only be stated in the most general terms. However, it is important for an understanding of the biology of this pteropod to emphasize the probability that there is a causal relationship between the seasonal expansions and contractions in its geographic range in the Gulf of Maine, on the one hand, and local and seasonal differences in the salinity of the water, on the other. We find in this a resasonable explanation for the fact that while winter chilling to 2° to 3° probably is the cause which banishes *L. retroversa* from the coldest parts of the gulf in winter,[64] it does not reappear near the coast in regions where the effect of the spring freshets in lowering the salinity persists longest into spring and summer (Massachusetts Bay, for example) until several months after the water has warmed to a point favorable for its existence, and until a considerable increase has taken place in the salinity of the upper 40 meters or so. In such locations, therefore, low salinity is probably responsible for its protracted absence, which continues until the water is once more salt enough for its liking.

Repopulation of the coastal zone by Limacina after its annual period of scarcity might take place in one of two ways—either by local survival or by immigration.

[64] From parts of the Bay of Fundy and from the inner parts of Massachutests Bay and probably from all along the shore in cold winters.

Alexander Agassiz's (1866) observation that Limacina often sinks to the bottom suggested to him, and to other students subsequently, that this habit may explain its sudden appearances and disappearances—that is, that it may endure unfavorable periods on the bottom, where salinity would always be sufficiently high for its existence in all parts of the gulf except in very shallow water. However, since this habit has not been observed in European waters, where *L. retroversa* is often far more abundant than we have ever found it in the Gulf of Maine, probably its disappearance from the coast water reflects either the death of the local stock or a migration out to sea, its reappearance there reflecting an actual immigration from offshore in toward land, which follows more or less closely on the reestablishment of a favorable environment in the coast water and depends on the precise distribution of Limacina at the time relative to the circulation in the central parts of the gulf.

The upper limit of salinity for Limacina is certainly as high as 36 per mille (35.9 per mille is the most saline water in which I find it actually recorded), and inasmuch as it thrives in water of 34 to 35 per mille in the North Sea region no part of the Gulf of Maine could ever be too salty to afford it a favorable environment.

Nothing is known of the reproduction of *L. retroversa* in the Gulf of Maine except that young as well as old individuals have been taken repeatedly in spring, summer, autumn, and winter, proving it endemic. Very little information is as yet available as to the actual numbers in which *L. retroversa* occurs in the gulf, and comparison of the catches of the horizontal nets with those of the verticals shows that whether it be scarce or plentiful, it is so prone to congregate in shoals (which one net may hit but the other miss) that it would take a great number of vertical hauls to yield even an approximation of its actual numerical strength over any considerable area of the sea. For example, the vertical haul from 70 meters yielded none at all at the station where we made our largest catch in the horizontal net (station 10215, northwest part of Georges Bank, 125 cubic centimeters of Limacina in a 50-meter haul of one-half hour's duration). An instance of the opposite sort is afforded by a station in the center of the gulf (March 2, 1920, station 20052), where the quantitative haul yielded enough (58 specimens) to indicate comparative abundance (theoretically 240 Limacina under each square meter of the sea's surface), whereas the surface haul yielded only a few dozen individuals, the horizontal net, working at 100 meters, none at all, and the closing net only a few at 160 meters. Instances of this sort, which might be multiplied, make any attempt to plot its actual numbers from the data yet in hand not only idle but apt to prove misleading. However, it can be stated as a general proposition that only on the rarest occasions does *L. retroversa* form any considerable proportion of the plankton in any part of the gulf, judged either by numbers of individuals or by bulk.[65] Nor have we ever found it in abundance to compare with the shoals recorded by Paulsen (1910) from the waters south and west of Iceland. Therefore, it is not likely that this pteropod is ever of as much importance as pasturage for the pelagic fishes in the Gulf of Maine as it is in Irish waters, for instance, where, says Massy (1909), it regularly serves as an important item in the diet of both mackerel and herring.

[65] The richest catches of Limacina are noted above (p. 119).

### Limacina helicina Phipps

The Arctic pteropod *L. helicina*, a close relative of the boreal *L. retroversa*, though characteristic of a different zoogeographic province, appears but rarely in the gulf, and then only as an immigrant from the colder waters to the east and north. Its status as such and its importance as an indicator of cold currents being discussed elsewhere (p. 59), this mention may be confined to a list of its recorded occurrence in the Gulf of Maine.[66]

May 6, 1915—off Cape Sable, station 10270, 150–0 meters and 50 meters.
May 10, 1915—near Lurcher Shoal, station 10272, 60–0 meters, occasional specimens on each occasion.

### Clione limacina (Phipps)

The large shell-less pteropod Clione, beautiful in the water and easily recognized, may be expected anywhere in the northern half of the Gulf of Maine in winter, spring, or summer (fig. 45). During the cold half of the year—December to May—it has appeared at nearly 50 per cent of our stations, both over the gulf as a whole and on the individual cruises. Not only are the records for these months very generally distributed over the deeper basins and along the coastal belt, but Clione may be more universal than the actual records suggest, for we have usually taken it in numbers so small that its failure to appear in the tow nettings at other stations may have been purely accidental.

In summer, too, we have found Clione repeatedly in the northern parts of the gulf, but during the period from June to August it has appeared at only about 20 per cent of our stations—that is, distinctly less regularly than in winter or spring. We have not found it at all in September, October, or November, though the few stations for those months have been occupied at localities where it has been taken at other times of year. From this it appears that Clione is distinctly seasonal in its occurrence in the gulf, reaching its maximum from February until May and its minimum in autumn.

Although Clione is oceanic in its general biologic status as opposed to neritic or coastwise, it shows no apparent predilection for the deeper rather than the shoaler parts of the Gulf of Maine; and while we have not found it in inclosed waters, and Doctor McMurrich detected it only once at St. Andrews (on February 16, 1916), it has been known to appear in swarms in Portland Harbor, an event referred to below (p. 127). Neither do our records suggest any seasonal onshore or offshore migrations on its part, such as appear to be executed by its relative, *Limacina retroversa*.

I should point out that Clione is no more regular in its occurrence and shows no more concentration in the eastern than in the western side of the gulf, such as might be expected of an organism the maintenance of whose numbers within our limits depends partly on immigrations around Cape Sable, and such as actually obtains for various Arctic animals (p. 59). On the contrary, no general portion of the open gulf north of a line from Cape Cod to Cape Sable appears more favored by it than another at its season of maximum abundance, but our few traverses of Georges

[66] Also off Halifax, Aug. 2, 1914; near Shelburne, Nova Scotia, and over the continental slope off that port, June 23 and 24, 1915 (Bigelow, 1917, p. 300).

Bank suggest that Clione is less common there than within the gulf proper to the north. Thus, in March, 1920, it was not detected at all at the three stations (20065 to 20067) on the eastern end of Georges Bank, though on the slope to the south

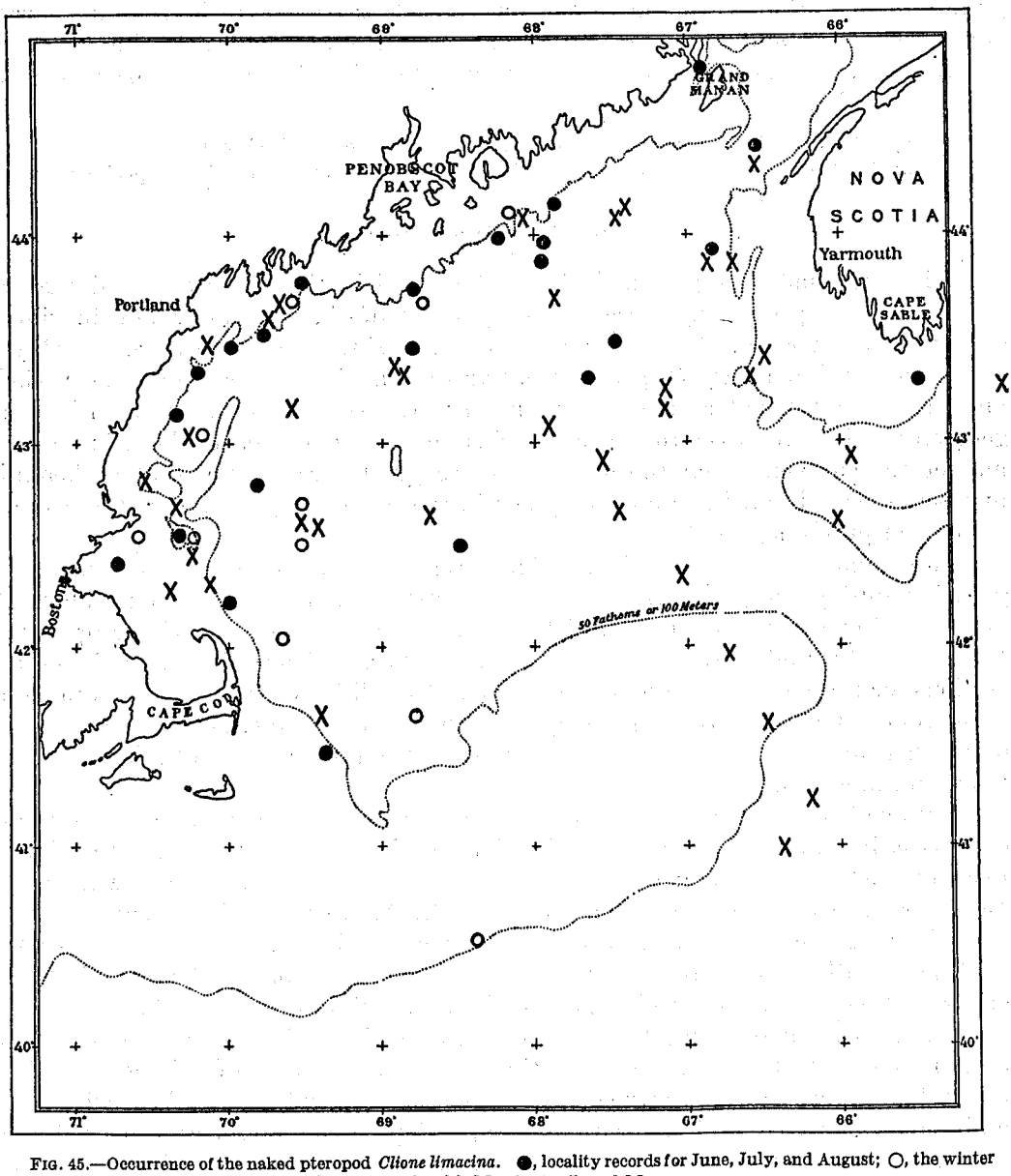


FIG. 45.—Occurrence of the naked pteropod *Clione limacina*. ●, locality records for June, July, and August; ○, the winter months; X, March, April, and May

(20068) a haul from 150–0 meters yielded four; and while it appeared again there (station 20109) and on the bank to the north (station 20110) on April 16, only one specimen was noted at each station. Apparently Clione vanishes from all parts of

Georges Bank as the season progresses, for we did not find it at any station there or along the continental slope abreast the gulf in July of 1913, 1914, or 1916.

We have never found Clione assuming any faunal prominence in the open waters of the Gulf of Maine, where it is usually represented by occasional specimens only among the mass of other plankton brought in by the nets. For example, in February, March, and April, 1920, all our hauls combined yielded not over 175 specimens of Clione, although it occurred at some 30 stations, whereas various other animals were captured in thousands—even millions in the case of the commoner copepods. Wood (1869, p. 185), it is true, found Clione so abundant in Portland harbor in May, 1868, that "the water appeared to be alive with them," but our experience ever since 1912 has been so consistent in this respect that I can only look on such local swarms of Clione as altogether exceptional for the Gulf of Maine, although this pteropod regularly appears in vast shoals in more northern seas.

It is still uncertain to what extent Clione is endemic in the Gulf of Maine. There is every reason to suppose that it immigrates more or less regularly into the gulf around Cape Sable via the Nova Scotian current, as do the various Arctic organisms, because it is far more numerous off the east coasts of Newfoundland and Labrador—where I found it swarming among the floe ice in the summer of 1900—about the Grand Banks of Newfoundland, and in the Arctic seas as a whole, than we have ever found it of late years in the Gulf of Maine or farther south. However, as I have elsewhere emphasized, in reality the local presence of Clione is not the sure index to Arctic currents many have supposed (Bigelow, 1917, p. 301, and 1922, p. 174), for it is as abundant in Atlantic as in Arctic waters around Iceland (Damas and Koefoed, 1907; Paulsen, 1910); and while Clione grows to a larger size in the latter than in the former, there is no reason to doubt, from their evidence, that it breeds successfully in both. Many authors have quoted its abundance south of Ireland, to which Massy (1909) called attention, and where there is no reason to credit it with an Arctic origin. According to Dr. A. G. Huntsman (in Bigelow, 1922, p. 135), its larvæ are found over the whole region from the Gulf of Maine to the Gulf of St. Lawrence and the Newfoundland Banks, at sea but not in estuaries.

Like many other animals, Clione decreases in numbers toward the boundary (in this case the southern) of its range, but it is probably impossible to draw any sharp line beyond which it can not maintain itself. No doubt as we pass from north to south it becomes more and more dependent on accessions of fresh blood from the north for the maintenance of the local stock, but in favorable seasons it may be expected to reproduce itself in unwonted numbers far beyond its normal zone of abundance. Probably the Portland swarm just mentioned resulted from an unusually successful wave of local reproduction; and the generality of its distribution over the gulf suggests that more or less Clione are produced there yearly, though probably immigration via the Nova Scotian current is the more important source of supply. On the whole, I see no reason to alter the view, earlier stated, that it probably rarely succeeds in breeding south of Cape Cod. Even in the Gulf of Maine Clione can reproduce itself in abundance only on the occasions when hydrographic conditions conspire in its favor, conditions occurring so rarely that only the one instance of this is known. I must caution the reader that very few

observations have been made on the occurrence of larval Clione that might or might not survive to maturity. Even in European seas, where the plankton has been much more intensively studied, little is known of the conditions of temperature and salinity under which its reproduction normally takes place (Paulsen, 1910).

Granting that Clione does reproduce itself to some extent in the Gulf of Maine, it follows that its presence at any particular time and place is not necessarily to be taken as evidence of a northern current; but in the last analysis Clione is essentially of northern origin in the gulf, and it is probable that a considerable proportion of the stock existing there at any given time are actual immigrants via the Nova Scotian current, some indirect evidence of which is yielded by the details of the records of its occurrence in the gulf. Thus, although the data yet at hand do not indicate any connection between the winter increase in the numbers of Clione and the fluctuations of the cold current (the latter is then at a low ebb), and although Clione shows no definite tendency toward concentration in the side of the gulf where this water is most in evidence, the spring maximum for Clione corresponds to the maximum annual intrusion of the latter into the gulf.

West and south of Cape Cod Clione may safely be classed as primarily an immigrant. As such it was long ago recorded as far south as the coast of Virginia (Rathbun, 1889), and probably it is a more or less regular if usually uncommon visitor along this part of the continental shelf in winter and spring, for the *Albatross* towed it off Delaware Bay on February 20, 1920 (station 20042), and Rathbun (1889) recorded it from localities on the outer part of the shelf between the latitudes of New York and Chesapeake Bay in April and May of 1887. Occasionally large numbers of them may drift south, De Kay (1843, p. 66) describing them as very abundant in the bays near New York in April, 1823, but only for a few days, after which they vanished. In warm summers, such as that of 1913, it vanishes beyond Cape Cod by July, but in the cool summer of 1916 its presence off Chesapeake Bay, off Delaware Bay, and off New York in August suggested temporary breeding activity under rarely favorable local conditions, a view supported by the fact that at one of these stations (10386) Clione larvæ were taken with the adults (Bigelow, 1922, pp. 156, 174). Evidently, however, Clione did not succeed in maintaining itself there much later into the season, because it was not taken in these southern waters at any of the November stations for that year. The high temperatures of the tropical "Gulf Stream" water are a fatal barrier to the offshore dispersal of Clione a few miles outside the continental edge, from abreast of southern Nova Scotia southward.

Probably Clione is never numerous enough, or locally numerous, in the Gulf of Maine for a long enough period to be of any importance in its natural economy. In more northern seas its great swarms afford a bounteous food supply for whales, and it is an important article of diet for both mackerel and herring in Irish waters, according to Paulsen (1910).[67]

[67] Station records of Clione in the Gulf of Maine have been published as follows: For July and August, 1912, in Bigelow, 1914, p. 118; for the winter of 1912–1913 and the spring of 1913, in Bigelow, 1914, pp. 403, 406, and 407; for the summer of 1913, in Bigelow, 1915, p. 302. In July and August, 1914, it was detected at stations 10213, 10243, 10249, and 10255; in the season of 1915 at stations 10276, 10277, 10278, 10280, 10281, 10282, 10286, 10287, and 10306; in July, 1916, station 10346; in October and November, 1916, not at all; in the spring of 1920, stations 20046, 20048, 20049, 20053, 20055, 20056, 20057, 20058, 20068, 20074, 20079, 20081, 20086, 20087, 20091, 20094, 20095, 20097, 20100, 20101, 20103, 20105, 20106, 20109, 20110, 20112, 20113, 20114, 20115, 20119, 20122, 20124, and 20126; in December, 1920, and January, 1921, stations 10489, 10491, 10493, 10495, 10496, and 10497.

## Other pelagic mollusks

Apart from the cephalopods and the three pteropods (*Limacina retroversa*, *L. helicina*, and *Clione limacina*) just discussed, very few adult pelagic Mollusca have ever been found within the southern rim of the Gulf of Maine.[68] The *Grampus* cruises have yielded an Atlanta and two specimens of the pteropod *Diacria trispinosa* from 10 miles north-northwest of Gloucester on July 8, 1913, and two of *Limacina inflata* taken off Cape Cod July 19, 1914 (station 10213). All these species are characteristic of the warmer parts of the North Atlantic, not of boreal waters, and hence reached the gulf as stragglers from the warm waters of the Atlantic to the south; but it is hard to account for their presence at the particular times and places of capture, because "they were taken with an otherwise typical boreal assemblage of plankton organisms" (Bigelow, 1915, p. 306).

A Pneumoderma, or some closely allied pteropod too young for identification, was taken near Lurcher Shoal on August 12, 1914 (station 10245); and, under the name Pseudoclione, Danforth (1907) has described a pteropod of doubtful relationship from Casco Bay, which showed sexual maturity combined with various larval characters (taken August 29 and again September 5 to 8, 1902). A *Cavolina tridentata* and two Pterotrachea from the southern edge of Georges Bank, respectively on July 21 (station 10219) and July 20 (station 10216) in 1914, complete the brief list.

In contrast to the Gulf of Maine, the waters along the continental slope from the longitude of New York eastward have proved extremely rich in warm-water pteropods and heteropods carried thither in the sweep of the Gulf Stream, whence considerable lists of them were obtained by the early expeditions of the Bureau of Fisheries (Smith and Hargar, 1874; Verrill, 1885; Johnson, 1915), as well as on our more recent *Grampus* cruises (Bigelow, 1917, p. 302). However, since it is only in the rarest instances that any of these find their way into the inner parts of the Gulf of Maine, little space need be devoted to them here.

The captures of this category made by the *Grampus* in July, 1913, and July, 1914, are noted elsewhere (p. 54; Bigelow, 1915, p. 301; Bigelow, 1917, p. 302). These two lists together comprise some 14 species, while Johnson (1915), in his more complete summary of previous records, mentions 25, representing the genera Firoloida, Carinaria, Atlanta, Clio, Cuvierina, Peracle, Corolla, and Glaucus. Others (e. g., Janthina) have also been recorded, but only from examples washed up on the beaches of southern New England or the outlying islands. To illustrate how seldom any of these oceanic Mollusca stray within the 500-meter contour and how sharply their range contrasts with that of their boreal relative *L. retroversa*, the accompanying chart (fig. 46), showing all records listed by Johnson (1915), is offered. All these are from summer and autumn. In winter and spring warm water, with its characteristic tropical-oceanic inhabitants, lies farther out from the continental edge.

[68] Leaving out of account the various pelagic bivalve and gastropod larvæ.

## CRUSTACEANS

### Adult decapods

The Gulf of Maine supports a host of decapods—that is, crabs, shrimps, and lobsters—the larval stages of which often swarm in the plankton, most often along

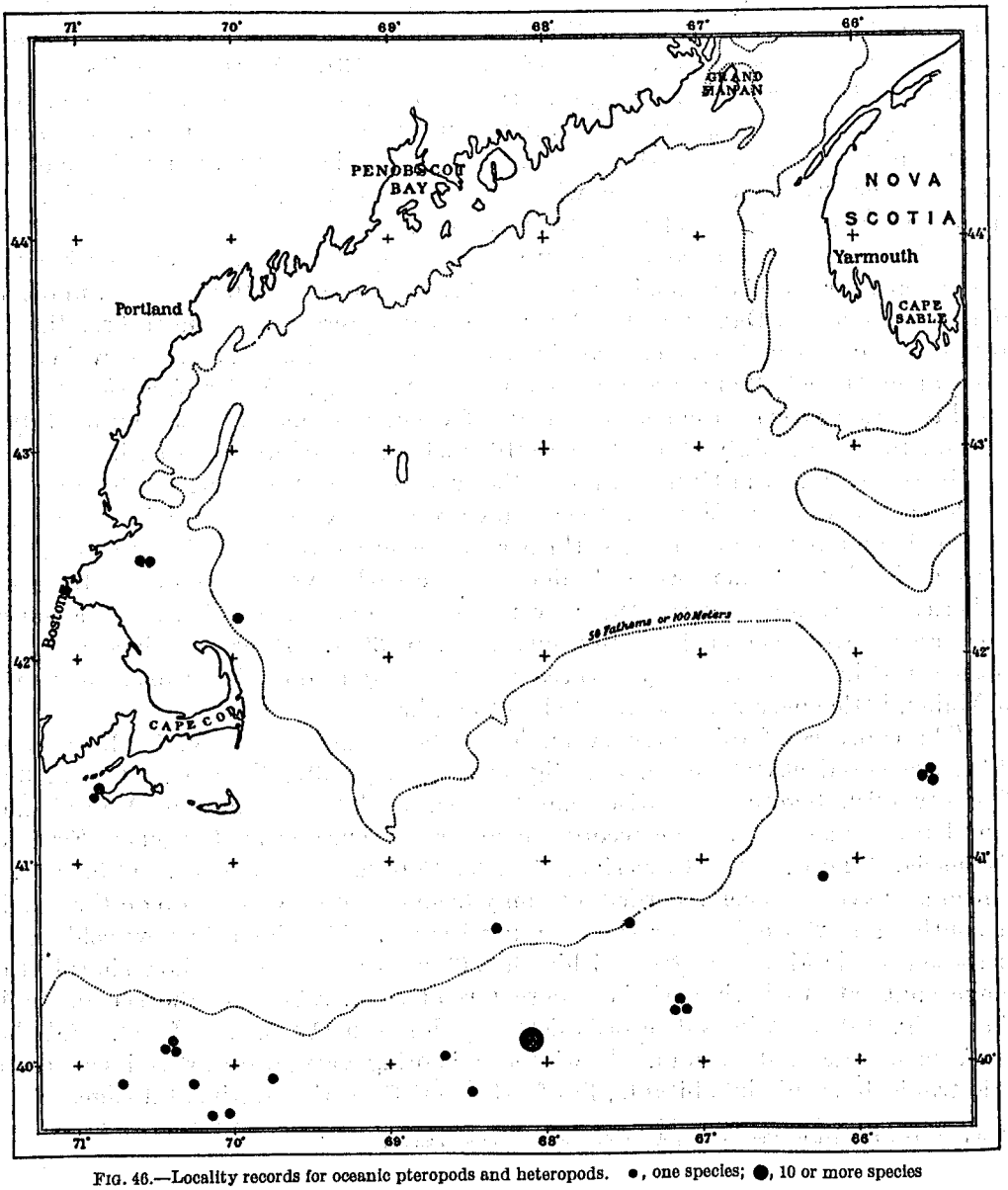


FIG. 46.—Locality records for oceanic pteropods and heteropods. •, one species; ●, 10 or more species

shore, as noted elsewhere (p. 34). The adults of nearly all of them live on the bottom, except when some of the shrimps make brief swimming excursions upward when disturbed, as, for instance, by the passage of the bottom net or trawl, or when

they are lifted by active vertical currents. The glass shrimps (genus Pasiphæa) are the only decapods regularly planktonic in the Gulf of Maine when adult.

### Pasiphæa

These shrimps are so much larger (80 to 90 millimeters long when adult) than any other crustaceans pelagic in the gulf that even a single specimen is sure to be detected in the tow. It is therefore safe to assume that the list presented herewith comprises our whole catch, which is not true of smaller organisms easily overlooked in the mass of other plankton unless abundantly represented in the catch.

We towed our first glass shrimps (three in number) in the western basin in a haul from 150 meters on August 9, 1913 (station 10088). Since then they have been taken there on August 22, 1914; August 31, 1915; March 5, 1920; and April 18, 1920 (stations 10254, 10307, 20087, and 20115), and likewise at two stations in the deep water in the northeastern part of the gulf (March 3, 1920, station 20055, and March 22, 1920, station 20081); once in the southeast corner (April 17, 1920, station 20112), and once at the outer edge of the shelf off Cape Sable (March 19, 1920, station 20076).

So far as I can learn, the only previous records of this genus for the Gulf of Maine are as follows: Western Basin, approximate latitude 42° 38′, longitude 69° 38′, two specimens dredged in 203 meters in August, 1877; two more near the same locality, 256 and 311 meters (dredge), on August 27, 1878 (Smith, 1879); others from Cape Cod Bay and from off Cape Cod, 25 meters and 212 to 223 meters, respectively (Rathbun, 1905).

These early captures were recorded as *Pasiphæa tarda*, which has long been spoken of as the characteristic northern representative of the genus (Wollebæk, 1908). Sund (1913), however, has more recently shown that at least three perfectly distinct and easily recognizable species have been confounded under this name, Smith's own illustration (S. I. Smith, 1879, pl. 10, fig. 1) showing that in reality the early American records were not based on *tarda* but on the *P. multidentata* of Esmark, which has also proved to be the commonest glass shrimp in Norwegian waters.[69] All the recent specimens from within the Gulf of Maine likewise are *multidentata*, a perfectly transparent species, whereas *P. tarda* is commonly blood red. Our records of *P. multidentata* have been from comparatively deep hauls, though not invariably from the deepest stratum in the Gulf (fig. 47) as follows:

| Station | Depth of haul in meters | Depth of water in meters | Station | Depth of haul in meters | Depth of water in meters |
|---|---|---|---|---|---|
| 10088 | 146–0 | 274 | 20076 | 200–0 | 250 |
| 10254 | 75–0<br>225–0 | 286 | 20081 | 140–0 | 206 |
| 10307 | 230–0 | 245 | 20087 | 200–0 | 255 |
| 20055 | 180–140 | 230 | 20112 | 200–0 | 290 |
| | | | 20115 | 200–0 | 290 |

So far as I can learn, Pasiphæa has never been taken on the surface or in plankton hauls shoaler than 75 meters in the Gulf of Maine, though it has been dredged in as shallow water as 25 meters; hence, it is clearly bathypelagic in the

[69] The several species are easily separable by the form of the rostrum, which is high and coniform in *multidentata*. For details I refer the reader to Sund (1913).

gulf, just as in the Norwegian fjords (Wollebæk, 1908), and very probably it lives on the bottom part of the time.

The material at hand is not sufficient to throw any light on the breeding habits of Pasiphæa in the Gulf, except that females carrying the very large eggs were taken

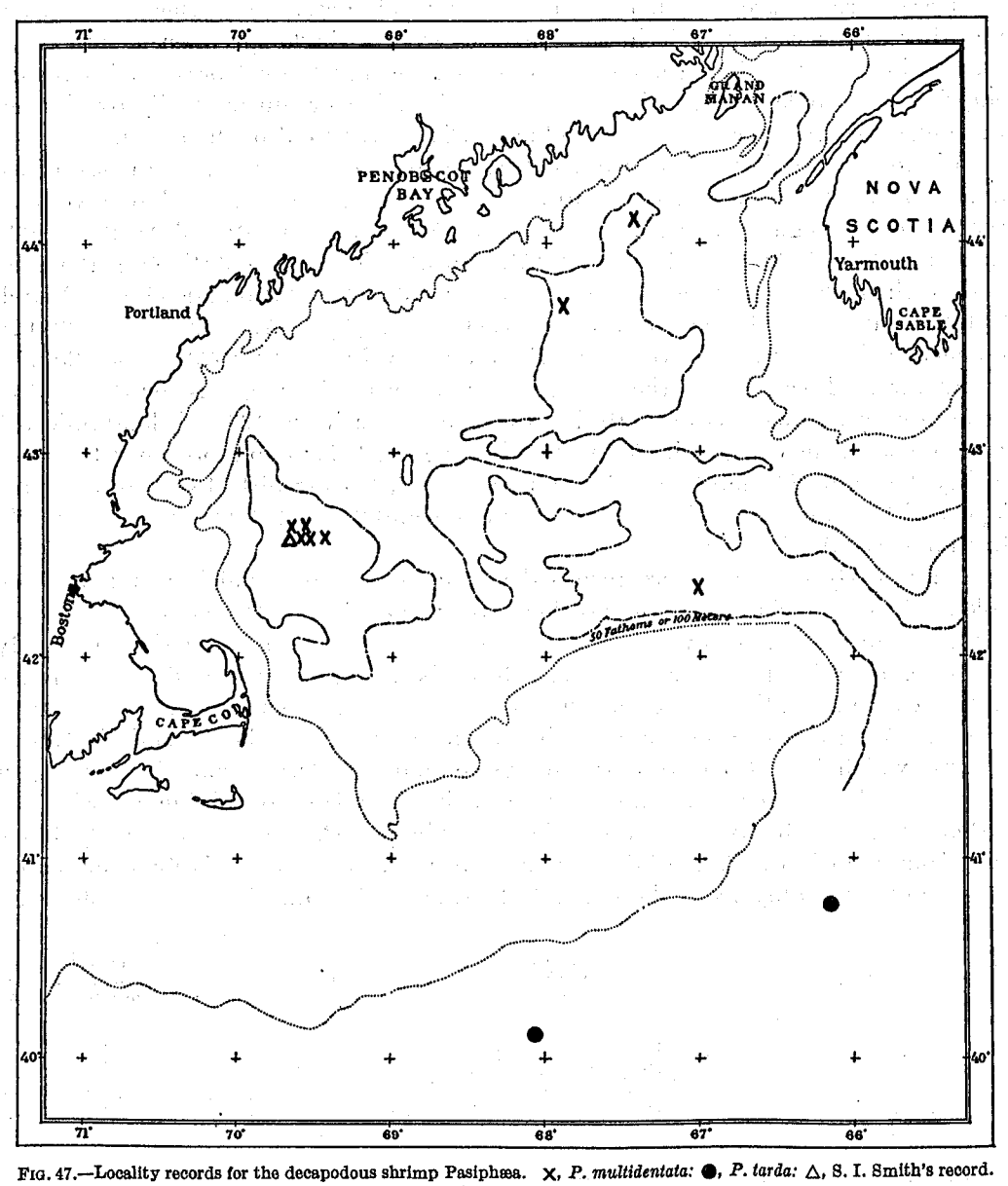


FIG. 47.—Locality records for the decapodous shrimp Pasiphæa. X, *P. multidentata:* ●, *P. tarda:* △, S. I. Smith's record. (See p. 131)

in August (station 10254) but not in March or April. The locations of capture suggest the western basin (where we have usually, though not invariably, found it in our deepest hauls) as the chief local center of abundance for Pasiphæa, but it is

to be expected anywhere in the gulf below 200 meters—witness the records from the eastern basin and from the southeast deep.

We have only two records for *P. tarda*, both over the continental slope off Georges Bank in hauls from 750 to 100 meters, February 22 and March 12, 1920 (stations 20044 and 20069), which agrees with Sund's (1913) experience that this species usually lives at a rather deeper level than *P. multidentata*, from which it is separable by the low rostrum, hardly rising above the general dorsal outline, and by its red color. We have not taken *P. principis*, but this species is recorded from south of Marthas Vineyard by Sund (1913).

## Euphausiids

We are indebted to Dr. H. J. Hansen, who identified the collections made during the summer of 1912 and winter of 1912 and 1913, and to Dr. W. M. Tattersall, who undertook the same task for the gatherings of 1914,[70] for ability to include a chapter on this economically important and faunistically instructive group of pelagic crustaceans. I have attempted the identifications of the euphausiids contained in the tow nettings of our subsequent cruises by comparison with specimens named by these two eminent specialists and by the aid of Zimmer's (1909) very clear keys and descriptions; but while it is easy to name the adults of all the species occurring regularly in the Gulf of Maine, by easily recognizable anatomical features, the larval stages, occasionally abundant (p. 134), still await reference to their proper parentage.

Knowledge of the occurrence of this group in the deep water outside the continental shelf abreast of the gulf, between the longitudes of 71 and 65°, is chiefly based on the collections made by the Bureau of Fisheries' vessels in past years, recently reported upon by Doctor Hansen (1915).

Only a few species of euphausiids are yet known to occur within the gulf, nor is it likely that the various oceanic members of the group will ever be found in its inner parts except as stragglers; but these few (to be treated in detail below) are among the most characteristic if not the most numerous members of its endemic plankton. True, they seldom dominate the catch, or even form any considerable part of it, except locally in the northeast corner of the gulf and near the mouth of the Bay of Fundy, and when they swarm in other parts of the gulf it is only for brief periods. But our tow nets have seldom failed to yield them in greater or less number, except at times and localities when the catch as a whole has been of the scantiest. Euphausiid shrimps are so important in the dietary of whales and of many fishes that pursue them eagerly (and indeed one can well believe them dainty morsels) that they are much more important economically than their small numbers, contrasted with the hosts of copepods, might suggest. This subject is discussed in another chapter (p. 97).

The occasions on which we have made notably rich hauls of euphausiids within the limits of the Gulf of Maine have been as follows: On Browns Bank, July 24, 1914 (station 10228), the haul at 60–0 meters yielded about 500 cubic centimeters of small Thysanoessa, representing three species (*Thysanœssa gregaria, Th. longicaudata,*

[70] For tables of occurrence of the several species in these years see Bigelow, 1914a, p. 411, and 1917, p. 282.

and *Th. inermis*), many large Meganyctiphanes, and a few Nematoscelis. Four days later we again encountered a euphausiid plankton over the continental slope off Shelburne, Nova Scotia (station 10233), where half-hour hauls on the surface, at 100–0 meters and at 200–0 meters, yielded, respectively, 125, 500, and 250 cubic centimeters, chiefly euphausiids. On this occasion the surface catch consisted mainly of Euphausia, but Nematoscelis dominated at 400 meters, with the two species mingled at the 100-meter haul. An abundance of these two genera is perhaps characteristic of this general location in summer, for we again found them in large numbers over the continental slope near by on June 24, 1915 (station 10295). This does not apply to Browns Bank, however, which was barren of euphausiids on June 24, 1915 (station 10296), though productive of them the previous July; nor did we find more than an odd specimen there in March or April, 1920 (stations 20072 and 20106). Small *Th. longicaudata* were numerous over the northeast part of Georges Bank on March 13 of that year (station 20070). By April 16 (station 20108) they had vanished thence, but the fact that we once more found small *Th. longicaudata* very plentiful off the southwest face of the bank on May 17 (station 20129) suggests that the swarm had drifted westward from one end of the bank to the other during the interval from March to May.

Turning now to the inner parts of the gulf, we have twice found the waters off northern Cape Cod supporting larval and very young Thysanoessa in abundance (July 8, 1913, station 10057, and August 28, 1914, station 10264). Medium-sized and adult specimens of this genus (particularly *Th. inernis*, p. 135) were also taken in large numbers in the eastern side of the basin in May (station 10270) and off Cape Ann in August, 1915 (station 10306). On August 22, 1914 (station 10254), we found Meganyctiphanes abundant in the deeper water layers of the western basin, but the most interesting swarming of shrimps of this group in the western part of the gulf was the sudden appearance of shoals of *Thysanoessa raschii* off the Isles of Shoals late in April, 1913, as described below (p. 145). Provincetown Bay was similarly invaded by "shrimps," very likely of this same species, in March, 1880, as described by A. H. Clark (1887), and in August, 1923, euphausiids of some sort were so plentiful at the surface off Penobscot Bay that Dr. George C. Shattuck wrote me of seeing "a good many shrimp in the water" while sailing from Isle au Haut to Matinicus Island during the last week of the month.

All the congregations of pelagic shrimps mentioned so far have been sporadic, or at least of brief duration; but euphausiids are often enough plentiful in the extreme northeast corner of the deep basin, some 50 miles southwest of Grand Manan, at various seasons, for this local abundance to be regarded as characteristic. Our first visit to this locality (in August, 1912) did not suggest this (indeed, not a single euphausiid was noted in the tow on that occasion), but many large specimens of *Meganyctiphanes norvegica* were taken at this general location on August 13, 1913 (station 10097), in a haul from about 160–0 meters; again on August 13, 1914 (station 10246, 150-0 meters); on May 10, 1915 (station 10273, 125–0 meters); on June 10, 1915 (station 10283, 100–0 meters); and in the basin, a few miles to the southward, on August 7, 1915 (station 10304). If the year 1920 can be taken as typical, this local abundance of Meganyctiphanes is as characteristic of spring as of midsum-

mer, for this shrimp was plentifully represented in that region on March 22 (station 20081) in hauls from 40 and from 200 meters, while the haul from 100 meters yielded about 50 on April 12 (station 20100), although the zooplankton as a whole was decidedly scanty on that occasion. I hesitate to extend this generalization to the winter, however, because only a few euphausiids were taken there on January 5, 1921 (station 10502).

Euphausiids [71] are often extremely plentiful near the surface in the Eastport–St. Andrews region at the mouth of the Bay of Fundy, where the smaller-sized herring can be seen chasing them to and fro right up to the docks (p. 102), and they are so conspicuous when schooling that they must have been seen and commented upon by local fishermen from the first settlement of that coast. The earliest published reference to their local abundance there, or in any part of the gulf, for that matter, seems to have been in 1879, when S. I. Smith (1879, p. 90) described *Meganyctiphanes norvegica* as occurring at the surface in the Eastport region in "swarms, filling the water for miles," and as "usually accompanied by schools of mackerel, young pollock, and other fish, and in autumn by immense flocks of gulls, the fish and smaller gulls appearing to feed almost exclusively on Thysanopoda at such times." Such occasions he recorded for April, August, September, and October, adding that Verrill found these shrimp swarming in myriads in the ripplings in the center of the Bay of Fundy in 1869, and that they are often so abundant among the wharves at Eastport that they may be caught there by the quart. Moore also wrote (1898, p. 401) that "during the summer and fall dense bodies of Thysanopoda are seen swimming about the wharves at Eastport and at other places in the vicinity, and they are also extremely abundant on the ripplings at Grand Manan, which has long been famous as a herring fishery. Excepting the eyes and the phosphorescent spots beneath, which are bright red, the bodies of these shrimps are almost transparent, yet such is the density of the schools in which they congregate that a distinct reddish tinge is often imparted to the water. In the summer and early fall of 1895 they were especially abundant about the wharves at Eastport, and on one occasion, at least, they were left at low water several inches deep over a considerable area of one of the docks." Moore believed that *Thysanoessa inermis* was the species chiefly concerned, but in the light of subsequent observations it is probable that then, as now, it was outnumbered there by Meganyctiphanes. Our own observations, with information communicated by Doctor Huntsman, show that the passage of time has seen no diminution in the abundance of the latter in the Eastport–St. Andrews region in summer and early autumn.

It is only in the extreme northeast corner of the gulf, perhaps east of Machias, that euphausiids appear regularly in estuarine situations; farther west and south the group, as a whole, are creatures of the open sea.

### Thysanoessa inermis (Krøyer) [72]

*Thysanoessa inermis*, as I have stated elsewhere (Bigelow, 1917, p. 283), occurs more regularly over the gulf as a whole than any other euphausiid, though it is not the most abundant locally. In July and August, as exemplified by the summers of

[71] Chiefly Meganyctiphanes, but Thysanoessa as well, according to Smith (1879), Moore (1898), and our own observations.

[72] I follow Hansen (1911) in including under this name both *Th. neglecta* and *Rhoda inermis*, which, as he has shown, are merely varieties of the one species.

1912, 1914, and 1915, it occurred at about 50 per cent of our stations (fig. 48), with the records for those months distributed generally throughout the offshore parts of the gulf as well as over Georges and Brown's Banks and over the shelf off Marthas Vineyard and Nantucket.

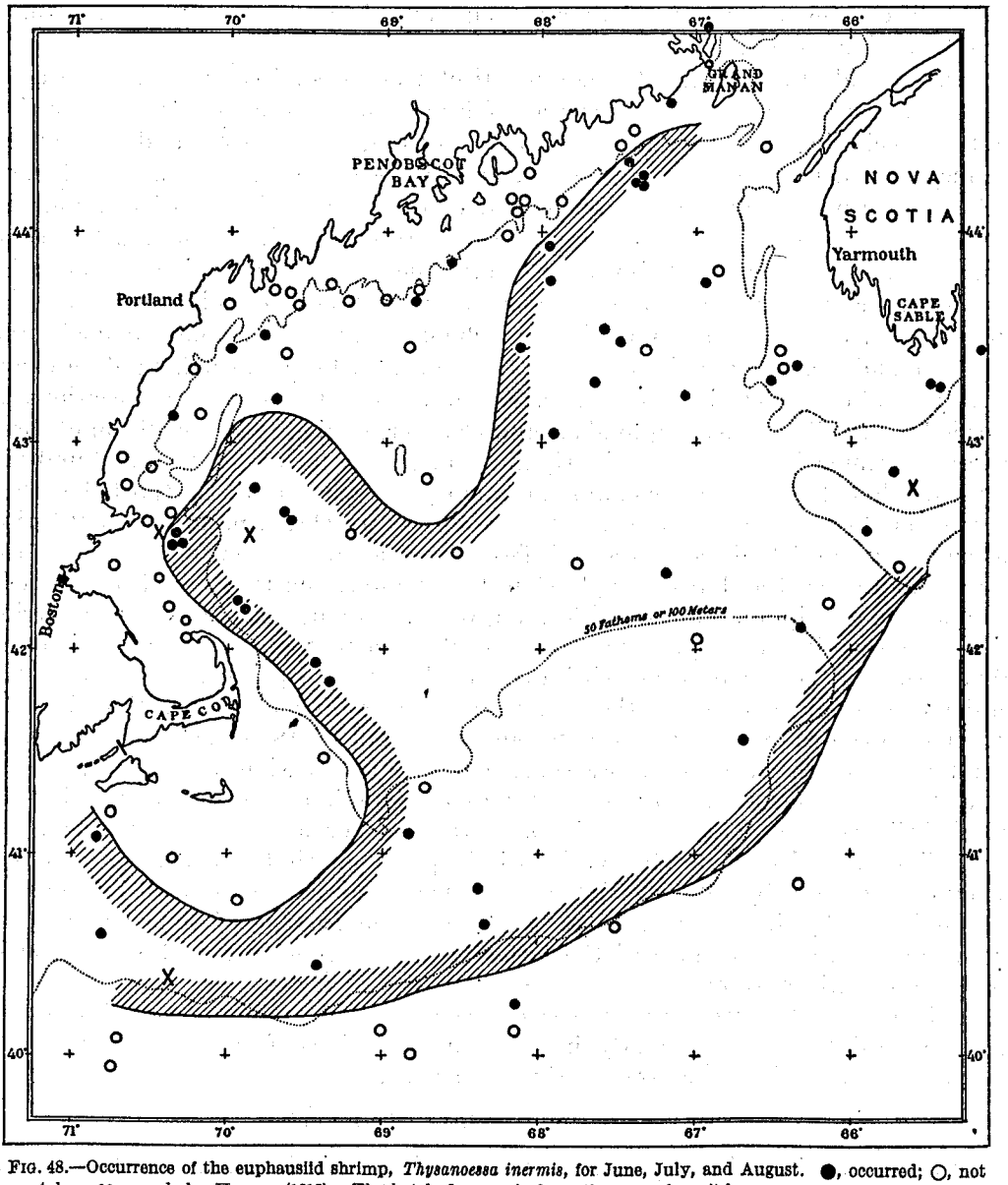


FIG. 48.—Occurrence of the euphausiid shrimp, *Thysanoessa inermis*, for June, July, and August. ●, occurred; ○, not taken; X, records by Hansen (1915). The hatched curve incloses the area where it has occurred at 50 per cent of the stations

This species (figs. 48 and 49) has occasionally been recorded close to land in Massachusetts Bay and may be abundant temporarily in Eastport Harbor, as just noted, but its presence in these estuarine waters is only sporadic in summer. Nor

did Doctor McMurrich detect it at all at St. Andrews at that season, though it occurred there in November, December, and January, and occasionally in February and March. In fact, we have usually found it wanting in summer throughout the

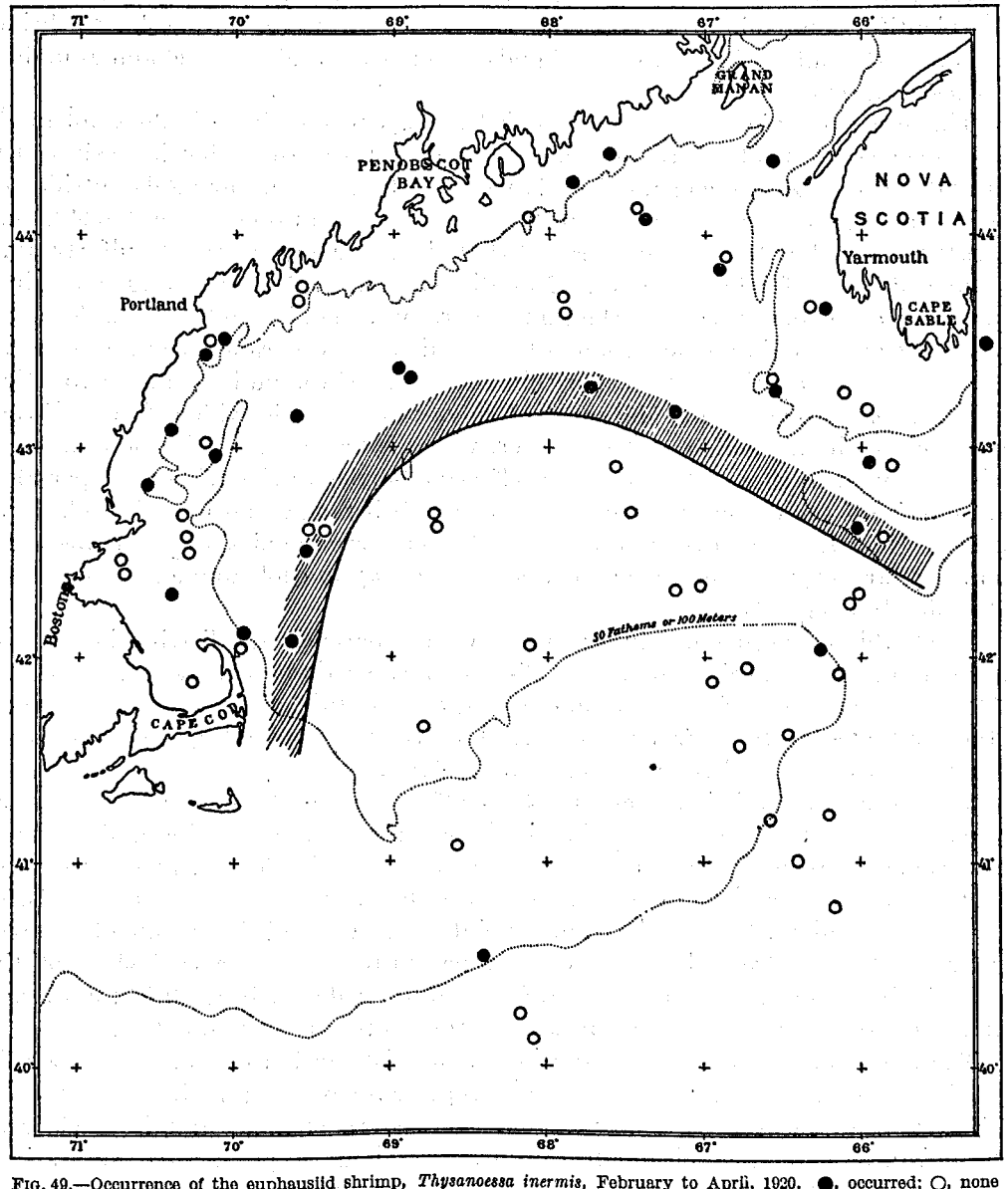


FIG. 49.—Occurrence of the euphausiid shrimp, *Thysanoessa inermis*, February to April, 1920. ●, occurred; ○, none taken. The hatched curve incloses the area where it occurred in about 50 per cent of the stations for March and April

coastal zone from Cape Cod to Grand Manan, with the 100-meter contour roughly marking its shoreward limit from Cape Ann to the mouth of the Grand Manan Channel at that season. But its regular presence over the shallow southern rim of

the gulf, as well as close up to the land off Cape Sable and in Eastport harbor during the warm months, shows that it is not the shoalness of the water which holds it offshore, but either some influence of the coast line itself or the physical state of the water. Thus it is rather more oceanic in the gulf than its omnipresent and much more plentiful companion, the copepod *Calanus finmarchicus*, for the latter thrives right up to the outer islands and headlands, though its adults are seldom abundant in inclosed waters.

The term "oceanic," however, as applied to *Thysanoessa inermis*, does not imply that it reaches the Gulf of Maine from the warm water of the Atlantic Basin to the east and south. On the contrary, we have never found it in our hauls outside the continental edge, either east or west of Cape Cod, except at one station (10349, July 24, 1916), where low temperature proved that the inner edge of the "Gulf Stream" lay some distance farther offshore. Nor did Hansen (1915) find it in gatherings taken over the slope abreast of the gulf, where other euphausiids—e. g., Nematoscelis— occurred in abundance, though he records it from various localities over the outer part of the continental shelf within the limits of the gulf—e. g., off Marthas Vineyard, near Browns Bank, and south of Nova Scotia. It is evident from this that the warm and highly saline tropical water, which is never far out beyond the edge of the continent in these latitudes, is an effective barrier to the offshore dispersal of *Th. inermis* off the eastern United States, although it ranges southward regularly to southern New England every summer, and even accompanies the Calanus community as far south as the latitude of Chesapeake Bay in cool summers (e. g., 1916) and probably every winter.

In all this its occurrence in American waters parallels its distribution on the other side of the Atlantic, where it is distinctively arctic-boreal, as Kramp (1913, p. 544) points out, occurring chiefly in the northern Atlantic and in the adjacent parts of the Arctic Ocean from Franz Josef Land to West Greenland, and southward as far as the North Sea and the waters around Ireland.

*Thysanoessa inermis* is present in the Gulf of Maine throughout the year, as proven by the fact that we have taken it there throughout the spring and summer, at several stations in September and October of 1915, twice (out of five stations) in November in 1916, and at about half the stations occupied during our midwinter cruise of 1920 and 1921. As I have just pointed out, winter is its season of greatest abundance at St. Andrews, but it shows no apparent tendency to work inshore off the coasts of Massachusetts at that season, for we did not detect it at all in tows taken near Gloucester every two weeks throughout the winter of 1912 and 1913.[73]

The most notable seasonal fluctuation in the distribution of *Th. inermis* within the gulf (supposing its status in 1920 to be representative) is that it almost totally disappears from the southern deeps, from the eastern channel, and from Georges Bank in March and April, although it occurred at about 50 per cent of our stations around the coastal belt at that season (fig. 49). Our failure to find it over the eastern

[73] For its occurrence from 1912 to 1916 see Bigelow, 1914a, p. 411; Bigelow, 1917, pp. 282 and 283; and Bigelow, 1922, pp. 133, 136, and 150. In the spring of 1920 it was detected at stations 20046, 20049, 20054, 20057, 20059, 20060, 20070, 20073, 20075, 20079, 20080, 20085, 20086, 20088, 20092, 20093, 20094, 20097, 20099, 20100, 20101, 20102, 20105, 20106, 20116, 20119, 20122, 20125, and 20126; as well as at the following stations from December, 1920, to January, 1921: 10490, 10494, 10497, 10499, 10500, 10502, and at stations 10507, 10508, 10509, and 10510 in March, 1921.

end of Georges Bank during these months certainly was not accidental, for we made two traverses of the bank four weeks apart, and it was equally wanting at our several stations on the western end of the bank on May 17, a month when we have previously found it widespread in the inner parts of the gulf.

It will require more than the one year's data to prove whether this vernal contraction of the range of *Th. inermis* on the offshore side, which must be followed by a corresponding expansion in June to repopulate these waters to the extent that obtains in midsummer, is an annual occurrence.

We have yet to learn how far the maintenance of the local stock of *Th. inermis* in the Gulf of Maine depends on the reproduction which takes place there and how far on immigration around Cape Sable from the colder waters of the Nova Scotian current, no attempt having yet been made to trace the life history of this shrimp in the gulf. It is probable that *Th. inermis* breeds successfully at least as far west as Cape Cod, and that it is represented among the considerable numbers of larval euphausiids which we have taken there side by side with medium-sized specimens and large adults of this species.

*Thysanoessa inermis* has never been found in abundance at the surface in any part of the gulf except at Eastport, though it has often occurred in small numbers in the catches of the surface nets. On the other hand, our deepest hauls in the gulf have never yielded many, and the largest catches have all been in nets working at 40 to 80 meters depth. Thus it tends to congregate at about the same level as Calanus and is not associated with the Euchæta community of the deep basins, as its relative *Meganyctiphanes norvegica* so often is.

I can offer no data bearing on the actual numerical strength of *Th. inermis* in the gulf, nor could much dependence be placed on the results of vertical hauls in the case of so active an animal unless with larger nets than we have used. Our largest catches of it have been made near Cape Ann (August 22, 1914, station 10253), on the eastern end of Georges Bank (July 23, 1914, station 10223), near Cape Sable (August 11, 1914, station 10243), and off Marthas Vineyard (August 25, 1914, station 10259).

### Thysanoessa longicaudata (Krøyer)[74]

This species, as Kramp (1913) and Holt and Tattersall (1905) have pointed out, is generally distributed in Arctic Seas and in the northern part of the Atlantic, ranging south to the west coast of Ireland and northern North Sea in European waters. On the whole, it is more northern and more oceanic in its affinities than *Th. inermis*, but, like the latter, the records for it in the Gulf of Maine are so widely distributed that it is to be expected anywhere in the offshore parts of the latter in summer (fig. 50), late winter, and early spring. Only three times in all our experience, however, have we detected it in the coastal zone inside the 100-meter contour at any season, and never in inclosed bays or estuaries.

*Thysanoessa longicaudata* is far less numerous in the gulf than its relative *Th. inermis*, and occurs there far less regularly, having been detected at fewer than 25 per cent of our summer stations (fig. 50), and then usually in small numbers; nor

[74] For the occurrence of this species in 1912 to 1916 see Bigelow, 1914a, 1917, and 1922. In the spring of 1920 it was taken at stations 20045, 20046, 20054, 20057, 20060, 20064, 20065, 20066, 20069, 20070, 20073, 20075, 20076, 20077, 20079, 20080, 20086, 20087, 20100, 20101, 20107, 20112, 20116, and 20129. It was also taken in December, 1920, and January, 1921, at stations 10490, 10494, and 10502.

does there appear to be much change in its status from season to season, for it was found at about 20 per cent of the stations occupied by the *Halcyon* during December, 1920, and January, 1921, and at about 25 per cent of the *Albatross* stations of Feb-

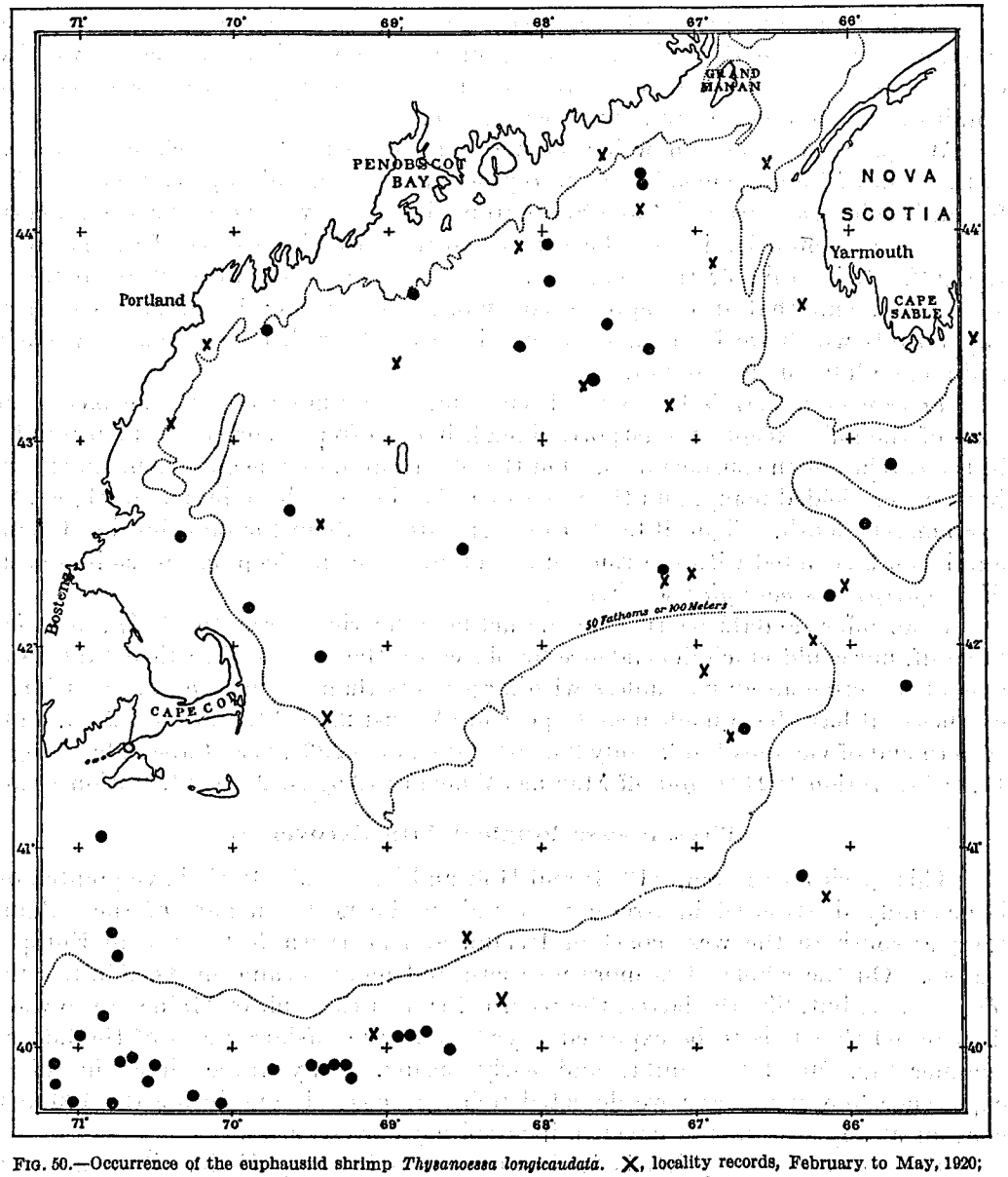


FIG. 50.—Occurrence of the euphausiid shrimp *Thysanoessa longicaudata*. X, locality records, February to May, 1920; ●, July to September, including Hansen's (1915) records

ruary to May, 1920 (fig. 50). Although the locations where *Th. longicaudata* has actually been taken are not concentrated in the one side of the gulf or in the other, we have usually made our largest catches of it in the eastern part, both in spring

and in summer. For instance, it was abundant on the edge of Georges Bank on March 13, 1920 (station 20071), and on Browns Bank on July 24, 1914 (station 10228). This phenomenon and the fact that we have found it at most of our stations along the continental slope abreast of Georges Bank and south of Nova Scotia, where *inermis* has usually proved wanting, is no doubt correlated with its oceanic nature, and Hansen (1915) records *Th. longicaudata* from many localities over the slope south of Marthas Vineyard, often in great abundance.

Evidently this shrimp is a characteristic inhabitant of the cool band of water of mixed origin which separates the tropical Atlantic (so-called "Gulf Stream") water from the continental shelf. Probably it comes as a wanderer from the east and north, and it may follow the outer part of the shelf at least as far south as the latitude of Chesapeake Bay in cool summers, as in 1916 (Bigelow, 1922, p. 151); but we have never found it at any station where the presence of a tropical planktonic community has betrayed a large admixture of "Gulf Stream" water. Judging from the boreal-Artic affinities of *Th. longicaudata*, it is probable that high temperatures and salinities form an impenetrable offshore barrier to its dispersal off the coasts of Nova Scotia and the United States.

*Bathymetric range.*—We have yet to find *Th. longicaudata* on the surface in the Gulf of Maine in summer, most of the records of it for the three months, July to September, being in hauls from 80 meters or deeper, the shoalest from 50–0 meters (two hauls). An interesting example of its preference for deep water is afforded by its vertical distribution in the western basin on August 22, 1914 (station 10254), when there were none on the surface, and, allowing for the use of different-sized nets, many more at 235–0 meters depth than at 75–0 meters (Bigelow, 1917, p. 282). Although it is not so closely confined to the deeper strata of water during the early spring (for we found many on the surface over the eastern end of Georges Bank on March 13, 1920 (station 20070), and a few on the surface in the western side of the basin 10 days later (station 20087)) most of the spring records of the species in the gulf have likewise been from depths greater than 75 meters. Thus, it finds its most favorable habitat at a deper level than that of *Th. inermis*.

Judging from the rather conflicting statements of European students (Holt and Tattersall, 1905; Hansen, 1908; Tattersall, 1911; Kramp, 1913), *Th. longicaudata* is equally a deep-water form on the other side of the Atlantic, though it comes right up to the surface of the water about Iceland (Paulsen, 1909). Probably the warm layer that forms over the surface of most boreal seas in late spring and summer acts as a barrier to its upward dispersal during the warm half of the year, just as high temperature confines it offshore, abreast of the Gulf of Maine. At any rate, its avoidance of the surface in summer and of the coastal zone at all seasons makes it an inhabitant of low temperatures and comparatively high salinities in the Gulf of Maine, where the water in which most of the stock lives ranges from about 2° to about 10° in temperature and upward of 32.5 per mille in salinity.

Whether *Th. longicaudata* breeds in the Gulf of Maine or appears there only as an immigrant from the north is yet to be learned. Probably it is endemic there in small numbers, like other planktonic animals with a similar affinity for low temperature, but depends as much on more or less constant immigration from

northern sources, either around Cape Sable or from the mixed water along the outer part of the continental shelf, for the maintenance of its numbers within the gulf.

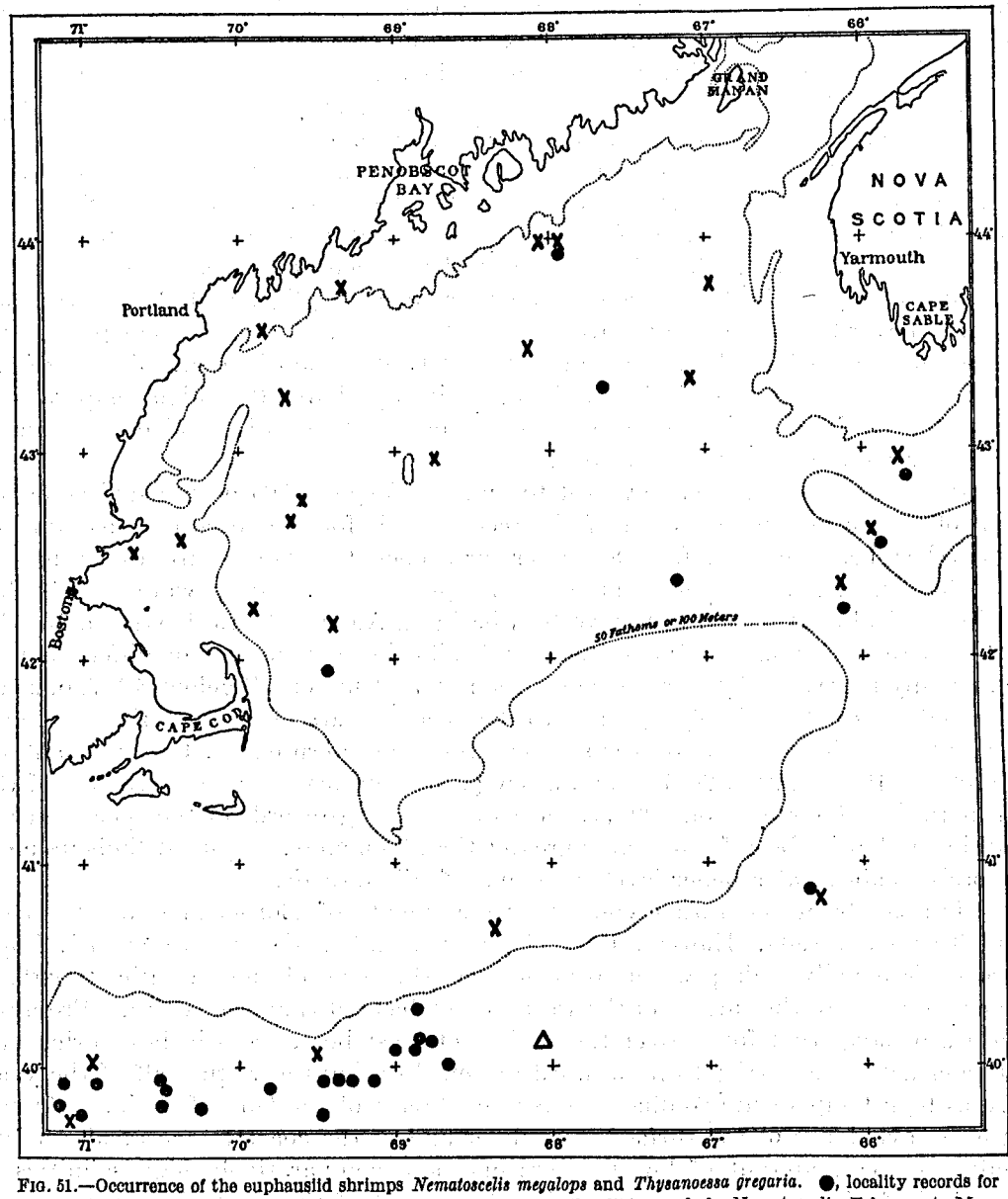


FIG. 51.—Occurrence of the euphausiid shrimps *Nematoscelis megalops* and *Thysanoessa gregaria*. ●, locality records for Nematoscelis, July to September, including Hansen's (1915); △, locality records for Nematoscelis, February to May, 1920; X, locality records for *Thysanoessa gregaria*

## Thysanoessa gregaria, G. O. Sars

The fact that *Thysanoessa gregaria* occurs side by side with its boreal-Arctic relatives *Th. inermis*, *Th. longicaudata*, and *Th. raschii* in the Gulf of Maine is, as Doctor Tattersall writes me, an interesting phenomenon; for, unlike them, it is a

tropical and warm-temperate form which undoubtedly reaches the gulf from the warmer waters offshore and not from the cooler seas to the east and north. Its local presence is sure evidence of an influx of such water into the gulf.

As I have noted elsewhere (Bigelow, 1917, p. 284), *Th. gregaria* is much less common in the gulf than *Th. inermis*, or, I may add, than *Th. longicaudata;* but the records for 1912 (Bigelow, 1914a, p. 412), 1914, and 1915 (Bigelow, 1917, p. 285), show that in summer it is to be expected anywhere on Browns and Georges Banks, along the continental slope south of Nova Scotia, in the Eastern Channel, and in the inner parts of the gulf as well (fig. 51). We have never found *Th. gregaria* in any abundance anywhere in the gulf north of the offshore banks, but we took it in numbers on the western part of Georges Bank on July 20, 1914 (station 10216), and Hansen (1915) detected it in the gatherings from two deep stations south of Marthas Vineyard. Curiously enough, however, in spite of its well-established warm-water origin, we did not find it at our saltest and warmest station east of Cape Cod, where the plankton was distinctly tropical in aspect (station 10218, July 21, 1914), nor did it appear in the tow nettings along the slope from Georges Bank to the latitude of Chesapeake Bay during July, 1916. Our records for this species [75] prove that it is more seasonal in its occurrence in the Gulf of Maine than are its northern relatives, nearly all being for August; and its history in 1915 in particular, when it was not detected until August, although we made frequent tows in various parts of the gulf during the spring and early summer, shows that it increases in numbers and penetrates farther and farther into the gulf with the advance of summer. Its presence there seems short lived, however, for we did not find it at all during October, 1915, or November, 1916; and although the tow yielded an odd specimen off Gloucester on December 23, 1912, we sought it in vain in December, 1920, and January, 1921, and during the late winter and spring of 1920. Probably the correct explanation for its absence from the Gulf of Maine during the cold half of the year is that the species vanishes thence when the stock that has entered the gulf during the summer perishes at the onset of autumnal cooling. It does not reappear until the surface waters are once more sufficiently warm for its existence, which means midsummer. Thus it closely parallels *Sagitta serratodentata* (p. 58) in its status in the gulf, and there is no reason to suppose that *Th. gregaria* ever breeds successfully there.

### Thysanoessa raschii, M. Sars

This species (fig. 52) resembles *Th. longicaudata* in its Arctic-boreal nature (Kramp, 1913; Zimmer, 1909), and ranges southward along the European coast to the northern part of the North Sea, to the longitude of Nantucket and probably still farther, off North America; but, as I have noted in an earlier report (Bigelow, 1917, p. 284), it is much less common in the Gulf of Maine in summer than is either *Th. inermis* or *Th. longicaudata.* It was not detected there at all in the hauls of July and August, 1912, and appeared at only three stations within the limits of the gulf during the summer of 1914—two of them in its northeastern part and the third off Marthas Vineyard (Bigelow, 1917, p. 282). It was not detected at all during the

[75] For lists of the Gulf of Maine records of *Th. gregaria*, 1912 to 1915, see Bigelow, 1914a, p. 411, and Bigelow, 1917, p. 282.

summer of 1915, was represented by occasional specimens only in Massachusetts Bay and over the continental slope south of Nantucket in July, 1916 (Bigelow, 1922, pp. 133 and 138),[76] and Hansen (1915) adds only one station on Browns Bank

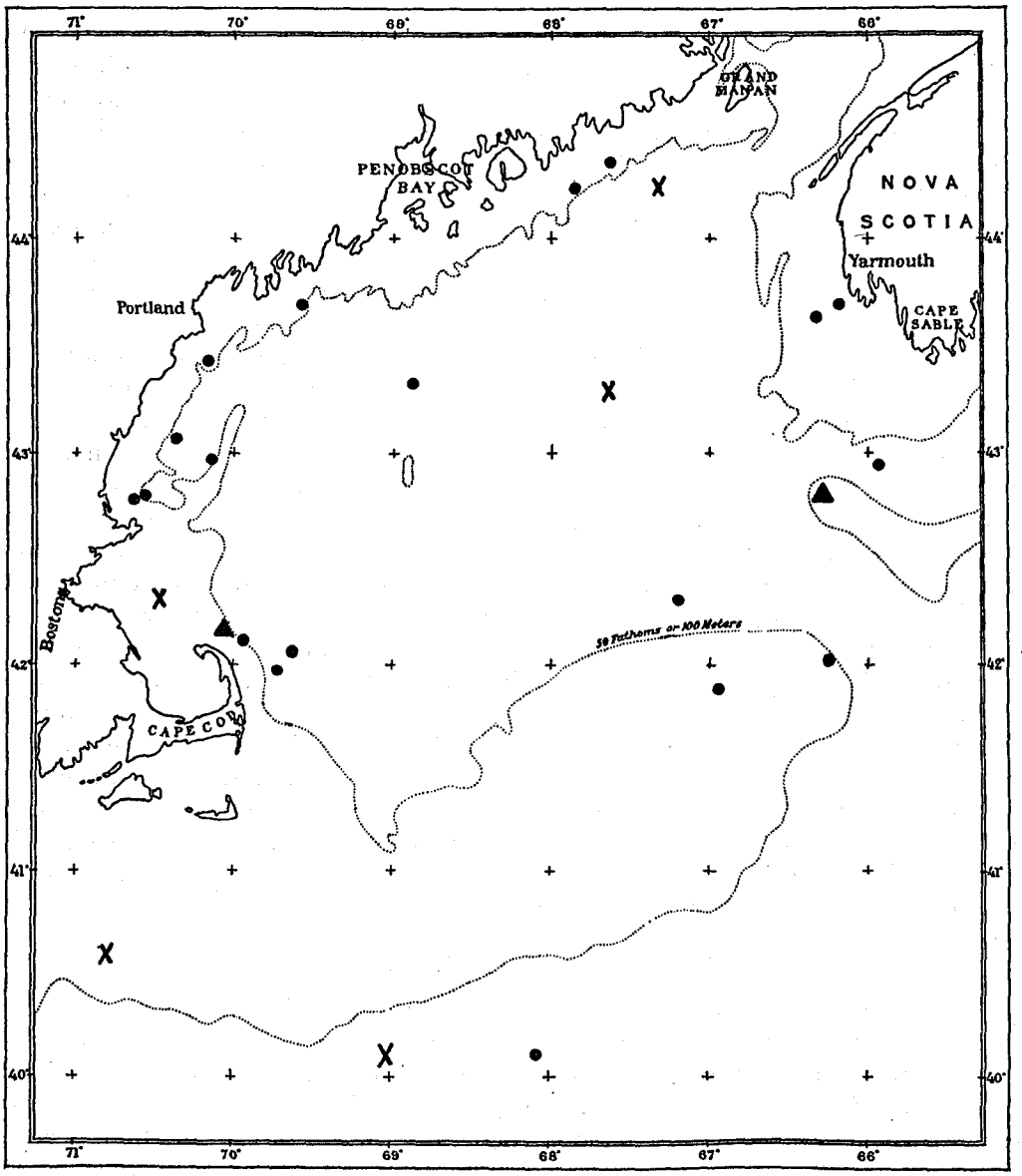


FIG. 52.—Occurrence of the euphausiid shrimp *Thysanoessa raschii*. ●, locality records, February to May, 1915, 1920, and 1921; X, August, 1912 to 1916; ▲, August records by Hansen (1915)

(August, 1877) and a second off the northern end of Cape Cod (for the same month in 1881) to this brief list.[77] Even during the cold July of 1916 we found no *Th. raschii* west of Nantucket, either near shore or over the slope, though the range of

[76] Doctor McMurrich did not detect it at St. Andrews.

[77] He lists many localities for it in the Gulf of St. Lawrence, where it is evidently a common species.

*Th. longicaudata*, a species equally northern in its faunal status, then extended southward beyond the latitude of Delaware Bay. In short, the Gulf of Maine and the continental shelf abreast of Marthas Vineyard and Nantucket together form the southern outpost of *Th. raschii* in summer.

*Thysanoessa raschii* is apparently no more plentiful in the gulf in autumn, for we have not noted it either in October or November and only twice during our December–January cruise of 1920–1921 (occasional specimens off Cape Elizabeth on December 30, station 10494, and off Lurcher Shoal on January 4, station 10500). Neither did we detect *Th. raschii* in any of the tows made off Gloucester from November, 1912, until March, 1913, but it swarmed a few miles north of Cape Ann during that April. The first specimens were noted on the 22d in the neighborhood of the Isles of Shoals; on the 23d (when, as it chanced, none were taken) Mr. Welsh wrote in his field notes of "the pollock schools feeding on shrimps, which were also in dense schools" (Bigelow, 1914a, p. 408); and a large catch of them made off Boon Island on the 25th, when Welsh saw "the feed (shrimps) breaking water trying to get away from the pollock, which are after them," established their identity as this species. At that time the shrimp, as he noted, were concentrated "in dense swarms apparently 6 inches to a foot below the surface," and although these schools had dispersed by the first week in May, so that they were no longer in evidence from the vessel, he still found them near the Isles of Shoals in abundance on the 12th and 13th of the month. There is no knowing how much longer they persisted there, for we did not revisit that region until the following August, when they had disappeared.

We have never found this species so plentiful in the gulf since then, but in 1920 it appeared at about 25 per cent of the stations occupied by the *Albatross* in March and April,[78] twice in considerable numbers—that is, off Cape Elizabeth on March 4 (station 10059), and a few miles north of Cape Ann on May 8 (station 20122). It again appeared in abundance in this same general region in the spring of 1925, when tows from the *Fish Hawk* at two stations 5 to 7 miles southwest from the Isles of Shoals yielded large catches of *Th. raschii* on April 7, with a few *Th. inermis*.

The facts just outlined are enough to show that the spring is the period of maximum abundance, the summer and autumn of minimum abundance, for *Th. raschii* in the Gulf of Maine, and the coastal zone between Cape Ann and Cape Elizabeth a center of abundance for it. Most of our records for it have been located either around the periphery of the gulf within or close to the 100-meter contour or in the shoal waters over Georges Bank (fig. 52), but more data are needed to show whether this apparent concentration in the coastal zone is significant.

Most of the specimens of *Th. raschii* that Welsh took during its period of abundance in April and May, 1913, were large, and we again found large adults in Ipswich Bay—that is, in the same general region—on May 8, 1920 (station 20122); but with this species so rare in the gulf in summer, few, if any, of the larvæ resulting from such local centers of reproduction can survive there. Thus it is chiefly as

[78] Stations 20044, 20059, 20060, 20070, 20073, 20075, 20080, 20085, 20092, 20093, 20096, 20097, 20099, 20102, 20105, 20116, 20122, and 20125.

an immigrant, not as a regular inhabitant, that *Th. raschii* occurs within the Gulf of Maine, where it occupies much the same faunal niche as the northern copepods, *Calanus hyperboreus* and *Metridia longa* (pp. 212 and 245).

### Nematoscelis megalops, G. O. Sars

The presence of this euphausiid at our outermost stations has been mentioned in an earlier chapter (p. 56), and we have also found it occasionally within the Gulf—that is, off Mount Desert Rock on August 16, 1912 (station 10032), and at eight stations during July and August, 1914 (Bigelow, 1917, p. 282), as illustrated on the accompanying chart (fig. 51). Most of these scattering records are from the eastern and southeastern parts of the gulf, as might be expected of a visitor from offshore, and it is probable that the few Nematoscelis that were present over Browns Bank and in the Eastern Channel in July, 1914, represented the innermost fringe of a swarm of this species that populated the waters over the continental slope southeast of Cape Sable at the time.

Our summer records for Nematoscelis within the gulf are based on very few specimens in each case; nevertheless, this is the season at which it most often occurs, for we have never detected it there or even on Georges Bank during autumn, winter, or spring; but the fact that the *Albatross* towed it in fair numbers off the western end of Georges Bank on February 22 (station 20044) and southeast from Cape Sable on March 19, 1920 (station 20077), is sufficient evidence that it is to be expected along the continental slope abreast of the gulf during the cold half of the year as well as the warm. It not only occurs more constantly along this belt than within the gulf, but is much more abundant there in actual numbers—witness the large catches made at our outermost stations off Cape Sable by the *Grampus* on July 28, 1914, and June 24, 1915, and off the southern slope of Georges Bank on July 24, 1916 (Bigelow, 1922, p. 138).

Hansen (1915) likewise records it from many localities over the continental slope off Marthas Vineyard, but not from the Gulf of Maine, from Georges Bank, or from anywhere on the continental shelf east of Cape Cod. This evidence supports the general thesis (Hansen, 1915; Zimmer, 1909; Kramp, 1913) that *Nematoscelis megalops* is typically an oceanic form of warm-temperate affinity, at home in the open Atlantic Basin; and since it is known to range as far north as Iceland and to the waters east of Newfoundland during the warm season, it is not surprising that it should occasionally enter the Gulf of Maine with the general indraught into the eastern side of the latter. We have no evidence that Nematoscelis ever breeds there successfully, however, nor is this at all likely, the probable fate of these rare immigrants being either to withdraw once more to warmer regions as the water cools in autumn (if they have been able to survive the vicissitudes of life in a foreign environment so long), or to perish like other visitors from offshore, such as *Thysanoessa gregaria* and *Sagitta serratodentata* (pp. 142 and 320).

### Euphausia krohnii, Brandt

*Euphausia krohnii* (the only species representative of this large genus so far detected in the Gulf) has not been taken in the inner parts of the Gulf of Maine but was sparsely represented off the southern slope of Georges Bank (station 10220)

and in the Eastern Channel (station 10227) in July, 1914. As has been noted above (p. 134), it occurred in abundance over the continental slope southeast of Cape Sable (station 10233) a few days later. We also found it at this general locality on June 24, 1915, which, with one record at the same relative position off Marthas Vineyard on August 26, 1914 (station 10261), completes the list for the Gulf of Maine cruises.

All the records given by Hansen (1915) are from well outside the continental edge, though he lists so many captures of *E. krohnii* that the species is evidently one of the commonest of euphausiids off the slope abreast of Cape Cod and at least as far east as off La Have Bank, and perhaps still farther. Thus, on the basis of actual record, Euphausia is hardly to be expected inside the outer rim of the Gulf of Maine except as a straggler from the warmer Atlantic.

### Meganyctiphanes norvegica (M. Sars) [79]

While this brilliantly phosphorescent shrimp, the largest and most familiar of all euphausiids in the Gulf of Maine, has not appeared as regularly in our tow nets in most parts of the Gulf as has *Thysanoessa inermis*, it occurs locally in such abundance that it is far more important economically than the latter. The locality records for Meganyctiphanes are distributed generally enough to show that it may be expected anywhere within the gulf north of the Cape Cod-Cape Sable line during the summer and early autumn, both in the deep basin and along shore. Nor does the chart (fig. 53) show any apparent concentration in distribution in one or the other side of the gulf at that season, if the considerable number of stations which the *Grampus* has occupied in the Massachusetts Bay region be allowed for.

I have just mentioned (p. 135) the swarms of Meganyctiphanes that regularly appear during the warm months about St. Andrews and in Eastport Harbor, where numbers of these shrimps can usually be seen darting to and fro at the surface on almost any calm day in August. It seems that this region of violent tidal currents is the only part of the Gulf of Maine where Meganyctiphanes regularly enters the estuaries, but it appeared in the shallows at the head of Frenchmans Bay for a brief period in June, 1923, when a number were collected by Dr. Ulric Dahlgren. Meganyctiphanes appeared there again in abundance in the summer of 1924 (Dahlgren, 1925, has already reported these incursions).

We have never taken it in our tow nettings inside the off-lying islands west or south of this at any season, and although neither comparatively shoal water, *per se*, nor the general neighborhood of the coast is any bar to its presence—witness its occurrence in Massachusetts Bay and in the Eastport-St. Andrews region—most of the *Grampus*, *Albatross*, and *Halcyon* records for it have been from the basin of the gulf outside the 100-meter contour. We have found it only once on German Bank (August 14, 1912, station 10029), once on Browns Bank (July 24, 1914, station 10228) and twice on Georges Bank (station 10223, July 23, 1914, and station 20124, May, 17, 1920), although it has been taken in the Woods Hole region and in shoal water south of Long Island (Hansen, 1915).

[79] For station records for this species from 1912 to 1916, see Bigelow, 1914, p. 118; 1914a, p. 411; 1915, p. 273; 1917, p. 282; and 1922, p. 133. During the spring of 1920 it was taken at stations 20049, 20052, 20053, 20054, 20055, 20056, 20057, 20076, 20079, 20081, 20087, 20088, 20093, 20097, 20098, 20100, 20102, 20113, 20114, 20115, 20122, 20126, and 20127. In December-March, 1920-1921, it was taken at stations 10490, 10491, 10494, 10497, 10499, 10500, 10502, 10507, 10509, and 10510.

The Gulf of Maine is the most southerly important center of abundance for this shrimp, and although it ranges much farther southward along the continental slope, most of Hansen's (1915) locality records of it from abreast of Cape Cod to the latitude

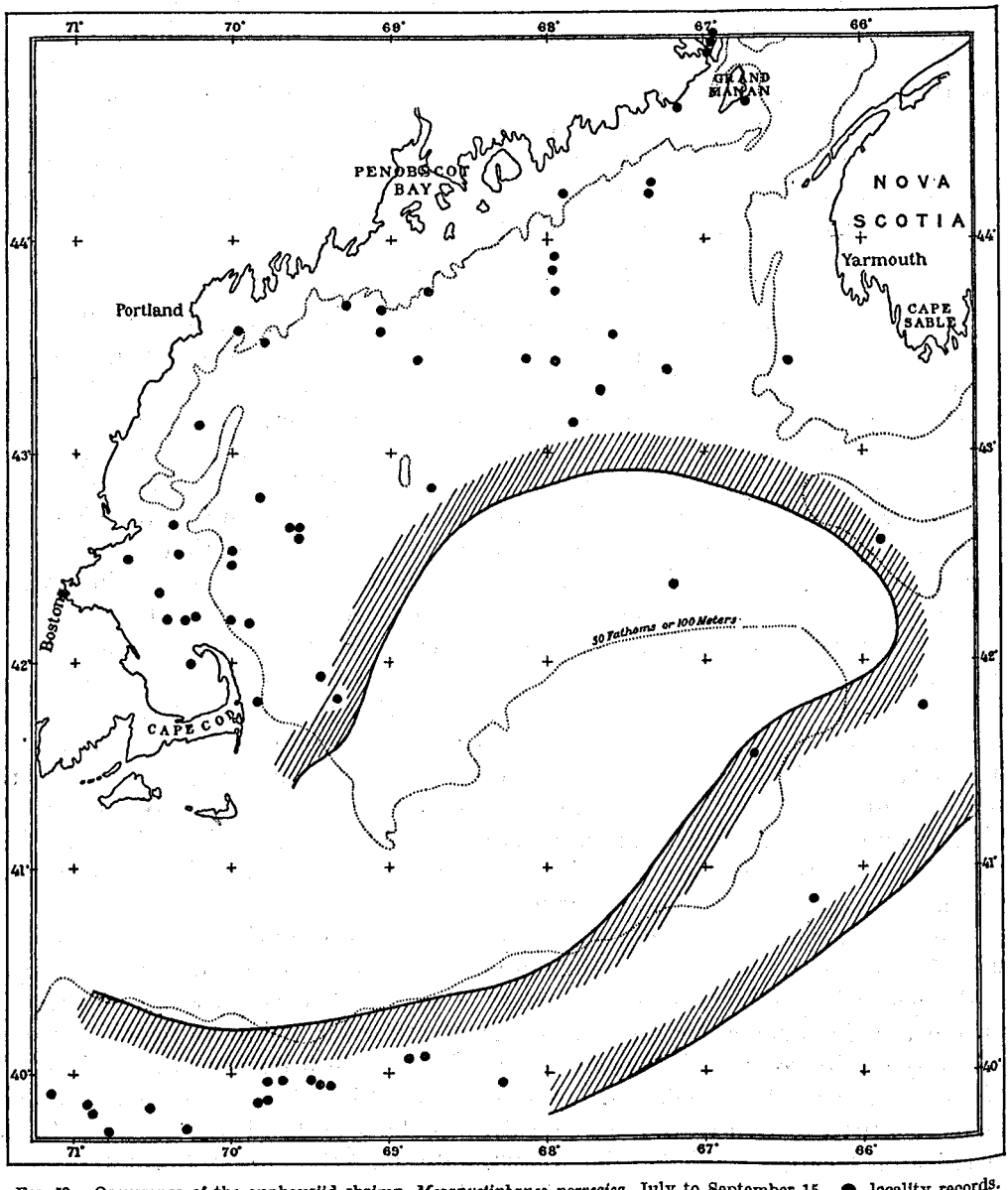


FIG. 53.—Occurrence of the euphausiid shrimp *Meganyctiphanes norvegica*, July to September 15. ●, locality records. The hatched curve incloses the area of regular occurrence in summer and early autumn

of Delaware Bay (37° 25′ N. lat.) were based on odd specimens only, and we did not detect it west of Cape Cod in the summers of 1913 or 1916. The frequency with which it has been recorded in deep water off Cape Cod and off southern New England

reflects the number of tow nettings that have been carried out along that part of the slope rather than any general abundance of Meganyctiphanes there, corresponding to which we have found it at only one of our stations off the slope of Georges Bank.

The scarcity of Meganyctiphanes over Georges Bank and in the southeastern deeps of the gulf generally, in spring as well as in summer, suggests that the few specimens that drift westward beyond Nantucket Shoals along the continental slope are migrants, either from along the Nova Scotian coast to the eastward (and possibly even from as far away as the Gulf of St. Lawrence) or from the western side of the Gulf of Maine, not from the eastern or central parts of the latter.

The alternation of the seasons sees a corresponding expansion and contraction in the area of distribution of Meganyctiphanes in the inner part of the Gulf of Maine. Probably this is at its narrowest late in the winter and early in the spring, for from February to April, 1920, we had only two records of it anywhere inside the 100-meter contour in the whole coastal zone on both sides of the gulf—one for half a dozen specimens near Mount Desert Island on March 3 (station 20056), and the other for a single specimen off Yarmouth, Nova Scotia, on April 9 (station 20102)—although we took it at many stations marked on the chart (fig. 54) in the central and northeast deeps of the gulf during that period. Nor did we find it anywhere on Georges or Browns Banks during these months. In fact, it is seldom that the local presence or absence of any one of the larger members of the zooplankton can be defined so sharply as in this instance. Thus it is evident that Meganyctiphanes withdraws altogether from the shallows of the gulf within the 100-meter contour during the coldest season, unless, perhaps, it persists locally around the shores of the Bay of Fundy; and our failure to find it at any of our February–May stations over the continental slope abreast of the gulf suggests that it vanishes similarly from this portion of its range in late winter and spring. Thus its area of distribution in the Gulf of Maine is then cut off from its more northerly centers of occurrence by an extensive zone off southern Nova Scotia and extending around Cape Sable, where there are no Meganyctiphanes at that season, which is not the case for *Thysanoessa inermis* (p. 135) or for *Th. longicaudata* (p. 139).

During the later spring and early summer Meganyctiphanes disperses in all directions in the Gulf of Maine, to occupy the much more extensive range over which we have found it occurring in midsummer, and reappears over the slope off Marthas Vineyard.

The contraction of the range of Meganyctiphanes, from its maximum in summer and early autumn to the spring state just outlined, may commence as early as October in the western side of the gulf, for we have not taken it anywhere in the Massachusetts Bay region in October, November, December, or during the winter of 1912–1913. It persists until later in the coastal belt north of Cape Ann, where we towed it near the Isles of Shoals and off Monhegan Island on November 1 and 2, 1916 (stations 10400 and 10402); off Cape Elizabeth, near Mount Desert Island, in the northeastern part of the basin, in the Fundy Deep, and off Lurcher Shoal during the last days of December and first week of January of the winter of 1920–1921 (stations 10494, 10497, 10499, 10500, and 10502).

I have already mentioned the fact that the deepest water in the northeast corner of the basin, off Grand Manan, has yielded an abundance of Meganyctiphanes in March, April, May, and June, as well as during the later summer (p. 134). Consider-

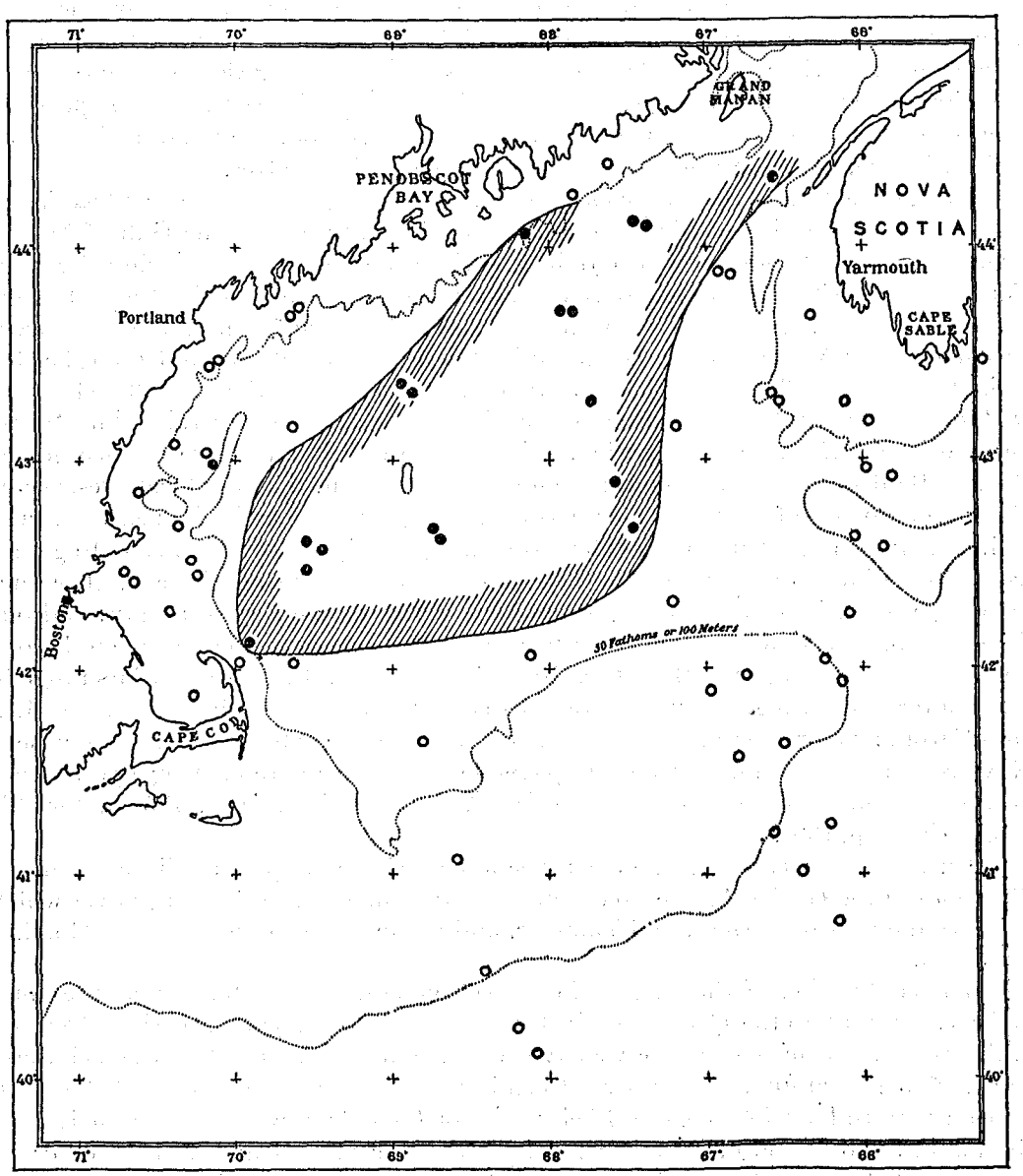


FIG. 54.—Occurrence of the euphausiid shrimp *Meganyctiphanes norvegica*, February to April, 1920. ●, locality records; ○, not taken. The hatched curve incloses the area where it occurs regularly in early spring

able numbers were also taken by the *Halcyon* in the deepest haul (150–0 meters) near-by on January 5, 1921 (station 10502), proving that this serves as a reservoir for Meganyctiphanes throughout the year. This shrimp has also been taken at most

of our stations in the western side of the basin of the gulf, except on May 5 and June 26, 1915 (stations 10267 and 10299).

The triangular extremity of the deep trough north of latitude 44° is the only offshore locality in the gulf where we have found it constantly abundant. Moderate catches of Meganyctiphanes were also made on Browns Bank on July 24, 1914 (though our hauls at about this same location just one month earlier in 1915 yielded none), in the Fundy Deep on March 22, 1920 (station 20079), in the center of the gulf on April 17 of that year (station 20113), and it has been found swarming in Massachusetts Bay at least once in the past (Hansen, 1915). However, we have never taken more than a few specimens at any station there in all our cruising; and the fact that, with the exceptions just recorded, our hauls in other localities have usually yielded only from one or two to a couple of dozens of these shrimps is evidence that Meganyctiphanes seldom swarms anywhere in the gulf except in the northeastern part.

It is not possible to estimate the actual numerical strength of Meganyctiphanes at any of our stations, because the small nets that have been used for the vertical tows in the Gulf of Maine do not yield reliable data for so active an animal and one which so commonly occurs in shoals. Two stations occupied by the *Albatross* in the center of abundance for this shrimp off Grand Manan during the spring of 1920 illustrate this imperfection of the record, for the vertical haul of April 12 (station 20100) did not yield a single specimen—that is, missed the school of shrimps altogether—although the catch of the horizontal haul—about 50 specimens—was about the same as on March 23 (station 20081), when the vertical haul indicated a Meganyctiphanes population of about 275 below each square meter of sea surface.

Although Meganyctiphanes is not neritic (for it is not dependent on the bottom at any stage in development or associated with the coast line in its distribution), it is a creature of the banks water on both sides of the Atlantic and is not oceanic in the typical sense, finding the high temperatures and salinities outside the edge of the continent an absolute barrier to its offshore dispersal along the American littoral. At one place and season or another Meganyctiphanes occurs over a very wide range of temperature in the Gulf of Maine, certainly from upward of 15° to as low as 2 to 3°, and possibly even colder; but it was rare at the coldest stations (0.5 to 2.5°) during March and April, 1920, with only three records from water as cold as 2°,[80] the temperature being higher than 3° and in most cases as warm as 4° to 5° at the five localities and at the deeper levels where it was most abundant during those months, although the surface strata might be colder.[81] It follows that almost the entire local stock of the species was then living in tempeartures of 3.5 to 5°. Therefore 3 to 4° may be set tentatively as the coldest favorable for the existence of Meganyctiphanes in the Gulf of Maine, a thesis corroborated by its absence from Ipswich Bay on April 9, 1920 (station 20092), when the temperature at 20 to 30 meters was still only 2.5°, coupled with its presence there on May 8 (station 20122), by which date the temperature had risen to 3 to 4° at that level.

[80] One specimen at station 20054, 100–0 meters, temperature 1.7 to 2.5°; occasional examples at station 20056, whole column of water, 0.5 to 1.9°; 3 specimens at station 20057, whole column of water, 1.9 to 2.2°.

[81] Station 20079, 180 meters, about 4°; station 20081, 140 meters, 4.5°; station 20100, 100–0 meters, about 4.5°; station 20113, surface, 3.3, and 4.5° at about 130 meters; station 20114, 110 meters, about 4°.

These observations make it probable that Megancytiphanes deserts the shallow coastal zone as winter draws to its close, in order to avoid the extreme chilling to which this part of the gulf is subject; but data for a single year, and especially for one as cold as 1920, are not enough to settle this point definitely. On the other hand, the great majority of our captures of Meganyctiphanes have been from water colder than 12°, both in the offshore parts of the gulf and on the surface about Eastport and St. Andrews. But off Cape Cod, on August 23, 1914 (station 10256), we found it indifferently on the surface at a temperature as high as 19.5° and in the much cooler (5 to 6°) layers deeper down, and probably the Massachusetts Bay swarm mentioned below (p. 153) was likewise living in water at least as warm as 16°.

Evidently the highest temperatures that ever obtain in the open waters of the Gulf of Maine are not immediately fatal to Meganyctiphanes, though it is doubtful whether it could long survive water so warm; nor does it always avoid it, although it may cease its upward swimming to do so or sink a few fathoms to escape it once it has come up to the surface. Nevertheless, judging from the distribution of Meganyctiphanes in other seas, it is probable that a constant high temperature is not favorable for it, and I think it safe to set 12 to 15° as the upper limit for its permanent existence, and especially for its reproduction. Within the limits of 3 to 15° it is practically eurythermal in the Gulf of Maine, both horizontally and vertically, and its distribution there is equally independent of local and vertical differences in salinity, for it occurs indifferently over the whole range—that is, from 31 per mille or less to 34 per mille—except perhaps in the very freshest water at the time of the spring freshets. This parallels its distribution in European seas, where it is common in the Skager-Rak in salinities ranging from as low as 28 to 30 per mille to as high as 34 to 35 per mille at different seasons (Kramp, 1913).

Apparently there is nothing in the physical state of the water over Georges Bank to account for the scarcity or absence of this euphausiid there, nor can a cause be assigned for this apparent anomaly in its distribution until its life history has been traced in more detail.

The bathymetric distribution of Meganyctiphanes in the Gulf of Maine remains puzzling. Most of our summer records for it in the offshore parts of the gulf have been from deeper than 40 meters or so, and when this shrimp has occurred on the surface at that season it has usually been represented more numerously at some deeper level, a rule illustrated by two stations in the western basin (August 22 and 23, 1914), when the number of Meganyctiphanes taken in the several hauls was as follows:

| Station | Depth in meters | Number of specimens | Station | Depth in meters | Number of specimens |
|---|---|---|---|---|---|
| 10254 | 0 | 13 | 10256 | 0 | 8 |
| | 45–0 | 38 | | 45–0 | 35 |
| | 225–0 | 50 | | | |

Not only have we taken it right down to the bottom of the deepest trough of the gulf, but it is only in the lowest strata of the latter that it occurs regularly and in numbers throughout the year, except in the Eastport region. To balance against

this apparent preference for considerable depths is the fact that the small surface net captured no fewer than 111 large specimens in the center of the gulf on April 17, 1920, at 2 p. m. (station 20113), while the haul from 120 meters took only three, though there were many of these shrimps at 110 meters, but none on the surface only 35 miles distant to the westward (station 20114), that same day. S. I. Smith (1879 p. 89) likewise found it in shoals on the surface "on the mackerel ground" off Casco Bay, both day and evening during the warm months 40 years ago. It swarms on the surface in the Eastport–St. Andrews region in midsummer and early autumn, as just remarked (p. 147), and although recent records for it in Massachusetts Bay have all been from depths of 40 meters or deeper, quantities of Meganyctiphanes were taken at the surface at the mouth of the bay on July 7, 1894, in dip nets from the rail of the *Grampus;* and they were so abundant there at a depth of less than 2 fathoms two days later that a large number found their way into the fish well of the vessel (Hansen, 1915). Thus, while the normal habitat of Meganyctiphanes is in the low temperatures and darkness of the deeper strata in the trough of the gulf, it may rise to the surface anywhere at any time. In the Eastport region it may be brought up involuntarily by the active stirring of the water which takes place there, and the constancy of this type of vertical circulation may account for the regularity of its presence at the top of the water there, expecially in view of the low surface temperature that characterizes that locality (10 to 12° in summer and early autumn). The Massachusetts Bay region, with surface readings of 16 to 18°, is nearly the warmest part of the gulf in midsummer, so Meganyctiphanes is not prevented from making occasional excursions upward to the top of the water even by temperatures so high that a prolonged stay would probably prove fatal. Furthermore, such excursions in this part of the gulf during the warm months involve voluntary upward swimming, the vertical currents being weak and the water highly stable, with its density much the lowest at the surface. Neither do they correspond to the diurnal vertical migrations shared in by many copepods (p. 25), because the appearances of Meganyctiphanes at the surface appear to be independent of the time of day. Therefore, the actual captures so far recorded do not indicate any definite phototropism on its part, positive or negative, although it is doubtful whether it could long survive the full illumination of bright sunlight.

Experience in most parts of the Gulf of Maine is therefore in line with Paulsen's (1909) conclusion that when Meganyctiphanes visits the surface in Icelandic waters it is not as a direct response to temperature (to which I may add salinity) or to the degree of illumination, but in pursuit of food. It is also brought up by vertical currents, where these are active.

The depth at which Meganyctiphanes is most plentiful is more definitely limited, and the relationship between its vertical occurrence and temperature is closer in North European waters than in the Gulf of Maine. Off Ireland, for instance, and in such parts of the North Sea as it visits, this euphausiid lives chiefly in the deeper layers of water, reaching its maximum, according to Tattersall (1911), at about 200 meters. In the Skager–Rak (Kramp, 1913, p. 542) it carries out a more or less definite vertical seasonal migration, always seeking the coldest level, which leads it to the surface in winter and down to lower levels in summer.

*Breeding habits.*—The spawning of Meganyctiphanes has not actually been observed either in American or European waters, but it seems certain that this genus either does not carry its eggs with it at all after they are extruded, as some other euphausiids do, or that it nurses them only for a brief period at most, both because ovigerous females have never been seen, so far as I can learn [82] (Holt and Tattersall, 1905), and because eggs probably ascribable to this species have been found free floating in the one-celled stage by Sars (1898) and by Lebour (1924a). It is true that the eggs of Meganyctiphanes have not been identified with absolute certainty from among the plankton. Sars (1898), however, thought it probable that at least some of the euphausiid eggs [83] about 0.7 to 0.8 millimeter in diameter, which he found in Christiania Fjord where Meganyctiphanes is plentiful, had that parentage. Similar eggs had already been recorded from the Clyde area, a center of abundance for Meganyctiphanes, by Brook and Hoyle (1888). Holt and Tattersall (1905, p. 103), too, have assigned to this genus certain loose ova found side by side with Meganyctiphanes and occasionally even clasped between its thoracic legs, among various articles of prey, though without describing the dimensions or appearance of the eggs in question. Lebour (1924) has recently ascribed to this same parentage certain euphausiid eggs from the English Channel, because of the characters of the larvæ hatching therefrom.

Brook and Hoyle, Sars, and Lebour all agree in describing these eggs (the correct identification of which is made practically certain by cumulative evidence) as inclosed by a perfectly transparent capsule 0.7 to 0.8 millimeter in diameter, the ovum proper having a diameter of approximately 0.3 to 0.4 millimeter. Thus, when first set free in the water they much resemble buoyant fish eggs with wide perivitelline membrane; but cleavage being holoblastic and the development of the nauplius plainly visible within the egg, thanks to its transparency, their crustacean nature is apparent almost from the beginning. Euphausiid eggs are so characteristic in appearance, also, that there is no danger of confusing them with any other buoyant eggs.

Our own hauls in the Gulf of Maine have yielded considerable numbers of eggs of this same type and size in various stages of development. We first detected them in a surface tow in the Grand Manan Channel, off Campobello Island, August 19, 1912 (in the report for that year (Bigelow, 1914, p. 104) they were referred to through error as "balanus" eggs). These were for the most part in early cleavage stages, a few in various stages up to the fully formed nauplius ready to hatch. Eggs of this same type, as well as the recently hatched nauplii, were again taken on the 22d of the month off Penobscot Bay (station 10039). Since that time we have detected similar eggs in the Fundy Deep and off Mount Desert Island in June (stations 10282, 10284, and 10286, June 10 to 14, 1915) and off the mouth of the Grand Manan Channel on July 15, 1915 (station 10301). It is not safe to say that all these eggs are Meganyctiphanes, for Lebour (1924) found eggs of *Thysanoessa inermis* indistinguishable from them; but the strong probability that at least part of them belong

[82] The considerable series of large adults which I have examined contained none.

[83] Metschinkoff (1871, pl. 34, fig. 1) first described the peculiar and very characteristic buoyant eggs of this group of pelagic Crustacea.

to the former suggests that Meganyctiphanes spawns in summer, which fits in with the season of abundance of euphausiid larvæ (p. 134) and points to the northeastern part of the gulf, where this shrimp is so abundant, as its chief spawning ground.

Nothing is yet known of the seasonal occurrence or distribution of the larvæ of Meganyctiphanes in the Gulf of Maine except that juveniles of the species were taken in some numbers off Cape Cod on July 19, 1914, in a haul from 70 meters (Bigelow, 1917, p. 282, station 10213). Very likely this genus was represented among the larval euphausiids taken on the surface off Cape Elizabeth on August 14, 1913 (station 10103); in Massachusetts Bay and off Cape Cod in July, 1916 (Bigelow, 1922, p. 133, and station 10343); and off the cape in August, 1914 (Bigelow, 1917, p. 283). These, however, have not been studied.[84] McMurrich, too, found young (unnamed) euphausiids common at St. Andrews from April until August, probably the offspring of the two pelagic shrimps Meganyctiphanes and *Th. inermis*, which are so plentiful in that region. However, larval euphausiids of any sort have always been very rare in our offshore catches in the northeastern part of the gulf, notwithstanding the constant presence of the adults there.

Hansen (1915, p. 68), I may add, records "immense numbers of older larvæ" of Meganyctiphanes taken on May 25, 1891, over the 50-meter contour south of Shinnecock Light, Long Island, which is more than 2° of longitude farther west than the adults of this euphausiid have ever been found in any number. The possibility that adult Meganyctiphanes, in company with the general Calanus community, may spread farther west and south over the shelf during the cold season than it does in summer makes it unsafe to assume that the larvæ in question had drifted to the locality of capture from a more easterly birthplace. (Compare, in this connection, the status of *Thysanoessa inermis* west of Cape Cod, p. 138.)

Although the evidence that the Gulf of Maine is a successful breeding ground for Meganyctiphanes still lacks something of proof positive, it is probable that this shrimp is not only regularly endemic there but that the northeastern part of the gulf is one of the most important centers of production for it off the American coast, and one, too, which receives few accessions from the north but forms a distinct and practically isolated colony. The relative distribution of euphausiid eggs and larvæ, like that of pelagic fish eggs and larvæ, is consonant with a general drift around the shore of the gulf with the dominant anticlockwise eddy, from the Bay of Fundy toward Cape Cod, on the part of the developmental stages.

### Thysanopoda acutifrons, Holt and Tattersall

The claim of this species to mention here rests on a single record—five specimens from the southeast corner of the gulf, July 23, 1914 (station 10225), identified by Dr. W. M. Tattersall (Bigelow, 1917, p. 282).

### Other euphausiids

The species discussed above are the only euphausiids actually identified from within the Gulf of Maine or from the shoal waters over its southern rim up to the present time. Sundry other members of this group have been taken at one time or

[84] According to Lebour (1924a) the larval stages of Meganyctiphanes and Thysanoessa are easily recognized.

another at the outermost stations, between longitudes 71 and 65° and north of latitude 39°, both in the earlier collections of the Bureau of Fisheries, reported on by Hansen (1915), and during the more recent Gulf of Maine explorations, the latter identified by Doctor Tattersall.[85] The combined list is as follows: *Bentheuphausia ambylops, Thysanopoda orientalis, Euphausia americana, E. mutica, E. brevis, E. tenera, E. hemigibba, Stylocheiron carinatum, S. abbreviatum, Thysanoessa parva, Nematoscelis atlantica, N. microps,* and *N. tenella.* These are all oceanic species, any of which may be expected to occur occasionally in the southeastern corner of the gulf; hence a lookout should be kept for them in future collections from that region.

## Hyperiid amphipods

### Euthemisto

The genus Euthemisto is one of the most characteristic, if not abundant, members of the plankton of the offshore waters of the Gulf of Maine. How regularly it is distributed there in summer (fig. 55) and over the shore banks as well appears from the fact that it has been taken at at least 90 per cent of our stations outside the immediate coastal zone, as bounded by the 100-meter contour on our July and August cruises of 1912, 1913, 1914, 1915, and 1916. Inside this zone, on the contrary, it fails almost as regularly at this season, with only four or five summer records for it from water shallower than 100 meters along the western side of the gulf. Similarly, it is so rare at St. Andrews that it finds no place in Doctor McMurrich's local plankton lists, and this is true, to a less extent, off western Nova Scotia as well, judging from its irregular occurrence on German Bank.

Euthemisto is usually only a minor factor in the plankton of the inner parts of the gulf. This rule has its exceptions, however, for we encountered swarms of its larvæ off Penobscot Bay on August 11, 1913 (station 10090), and of adults as well as young in the deep basin farther east (station 10092), while it was so plentiful in the western basin on August 31, 1915 (station 10307), that the haul from 40 meters yielded about 200 cubic centimeters of adults and multitudes of newly-hatched larvæ.

We have usually found Euthemisto an important element in the tow nettings at the mouth of the gulf and over the outer part of the continental shelf generally from off Halifax to abreast of New York. For example, *E. compressa* abounded on the south side of Nantucket Shoals on July 9, 1913 (station 10060), while young *bispinosa* swarmed in the water southwest of Nantucket on August 22 of that same year (station 10112). We took about 1,000 cubic centimeters of medium-sized Euthemisto in a half hour's tow at 40 meters near Cape Sable on August 11, 1914 (station 10243), an equal volume of large specimens in a surface haul of the same duration with a net 1 meter in diameter on Browns Bank, July 24. 1914 (station 10228), and 750 cubic centimeters on the surface off Shelburne, Nova Scotia, three days later (station 10231). Euthemisto "again formed a considerable part of our catches on the shelf south of Nova Scotia (stations 10291 to 10294), on Browns Bank (station 10296), and off Marthas Vineyard (stations 10332 and 10333) in

[85] For the actual details of capture I refer the reader to Hansen (1915) and Bigelow (1917).

the summer of 1915" (Bigelow, 1917, p. 286), as well as over the southwest part of Georges Bank in July, 1916 (stations 10351 and 10353), which substantiates the tow nettings made by vessels of the Bureau of Fisheries in past years.

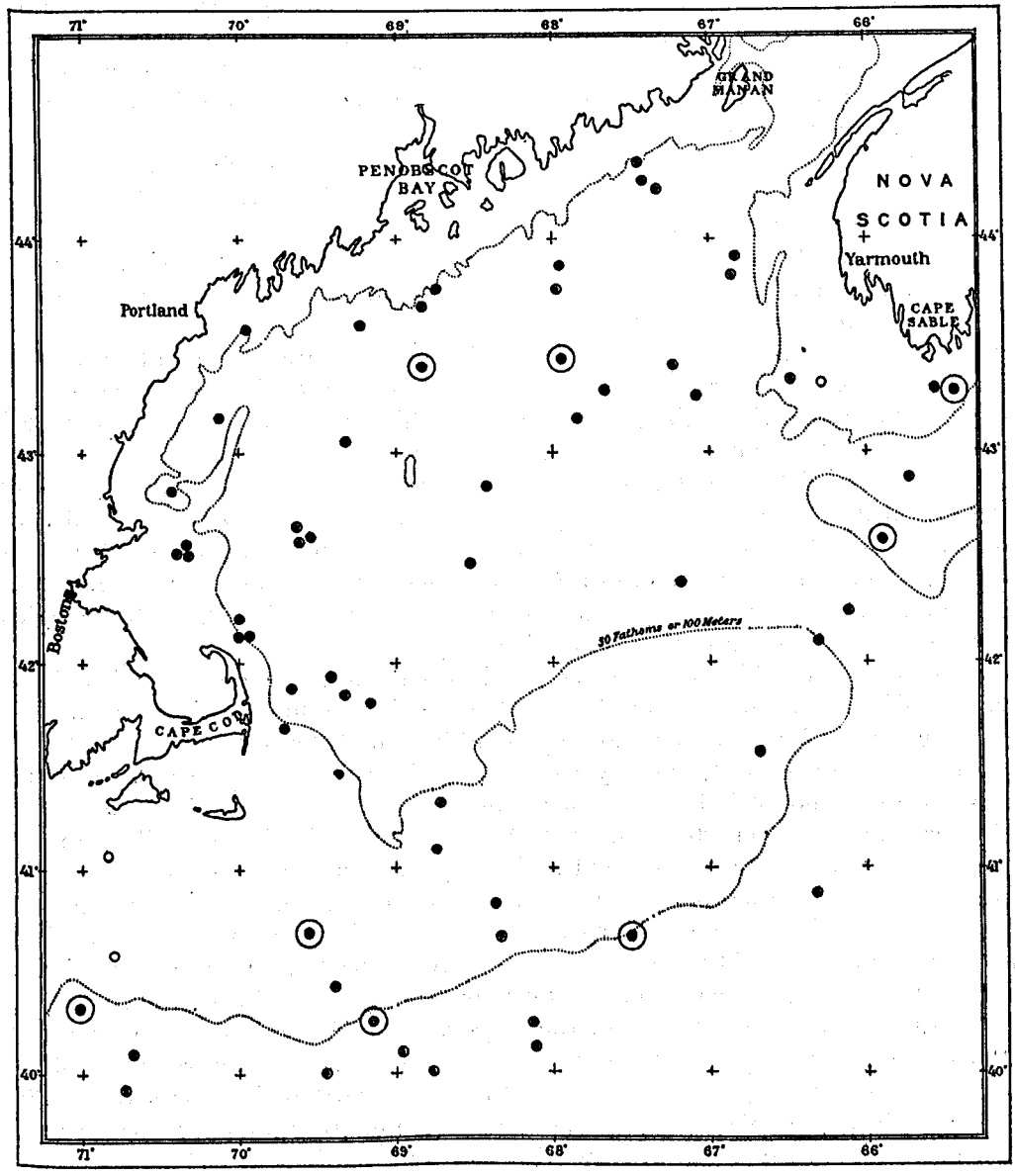


FIG. 55.—Occurrence of the amphipod genus Euthemisto, July, August, and the first week of September. ●, locality records for *E. compressa*; ○, locality records for *E. bispinosa*; ⊙, locality records for both species together. The large symbols are for the more notable swarms

This zone of abundance can hardly extend out beyond the continental edge, for, generally speaking, we have found Euthemisto decidedly less common over the continental slope and rare at the deep stations where the plankton is characterized

by a large tropical element (e. g., station 10218, July 21, 1914). Thus its abundance along the outer edge of the shelf does not imply an oceanic origin, but, like Calanus, it is typical of the water of the coastal banks off the Gulf of Maine and along the American litoral as a whole, finding the inner edge of the so-called Gulf Stream a fluctuating barrier to its seaward dispersal, which is in line with its boreal nature.

Euthemisto is not only more numerous over the outer part of the shelf than within the Gulf of Maine, but it grows larger there, although very large specimens occasionally occur even close to land. When adult females with eggs are taken in our coastwise hauls they are seldom over 10 millimeters long, with the general run of the catch still smaller, whereas the numerous adults taken over the offshore banks are often as long as 20 millimeters.

Although we know little of the status of Euthemisto in the offshore parts of the gulf in autumn, there can be little doubt that an inshore movement of greater or less extent takes place at that time, for in 1915 this genus occurred in some numbers in October in Massachusetts Bay, where it is usually scarce or absent in summer (p. 156). Apparently it reaches its maximum abundance in the coastal zone of the gulf in October and November, and during the third week of November in 1912 it was comparatively common near Gloucester (Bigelow, 1914a, p. 403). To judge from the season of 1920 and 1921, however, this autumnal increase is followed by shrinkage in its numbers with the onset of winter, for in late December and early January we took Euthemisto at only 5 out of 14 stations in the northern and western parts of the gulf—never more than a few specimens in any haul—nor did it appear in any abundance later than November during the winter of 1912–1913, though a few were noted at all our stations until February.

In February and March, 1920 (fig. 56), Euthemisto was as generally distributed over the gulf and over Georges and Browns Banks, as it is in summer (fig. 55); but it was far less numerous, for it appeared at only about half the February and March stations (occasional examples only), the only exception to this rule being the waters off southern Nova Scotia (not strictly within our limits), where it was taken in some numbers on two occasions (stations 20074 and 20075). Its numbers in the gulf fell to an even lower ebb in April, when we detected it (in very small numbers) at only 6 out of 30 stations, a shrinkage due to an actual decrease in the stock and not to an emmigration out of the gulf, for, as it happens, these few records were near Cape Elizabeth, on the one hand, and off the western shores of Nova Scotia, on the other, with no Euthemisto whatever taken at our stations farther out at sea during the month.

In 1920 none were detected in the western side of the gulf in May (stations 20120 to 20126), though a few (both *bispinosa* and *compressa*) were taken off the seaward slope of Georges Bank on the 17th (station 20129), in a haul from 100–0 meters; but in 1915 (which was also an earlier season in other respects) a scattering of Euthemisto was noted at most of the May and June stations at the mouth of Massachusetts Bay, in the gulf generally outside the 100-meter contour, off Lurcher Shoal, on German and Browns Banks, and over the outer part of the continental shelf outside the continental edge off Shelburne, Nova Scotia.[86] During these months

[86] Recorded in my field notes from stations 10269, 10270, 10272, 10273, 10278, 10279, 10281, 10282, 10284, 10288, 10290, 10291, 10293, 10294, 10295, and 10296.

it was noted at only one of the stations (10287) inside the 100-meter contour along the eastern coast of Maine.

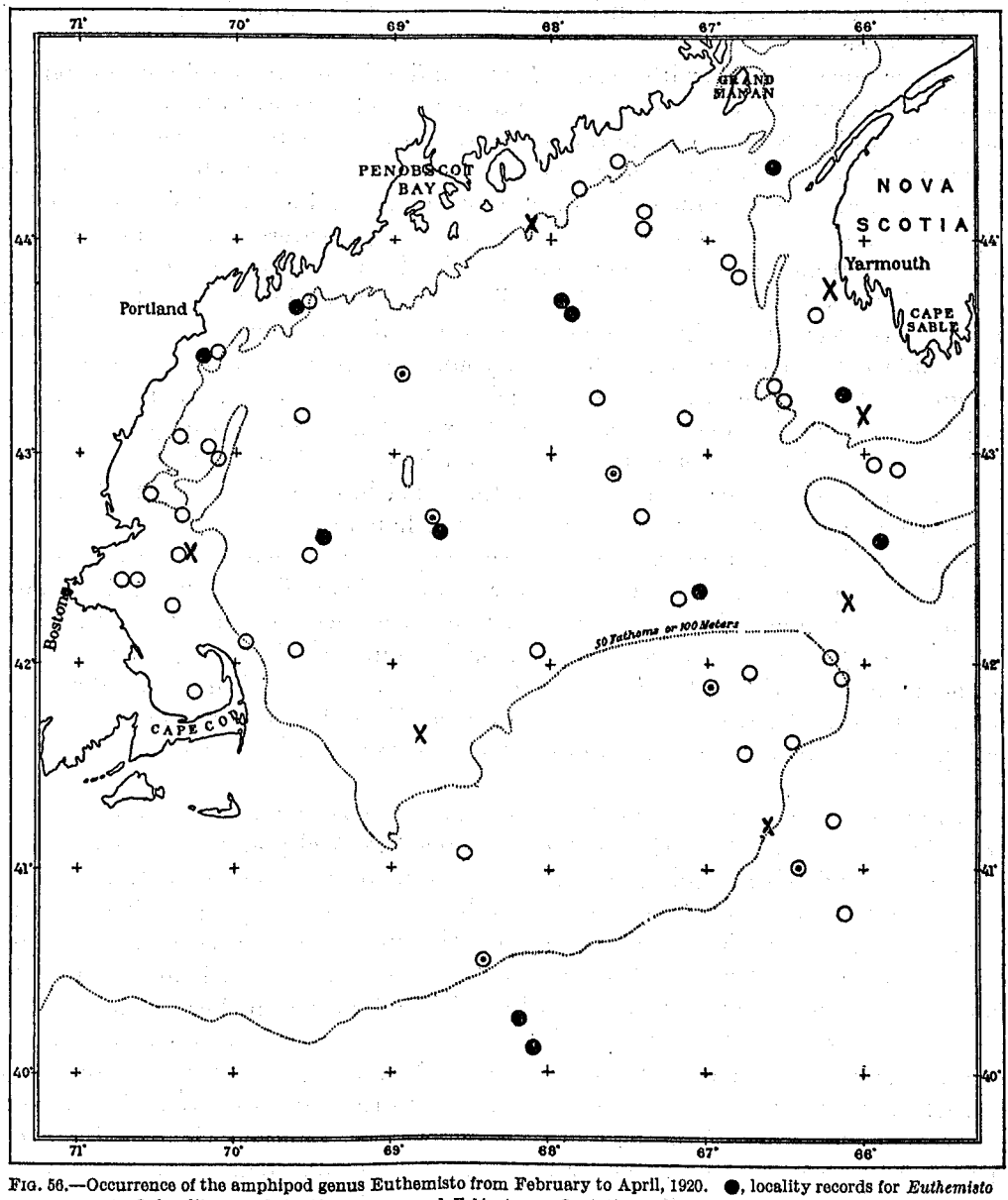


FIG. 56.—Occurrence of the amphipod genus Euthemisto from February to April, 1920. ●, locality records for *Euthemisto compressa:* ⊙, locality records for *E. compressa* and *E. bispinosa;* ○, stations where neither occurred; X, locality records for larvæ too young for identification as the one species or the other.

Euthemisto thus exhibits a more or less definite summer and early autumn maximum contrasted with an early spring minimum in the Gulf of Maine, disappearing from the coastal zone, as its numbers dwindle in late winter or early spring, to

reappear there in October and later. This seasonal cycle is just the reverse of what obtains in the North Sea region, where *Euthemisto compressa* occurs commonly in winter with the indraught of Atlantic water (Tesch. 1911), but only in small numbers at other seasons.

The presence of adults with eggs, of larvæ, and of immature specimens at various stages in development shows that Euthemisto [87] breeds successfully over the entire area of the Gulf of Maine outside the outer islands and headlands—perhaps even in Massachusetts Bay. Large numbers of young are sometimes produced in the inner parts of the gulf—for instance, the swarms of young off Penobscot Bay in August, 1913, mentioned above (p. 20)—as well as in the surface waters of the western basin, where newly hatched as well as medium-sized Euthemisto were plentiful on August 31, 1915 (station 10307). The chief breeding areas, as indicated by relative abundance, lie over the outer edge of the continental shelf, extending as far west at least as longitude 71°, where we found shoals of young specimens as well as of adults late in August in 1913 (Bigelow, 1915, p. 281); likewise on the central, northwestern, and southwestern parts of Georges Bank, on Browns Bank, and in the coastal waters off Cape Sable. In this general zone we have not only found breeding adults as well as young on many occasions, but more than once have taken young in abundance on the surface and adults with eggs in the deeper hauls (p. 163).

The breeding season of Euthemisto certainly extends over a large part of the year, for we have found its larvæ in every month from February until October. Probably it also breeds during the late autumn, when we have not visited its chief offshore areas of reproduction, for occasional young specimens appeared in our tows near the Isles of Shoals and off Cape Cod in the first week in November, 1916 (stations 10400 and 10403), and in the deep near Cape Ann late in December, 1920 (station 10389); but young are produced in greatest number in June, July, and August.

No attempt has yet been made to estimate the actual numerical strength of Euthemisto in the Gulf of Maine, but at times the local population must be considerable to yield the abundant tow-net catches mentioned above (p. 156).

In the preceding lines the genus has been treated as a unit. The relative fluctuations of its two local representatives, the species *compressa* and *bispinosa*,[88] are next to be considered. Although these two species of Euthemisto are often taken side by side, they occupy somewhat different faunal niches, with *bispinosa* the more oceanic of the two and showing a more definite seasonal movement toward and away from the coast than *compressa* does.[89] During the period February to May, when the genus as a whole is at a low ebb in the Gulf, *compressa* is decidedly the commoner member of the pair in its inner waters, while on Georges Bank and south of Nova Scotia the two occur in roughly equal numbers at that season (at least such was the case in 1920). In June, when the numbers of the genus as a whole increase, *compressa* still predominates within the gulf, but we found *bispinosa*

[87] Both *E. compressa* and *E. bispinosa*.

[88] For descriptions and the distinguishing features of these two see Sars, 1895. I have elsewhere given tables of the relative abundance of the two for several of our cruises (Bigelow, 1914a, p. 4; 1915, p. 279; 1917, p. 287; 1922, pp. 133 and 148).

[89] For tables of the relative abundance of the two species of Euthemisto from 1913 to 1915 see Bigelow, 1915, p. 282, and Bigelow 1917, pp. 287 and 288.

outnumbering it off Shelburne (station 10294) and on Browns Bank (station 10296) during that month in 1915.

| Station | Species present | Station | Species present |
|---|---|---|---|
| 20044 | Compressa. | 20074 | Compressa and bispinosa. |
| 20045 | Do. | 20075 | Do. |
| 20046 | Compressa and bispinosa. | 20077 | Compressa. |
| 20050 | Juveniles. | 20079 | Do. |
| 20052 | Compressa and bispinosa. | 20087 | Do. |
| 20055 | Compressa. | 20095 | Do. |
| 20057 | Compressa and bispinosa. | 20102 | Juveniles. |
| 20065 | Do. | 20104 | Do. |
| 20067 | Juveniles. | 20112 | Compressa. |
| 20068 | Compressa and bispinosa. | 20113 | Compressa and bispinosa. |
| 20071 | Juveniles. | 20114 | Compressa. |
| 20072 | Compressa. | 20129 | Compressa and bispinosa. |

With the advance of summer the ratio of *bispinosa* to *compressa* increases. Thus, in July, 1914, *bispinosa* outnumbered the latter on the southern part of Georges Bank (stations 10216 and 10223) and on Browns Bank (station 10228) and about equalled it on the northwest part of Georges Bank (station 10215) and in the eastern channel (station 10227); but *compressa* was still the dominant member of the pair off Massachusetts Bay (station 10213), in the southeastern part of the basin of the gulf (station 10225), over the northeastern edge of Georges Bank (station 10226), along the continental edge off the southeast and southwest slopes of Georges Bank (stations 10220 and 10218), and abreast of Shelburne, Nova Scotia (station 10233).

In August of that year *bispinosa* was the dominant member of the pair near Cape Sable (station 10243) and in the eastern side of the basin (stations 10245 and 10249). The two species were about equal off Mount Desert and Penobscot Bay (stations 10248 and 10250). In the deep water off Cape Ann (station 10254) *compressa* was the more numerous at the surface, but *bispinosa* predominated in the haul from 225–0 meters. *Compressa* still dominated at the mouth of Massachusetts Bay and in the south central parts of the basin (stations 10253, 10255, and 10256), but *bispinosa* was much the more numerous of the two at two stations on the continental shelf off Marthas Vineyard at this time (stations 10258 and 10259), and while it dominated at one station at the continental edge (station 10260), *compressa* outnumbered it at another station a few miles farther out (station 10261).

*Bispinosa* is not so important, relatively, in the inner parts of the gulf every summer, for in 1913 *compressa* outnumbered it at all the August stations east of Cape Cod and north of Georges Bank, though *bispinosa* was more plentiful then than it had been a month previous (we have no autumn records for that year in the gulf), and with the same center of abundance as in 1914—that is, the central and eastern parts of the deep basin. *Bispinosa* outnumbered *compressa* in Massachusetts Bay, off Cape Cod, and locally south of Marthas Vineyard in October, 1915 (stations 10258 to 10267); and in the first week of November, 1916, it again predominated off Cape Cod (station 10404) but was detected at only two of five stations farther north in the gulf at this time, whereas *compressa* was at all of them. *Compressa* was also the only Euthemisto noted close to land near Marthas Vineyard

on November 10 (station 10405), but farther out on the continental shelf on this line *bispinosa* predominated in the rich catches of these amphipods (stations 10406 and 10407).

In Massachusetts Bay, which may be taken as fairly representative of the western coastal waters of the gulf, *E. bispinosa* attains its greatest numerical strength, compared to *E. compressa*, during late autumn or early winter, dwindling rapidly thereafter, as appears from the following table of the relative abundance of the two species in samples of the catches made off Gloucester during the winter of 1912–1913.

| Station | Date | Compressa | Bispinosa | Station | Date | Compressa | Bispinosa |
|---|---|---|---|---|---|---|---|
| 10047 | Nov. 20, 1912 | 20 | 12 | 10051 | Jan. 30, 1913 | 4 | 0 |
| 10048 | Dec. 4, 1912 | 15 | 25 | 10052 | do | 25 | 3 |
| 10049 | Dec. 23, 1912 | 15 | 12 | 10053 | Feb. 13, 1913 | 30 | 5 |
| 10050 | Jan. 16, 1913 | 30 | 2 | 10054 | Mar. 4, 1913 | 20 | 0 |

Although it is not yet possible to outline the relationship of the two species more in detail, it is safe to say that *E. compressa* is a permanent and characteristic inhabitant of all parts of the Gulf of Maine except the immediate coastal zone, occurring there wherever the genus is known at all, and at all seasons. *E. bispinosa* is to be found over the outer parts of the continental shelf throughout the year, but it is only a seasonal visitor to the inner parts of the gulf, spreading first into its eastern half in summer. By autumn and early winter it may rival *compressa* locally right up to the western and northern shores of the gulf, but in the western coastal zone it is usually outnumbered by the latter even at that season, and either perishes or withdraws seaward once more with the advance of winter.

Thus, *E. bispinosa* is decidedly more oceanic than *E. compressa*, as it occurs in the inner parts of the gulf, which corresponds to the fact that it usually equals or predominates over the latter in the coast waters south of Nova Scotia, over the whole southern part of Georges Bank, and in the shallow waters south of Marthas Vineyard and Nantucket. It is also more oceanic than *compressa* on the European side of the Atlantic, seldom appearing within the North Sea, but regularly present off the west coast of Ireland (Tesch, 1911; Tattersall, 1911), well out from the west coast of France, at least in autumn (Le Danois, 1921), and in the colder waters of the Norwegian and Arctic Seas. But with the two species in roughly equal numbers in the rather scant catches outside the continental edge, or with *compressa* and not *bispinosa* predominating there (sometimes, in fact, the only member of the pair represented, as at station 20064 on March 11, 1920), the relative status of the two species off the North American littoral can not be established without further study.

As a general rule, when *bispinosa* outnumbers *compressa* its preponderance is greatest in the deep hauls, whether in the gulf, over the banks, or west and south of Cape Cod.

The adult Euthemisto are not characteristic of any precise depth level in the water, as is the large copepod *Euchæta norvegica*, for example (p. 29), but occur at all depths from the surface down to the deepest strata of the Gulf of Maine.

Large ones, however, especially the females with eggs, have rarely been taken in our surface nets; and even medium-sized individuals have usually been but sparsely represented in the surface hauls, although we have occasionally met exceptions to this rule, notably in the northeastern part of the gulf during August in 1912 and 1913 (stations 10032 and 10096) and off Marthas Vineyard on July 10, 1913 (station 10062). On the other hand, *E. compressa*, like Calanus, has usually proved more abundant above than below 100 meters depth whenever two or more subsurface hauls have been made at different levels.

The bathymetric distribution of the larvæ of Euthemisto differs from that of the adults, for they are usually most numerous at or close to the surface. The fact that we have taken them in swarms in the surface nets at several stations where their parents (or at least females with eggs) were plentiful at deeper levels is evidence that they rise through the water immediately after they are hatched—one of the innumerable provisions of nature for the perpetuation of the species, for otherwise they would inevitably be devoured by their own voracious progenitors (p. 107). Examples of a bathymetric stratification of this sort as between adults and larvæ were noted in the eastern part of the gulf (stations 10092 and 10093) and off Marthas Vineyard (station 10112) in August, 1913; over Georges Bank in July, 1914 (stations 10215 and 10219); off Shelburne in June; in the western basin in August, 1915 (stations 10293 and 10307); and off Marthas Vineyard in July, 1916 (station 10353).

Both species of Euthemisto—*compressa* and *bispinosa*—like *Calanus finmarchicus* and *Sagitta elegans*, tolerate very wide fluctuations of temperature and salinity, as, indeed, they do in European waters as well (Tesch, 1911). So far as actual occurrence goes, we have taken them over the whole range of temperature prevailing within the limits of the gulf, from the icy waters of winter and of the Nova Scotian current, on the one hand, to the summer-heated surface of the western basin and the warm waters along the outer edge of the offshore banks, on the other; likewise over the entire range of salinity proper to the open waters of the gulf, except for the very lowest. It is not possible to draw any close parallel between the abundance (or reverse) of Euthemisto and the temperature from the data so far obtained, but we have never found it abundant in the coldest season, and most of the rich catches have been made in temperatures warmer than 5°, as appears from the following list of the readings at and above the levels at which the horizontal parts of the hauls were made, at several stations productive in large Euthemisto.

| General locality | Station | Date | Depth in meters | Temperature in degrees |
|---|---|---|---|---|
| Eastern basin | 10092 | Aug. 11, 1913 | 170 | 5+ |
| Western basin | 10307 | Aug. 31, 1915 | 40 | 7-8+ |
| Off Cape Sable | 10229 | July 25, 1914 | 80 | 5-6+ |
| Do | 10243 | Aug. 11, 1914 | 40 | 7.5+ |
| Browns Bank | 10296 | June 24, 1915 | 50 | 3+ |
| Do | 10228 | July 24, 1914 | (1) | 14.72 |
| Do | 10228 | do | 60 | 8.3+ |
| Georges Bank | 10216 | July 20, 1914 | 50 | 12+ |
| Do | 10219 | July 21, 1914 | 40 | 13+ |
| Off Marthas Vineyard | 10258 | Aug. 25, 1914 | 25 | 12+ |
| Do | 10351 | July 24, 1916 | 160 | 4.8+ |
| Off Shelburne, Nova Scotia | 10231 | July 27, 1914 | (1) | 6.62 |

[1] Surface.

The last of these records is especially instructive, because there were very few, if any, Euthemisto in the icy water below the surface at that station. The autumnal augmentation of the stock of Euthemisto in the coastal belt of the gulf likewise takes place in comparatively high temperatures (e. g., 7 to 11° on October 26 and 27, 1915, in Massachusetts Bay, stations 10337 to 10339), and our largest November catch was on the surface in water of about 10.3° (station 10404). Thus, whether or not the relation be a causal one (and this is not safe to postulate, in view of the wide distribution of Euthemisto in northern seas), the maximum abundance of Euthemisto in the Gulf of Maine coincides with rather high temperature, both in season and in the depth at which it congregates, corroborating Le Danois's (1921) observation that off the French coast *E. bispinosa* is common only in water as warm as 14°. The adults, however, whether of *compressa* or of *bispinosa*, certainly show no tendency to accumulate in the warmest waters of the gulf, which they could easily reach by swimming upward for a few meters. On the contrary, when they have been found in any number on the surface it has been at times and places where the water was at least no warmer than 15°. Only once have we found large Euthemisto in any number at a temperature higher than 14°.

For the adult, then, the optimum range of temperature in the Gulf of Maine is from 4° to about 12°. We have no evidence that any considerable reproduction of Euthemisto takes place in the gulf in temperatures lower than 5° or higher than 12 to 14°, but the fact that we towed occasional very small specimens in February, March, and April, 1920, both off Massachusetts Bay, in the western basin, near Cape Sable, on Browns Bank, and on the southwest part of Georges Bank (stations 20045, 20048, 20050, 20072, and 20104), proves that a certain amount of breeding takes place in water as cold as 2 to 3°. The larvæ, however, are most often abundant in considerably warmer water, thanks to the fact that summer is the chief breeding season, and to their habit of rising to the surface. Here, again, we hesitate to assume any causal connection between temperature and the depth which they seek, it being as likely that their tendency to congregate at the warmest level is due to some quite different cause; such, for example, as the available supply of food, the density of the water, or the influence of sunlight.

Within the Gulf of Maine Euthemisto is usually most numerous in comparatively high salinities, say, upwards of 32.5, per mile, and while we have made very rich catches in water as little saline as 31.6 per mille along the Nova Scotia coast, this is the lowest salinity in which we have found it in any numbers. Hence, 31.5 per mile may be set arbitrarily as the lower limit to its common occurrence in the Gulf of Maine. When the superficial layers of the coastal zone of the gulf are fresher than this—that is, throughout the period of spring freshets and in early summer—Euthemisto is usually rare there, if not absent; but it would be no surprise to meet exceptions to this rule, for Euthemisto has been found swarming off the English coast in water of only 30.26 per mille (Tesch, 1911).

It is questionable whether high salinities ever act as a barrier to the migrations of Euthemisto in the one direction as low salinities do in the other. It certainly occurs regularly in water as saline as 35 per mille in the eastern North Atlantic, and while it is not a characteristic inhabitant of salter seas (the highest salinity we have actually found it in was about 35.2 per mille (Bigelow, 1915, p. 283) ) it is

more likely that constantly high temperature, not high salinity, is its outer barrier off eastern North America, and bars it from the warmer parts of the Atlantic in general. Within these wide limits, however, Euthemisto is very tolerant of varying salinity, both in the western Atlantic and in the eastern.

At times and places where Euthemisto is abundant it probably serves as a valuable food for pelagic fishes in the Gulf of Maine, though little information is available. In Irish seas Tattersall (1906) found it forming a very large part of the food of two of the principal food fishes—herring and mackerel—as well as of the sea trout, while at times it forms the chief sustenance of the long-finned tuna (*Germo alalunga*) off the French coast (Le Danois, 1921). Euthemisto, in its own turn, is extremely destructive to copepods and to other small planktonic animals (p. 107).

Before closing the brief account of this genus, I must emphasize our failure to find even a single specimen of the arctic Euthemisto (*E. libellula*) within the limits of the Gulf of Maine. Certainly it does not reach it unless as the rarest of stragglers.

## Other hyperiids

The two species of Euthemisto are the only hyperiids that are of any numerical importance in the plankton of the Gulf of Maine. Their relatives, Hyperoche and Hyperia (similarly boreal in faunistic status), have been taken at several stations but always in small numbers.

### Hyperia

Hyperia is represented locally by two species—*galba* and *medusarum*—both of which usually live commensal with the large medusæ Aurelia or Cyanea. This is not invariably the case, however, for Hyperia has repeatedly appeared in the catches of the tow nets at stations where no medusæ were taken or seen—for example, on German Bank, August 14, 1912 (Bigelow, 1914, p. 103). Associated with their occasional independence of the medusæ we have found one or other species of the genus widely distributed in the northern half of the gulf, over deep water as well as shallow, but our nets have never yielded more than four or five specimens of Hyperia at any one station. *Hyperia medusarum* has been taken both in summer and in winter, but *H. galba* has so far been taken only in July and August.

In the case of animals as comparatively scarce as Hyperia is in the Gulf of Maine, captures in tow nets are so largely a matter of accident that they do not give a reliable picture of the numerical strength of the species in question from season to season and from place to place. It seems, however, that Hyperia was decidedly more numerous in 1913, when we found it at some half dozen stations in the gulf (Bigelow, 1915, p. 279), than in the summer of 1914, when it was not found at all at the same localities and season (Bigelow, 1917, p. 289), or in 1915, when only odd individuals were taken during the summer.

### Hyperoche

*Hyperoche tauriformis*[90] has appeared rather more commonly in our tow nettings than has either species of Hyperia, having been taken at 10 stations in the

[90] In an earlier report (Bigelow, 1915) this amphipod appears as "*H. kroyeri* Bovallius," but recent students of the group—e. g. Tesch, (1911) and Tattersall (1906)—agree that while it has passed most often as "*kroyeri*" or as "*abyssorum*" Boeck, its correct designation is "*H. tauriformis*" Bate and Westwood. This name is accepted here for the sake of uniformity, the question not being of specific identity but simply of the distribution of the only species of Hyperoche known to exist in northern seas.

gulf during August, 1913 (Bigelow, 1915, p. 279). Like Hyperia, it was far less common in 1914, when we took it only once within the gulf limits and occasionally off the Nova Scotian coast east of Shelburne (Bigelow, 1917, p. 289); in 1915 it was taken at several stations, but never more than one or two specimens at any. Judging from the regularity with which it appeared in Massachusetts Bay during the winter of 1912–1913 (Bigelow, 1914a, p. 410; six out of nine stations, but only one or two examples on each occasion), Hyperoche is at least as common during the period from November to February as during the warm months; but it has not been detected at all at any of the stations occupied in late February, March, April, or May, suggesting that it becomes very rare in the gulf, if it does not entirely vanish thence, when the water is at its coldest for the year.

Our captures of Hyperoche in the Gulf have all been near shore, for the most part within the 100-meter contour (Bigelow, 1915, p. 284), but the numbers of specimens concerned are too small to throw any light on its bathymetric distribution or on the relationship which its occurrence bears to the physical state of the waters of the gulf.

### Parathemisto oblivia

*Parathemisto oblivia* has been detected twice in our hauls in the open gulf (stations 10032 and 10036, August 16 and 20, 1912) and at three stations off the outer coast of Nova Scotia (Bigelow, 1917, p. 289), all in late summer. Doctor Huntsman informs me that it breeds locally under estuarine conditions in the Bay of Fundy also. This amphipod is far more abundant in North European waters, where it plays much the same rôle as does Euthemisto in our gulf and sometimes occurs in shoals right up to the land (Edward, 1868; Tattersall, 1906; Tesch, 1911).

### Oceanic hyperiids

Our stations along the continental slope have occasionally yielded oceanic and warm-water hyperiids in some numbers, but it is only on the rarest occasions that any of them encroach more than a few miles on to the shelf within the limits of the gulf, nor are any of them known from within Georges and Browns Banks (p. 56). For the sake of completeness, such records as have been obtained within the geographic limits of the present study since 1912 are listed below [91] (for earlier records for New England waters, see Holmes, 1905).

| Species | Date and stations | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | July, 1913,[a] 10061 | July and August, 1914 [b] | | | | | June to August, 1915 | | February to May, 1920 | | | |
| | | 10218 | 10219 | 10220 | 10260 | 10261 | 10296 | 10333 | 20044 | 20045 | 20076 | 20129 |
| Oxycephalus sp. | | 3 | | | | | | | | | | |
| Phronima sedentaria | | 4 | 1 | 2 | | 1 | | | | | | |
| Phronima atlantica | | × | 1 | | 1 | | | | | | | |
| Phronima sp. | | | | | | | × | × | × | × | × | × |
| Phrosina semilunata | | × | | | | | | | | | | |
| Phronimella elongata | | 3 | | | | | | | | | | |
| Vibilia sp. | 1 | 2 | | | | | | | | | | |

[a] For records between the latitudes of New York and Chesapeake Bay during that summer see Bigelow, 1915, p. 279.

[b] Previously listed in Bigelow, 1917, p. 289.

[91] For descriptions and an account of the general distribution of these hyperiids on the high seas see Bovallius, 1887 to 1899.

The distribution of these and of other warm-water planktonic animals is discussed in a preceding chapter (p. 53).

## Copepods

Except in certain restricted localities, or for brief periods when some other animal swarms, the animal plankton of the Gulf of Maine consists chiefly of copepods at all seasons. The seasonal fluctuations of the group as a whole are touched on above. The following chapter gives brief discussions of most of the species so far detected in the plankton of the open gulf or at St. Andrews (Doctor McMurrich's lists, p. 12). The great majority are forms that are not only typically pelagic but widespread in northern seas; but at St. Andrews, where strong tides stir the water from bottom to top, sundry dwellers in the littoral zone are brought up to or near the surface, and probably this takes place more or less in estuarine situations all around the shore line of the gulf. Samples of the copepods collected in 1912, 1913, and 1914 were identified by Dr. C. O. Esterly, and lists for those years have been published elsewhere (Bigelow, 1914, p. 115; 1914a, p. 409; 1915, p. 287; 1917, p. 290). It is not necessary to repeat them here. Only a preliminary survey has been made of the copepods towed by the *Grampus* in 1916 (Bigelow, 1922), but Dr. C. B. Wilson has supplied lists for the vertical hauls made in 1915 and the spring of 1920 and for the horizontals for the winter of 1920–21, which are tabulated below (p. 297). Doctor McMurrich's manuscript lists of plankton for St. Andrews, New Brunswick, have been especially instructive for the seasonal periodicity of the copepods.

Previous to the inception of the *Grampus* cruises in 1912, almost no attention had been paid to the copepods of the Gulf of Maine, the only published data for that precise region being a few notes on species from Plymouth Harbor, Mass. (Wheeler, 1901). Subsequently Willey (1919, 1920, and 1921) has given some notes on the copepods of the St. Andrews region in the Bay of Fundy. The Copepoda of southern New England have been studied by Wheeler (1901), Williams (1906 and 1907), Sharpe (1911), and Fish (1925); those of the outer coasts of Nova Scotia and of the Gulf of St. Lawrence by Herdman, Thompson, and Scott (1898), by T. Scott (1905), and by Willey (1919), whose lists of the species collected by the Canadian fisheries expedition of 1915 are referred to repeatedly in the following accounts of the several species.

All living copepods are small—the largest up to 10 to 11 millimeters, the smallest less than 1 millimeter in length. The commonest Gulf of Maine species (*Calanus finmarchicus*) is about 2 to 5 millimeters long when adult. They are present in such immense numbers in the plankton, and they reproduce so rapidly, that they are the most important of all pelagic invertebrates from the economic viewpoint, furnishing the primary food for the young of most marine fishes until these attain considerable size, as well as for many of the larger planktonic animals of various groups. Copepods are the major article in the diet of the adults of such plankton-feeding species as the mackerel and all the herring tribe. This aspect of copepod economy is touched on in another chapter (p. 97). I need only emphasize here that evidence is constantly accumulating to prove that the fertility of any part of the northern seas in

commercial fishes depends very largely on the stock of copepods. As Dr. C. B. Wilson writes, it is not too much to say that "their presence and abundance count as much for the higher animal life in the ocean as does that of nitrates in the soil or carbon dioxide in the air for plant life upon the land," for they are the chief intermediary through which the elemental foodstuffs elaborated by the marine plants on which the copepods feed are made available for the support of the larger marine animals that feed on them.

Copepods are the only animal group that has been systematically counted in the catches of the vertical nets in the Gulf of Maine; and while the numerical calculations include so many indeterminate sources of error that they can be taken only in a general way, they have proved undeniably instructive in tracing the seasonal periodicity and relative regional abundance of several of the more common species. I must emphasize, however, that the counts given are only a rough indication of the relative abundance or scarcity of the several species, and that the "probable error" (unknown) may amount to as much as 80 to 100 per cent in extreme cases. (For a discussion of the allowance that must be made on this account see Johnstone, Scott, and Chadwick, 1924, p. 180.)

For the group as a whole the numbers present per square meter have varied from next to none at occasional stations in the coastwise zone during the early spring, when diatoms are flowering and copepods are scarcest (p. 39), to upwards of 500,000 in May, when *Calanus finmarchicus* is swarming (e. g., station 10266, May 4, 1915). Copepods are at their lowest ebb in the gulf in February and March, when the maximum per square meter at any station within the edge of the continent in 1920 was 37,500 (station 20049, in the western basin), the minimum 55, in the inner part of Massachusetts Bay, and the average about 6,600. Generally speaking, at this season there are more copepods under any given area of the sea surface in the deeper parts of the gulf than in the shoal, the numbers caught being roughly proportional to the amount of water strained by the net in its journey from the bottom up to the surface. Thanks to a swarm of Calanus (p. 189), there were more copepods outside the south eastern edge of Georges Bank than anywhere within the gulf.

In April, 1920, the average within the continental waters of the gulf was about twice as large (13,300) as it had been in March, the maximum more than three times (130,000 in the northern channel), and the minimum had risen from 55 to 900.

In another chapter (p. 41) I have commented on the tremendous augmentation of copepods which takes place in May and for which the vernal wave of reproduction of *Calanus finmarchicus* is chiefly responsible. In 1920 this was hardly under way by the middle of the month, but in 1915 it had raised the average number of copepods over the inner parts of the gulf to upwards of 140,000 by the 4th to the 14th (stations 10266 to 10278), with maxima of 511,000 off Cape Ann on the 4th and 411,500 in the eastern side of the basin on the 6th.

Fewer copepods were taken in June, the average being only about 23,000 per square meter. The fact that the vernal reproductive activity commences later in the northeastern and eastern shallows of the gulf, where most of the June stations were located, than in its western side is chiefly responsible for this apparent shrinkage; but with only about one-seventh as many copepods in the eastern basin on June 19,

1915 (station 10288) as at a near-by location (station 10270) on May 6, it seems that the swarm resulting from this local center of active reproduction had dispersed in the interim. Unfortunately no vertical hauls were made later than June in the summer of 1915, but in July and August, 1914, the average number of copepods per square meter for the gulf, as a whole, inside the continental edge but including the offshore banks, was between 72,000 and 73,000 (see Bigelow, 1917, p. 315, for table of counts)—i. e., something less than half the May average for 1915, with a maximum of 227,000 in the northern channel and a minimum of 6,000 on the northern edge of Georges Bank at this time.

Copepods were then most numerous per square meter (70,000+) in four distinct regions as follows: (1) Over a V-shaped area, with one arm extending from Cape Cod

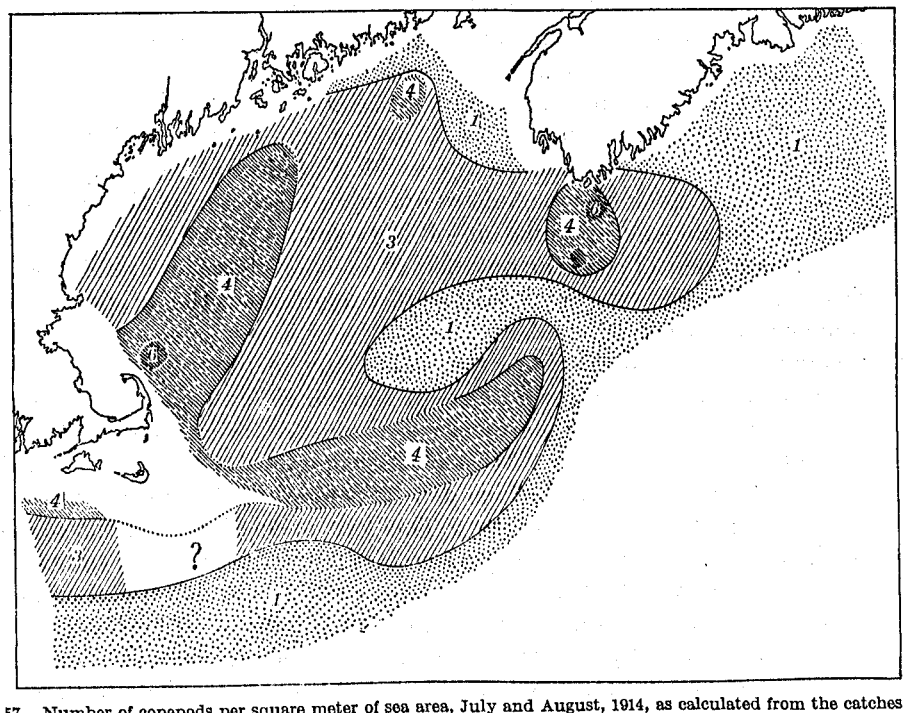


FIG. 57.—Number of copepods per square meter of sea area, July and August, 1914, as calculated from the catches of the vertical hauls. 1, scanty (less than 20,000); 2, intermediate (20,000 to 70,000); 4, rich (70,000 to 150,000); 6, very rich (150,000 or more). Reproduced from Bigelow, 1917, fig. 94.

toward Penobscot Bay, the other to the eastern part of Georges Bank; (2) off Cape Sable; (3) in the extreme northeast corner of the basin of the gulf; and (4) south of Marthas Vineyard (fig. 57). The maxima were off Cape Cod, off Cape Sable, and in the northern channel (stations 10213, 10243, and 10229; Bigelow, 1917, p. 316). On the other hand, we have found very few copepods in the coastal zone in the extreme northeast corner of the gulf, in the southeastern part of the basin, in the eastern channel, or in the oceanic water outside the edge of the continent during the summer. The distribution of copepods on the basis of numbers per cubic meter has paralleled this, except that the region northeast of Cape Cod was shown to be relatively less productive by this than by the other calculation in July, 1914. The numbers per

square and cubic meter for that summer and for the season of 1915 are tabulated in an earlier report (Bigelow, 1917, pp. 315 and 319). September stations for 1915 yielded an average of about 65,000 copepods per square meter in the northern half of the gulf—no noticeable change, that is, from the midsummer state—but the fact that the maximum (173,000) was considerably less and the minimum (14,700) considerably greater is interesting as evidence that copepods tend to become progressively more and more nearly equalized in number over the gulf as the season advances.

In the earlier chapter I have pointed out that we have observed an autumnal increase in the amount of plankton present in the western and northwestern parts of the gulf (p. 87). In 1915 this was due to a multiplication of copepods from the September average just given to an average of about 107,000 per square meter at ten stations for the month of October (stations 10323 to 10329 and 10336 to 10339; table, p. 297). As evidence that this multiplication was due to increased local reproduction we found upwards of 200,000 off Cape Cod (station 10336) and in Massachusetts Bay (station 10338) on the 26th and 27th.

Unfortunately no vertical hauls have been made in the gulf in November, December, or January. It is therefore impossible to follow numerically the gradual decimation of the local stock of copepods which takes place during the winter (p. 88), leading to the sparse copepod population of early spring (p. 82).

Outside the continental edge the numbers of copepods have invariably been small, except for the one Calanus swarm of March just mentioned, the origin of which is discussed under that species.

The pelagic copepods are perhaps the most truly planktonic of all animals, for although some of them dart actively through the water, and all swim more or less vigorously, they are utterly at the mercy of the current so far as directive journeyings from place to place are concerned. Most of the copepods of the Gulf of Maine are eupelagic ocean forms, floating at various depths beneath the surface of the water by means of their elongated first antennæ. The two species of Acartia (*clausi* and *longiremis*), the two species of Calanus (*finmarchicus* and *hyperboreus*), the two species of Metridia (*longa* and *lucens*), and *Pseudocalanus elongatus*, which together constitute 80 per cent of the copepod plankton of the gulf, all belong to this class.

The scope of the present paper being ecologic and geographic, not systematic, the copepods are arranged alphabetically here, the list of species, the distribution of which is discussed, being as follows. Those starred are only accidental in the plankton. For supplemental notes on a few other rare species detected by Dr. C. B. Wilson after the body of the report was ready for the press see p. 305.

Acartia clausi.
Acartia longiremis.
Acartia tonsa.
Aetidius armatus.
Anomalocera pattersoni.
Asterocheres boecki.
Calanus finmarchicus.
Calanus hyperboreus.
Candacia armata.
Centropages bradyi.
Centropages hamatus.
Centropages typicus.
*Dactylopusia thisboides.
Dwightia gracilis.
*Ectinosoma neglectum.
Eucalanus attenuatus.
Eucalanus elongatus.
Euchæta media.
Euchæta norvegica.
Euchirella rostrata.

Eurytemora herdmani.
Gaidius tenuispinis.
Halithalestris croni.
*Harpacticus litoralis.
*Harpacticus uniremis.
Heterorhabdus spinifrons.
*Idya furcata.
Labidocera æstiva.
Lucicutia grandis.
Metis ignea.
Mecynocera clausi.
Metridia longa.
Metridia lucens.
Monstrilla serricornis.
Oithona similis.
*Parathalestris jacksoni.
Phyllopus bidentatus.
Pleuromamma (genus).
Pseudocalanus elongatus.
Rhincalanus cornutus.
Rhincalanus nasutus.
Scolecithricella minor.
Temora longicornis.
Tortanus discaudatus.
Undeuchaeta major.
Undeuchaeta minor.
*Zaus abbreviatus.
*Zaus spinatus.

### Acartia clausi Giesbrecht

This species has a more southerly distribution than *A. longiremis*, ranging widely on both sides of the temperate North Atlantic, southward from western Norway on the one side and from the St. Lawrence River on the other; but it was not found in any of the samples of Arctic plankton examined by Sars (1900) and at only one station north of the Arctic Circle in the collection of the Canadian Arctic expedition (Willey, 1920). In general, it may be described as neritic, as opposed to oceanic, for although it is widely distributed in the oceanic areas of the North Atlantic, European students have found it most plentiful in coastal waters such as the Irish and English Channels and the southern parts of the North Sea. It is found plentifully in water as little saline as 18.42 per mille, but salinities much lower than this apparently bar it (Farran, 1910). Willey (1920) has characterized it as more of an estuarine form than *A. longiremis*, but the distribution outlined below for the Gulf of Maine shows that this can hardly be laid down as a general rule. Steuer (1923) has recently charted its distribution in the Eastern Atlantic and generally.

In a continuous collection of plankton from Liverpool to Quebec, made by Sir Wm. Herdman in 1897, it disappeared at longitude 38° 6′ W. and did not reappear until the ship was well up the St. Lawrence River (Herdman, Thompson, and Scott, 1898). T. Scott (1905) reports it from the Gulf of St. Lawrence, but Willey (1919) did not find it among the many samples which he reported on thence, and if not wholly wanting it is at least so rare over the continental shelf off Nova Scotia and south of Newfoundland that the Canadian fisheries expedition took it at only one station—this, curiously enough, the outermost on the line off Cape Sable (Willey, 1919).

It was not detected among the collections made by the *Grampus* between Cape Cod and Chesapeake Bay in 1913 or in 1916, though its relative *A. tonsa* swarmed locally off Delaware Bay during August of the latter year (Bigelow, 1922, p. 146). Neither did Wheeler (1901) nor Sharpe (1911) find it at Woods Hole, where *A. tonsa* is one of the commonest of copepods. It is not uncommon there during some winters, for Fish (1925, fig. 46) found it regularly from October, 1922, to February, 1923. It does not appear in Fowler's (1912) list of Rhode Island copepods, but Williams (1906 and 1907) describes it as abundant in Narragansett Bay in January and

February, and Dr. C. B. Wilson contributes the statement that in and around Chesapeake Bay *A. clausi* is more abundant than *A. longiremis*.

The earlier cruises in the Gulf of Maine gave no grounds for supposing that *A clausi* was ever plentiful there, Esterly having detected it at one station only (Gloucester Harbor) in the towings taken during the summer of 1912, and not at all for July and August, 1913 or 1914, nor for the winter of 1912–13 (Bigelow, 1914, 1914a, 1915, and 1917). Willey (1919), however, reported it from Passamaquoddy Bay in August, 1915, and on January 16, 1920, he found that adults and juveniles of *A. clausi* formed 68 per cent of the total catch of copepods there (Willey, 1921). Dr. C. B. Wilson has detected it in so many of the Gulf of Maine towings made during the summer of 1915 (fig. 59), the spring of 1920 (fig. 58), and the winter of 1920–21, that it was certainly widespread and locally abundant in the gulf during those years at least.

The counts tabulated here may be considered from two aspects—*a*, the relative importance of *A. clausi* in the copepod community, and *b*, its absolute abundance. It constituted 0–15 per cent of a comparatively scanty copepod plankton during December, 1920, and January, 1921, but was so nearly universal in the inner parts of the gulf that it occurred at 85 per cent of the stations. In February, 1920, however, it was not taken at all, either in the surface or in the vertical hauls, at the few stations occupied in the southwest deep and on Georges Bank during that month. It is probably at its minimum in early spring, because it averaged only 41 specimens per square meter inshore of the 100-meter contour, and 47 in the deeper parts of the gulf, in March, 1920, occurring in 15 of the 35 hauls. In April, however, it was detected in 25 of the 30 vertical hauls, having risen, on the average, to 10 per cent of the total catches of copepods and in absolute abundance to an average of 2,390 individuals per square meter within the 100-meter contour, 180 in the deeps. In May it occurred in all the vertical hauls, both in 1915 and in 1920, averaging 6 to 9 per cent of the total copepods, with an average of 2,787 per square meter in shoal water in 1920, and 7,857 in shoal and 8,469 in deep water in 1915. The augmentation which takes place in its numbers during the spring is further illustrated by counts of the numbers taken at pairs of stations in the western part of the gulf in February and March and again in May of 1920, as follows:

| Locality | Date | Station | Number of specimens in surface tow | Number of specimens per square meter in vertical tow |
|---|---|---|---|---|
| Southwest part of Georges Bank | Feb. 22 | 20046 | 0 | 0 |
| | May 17 | 20128 | 60 | 1,425 |
| Southwest corner of basin | Feb. 23 | 20048 | 0 | 8 |
| | May 17 | 20127 | 162 | 1,437 |
| Off Gloucester | Mar. 1 | 20050 | 115 | 0 |
| | May 4 | 20120 | 1,750 | 5,500 |

In 1915 it continued universal in June, averaging 14 per cent of the total copepods in the vertical hauls and 45 to 50 per cent at two of the stations, but its absolute abundance was somewhat less (averaging about 4,000 per square meter in shoal water

and 1,600 in deep). There are no vertical-net collections for July, 1915, and the normal summer status of *A. clausi* in the Gulf of Maine can not be stated from the other data at hand. In 1915 it varied in abundance from about 500 to upwards of

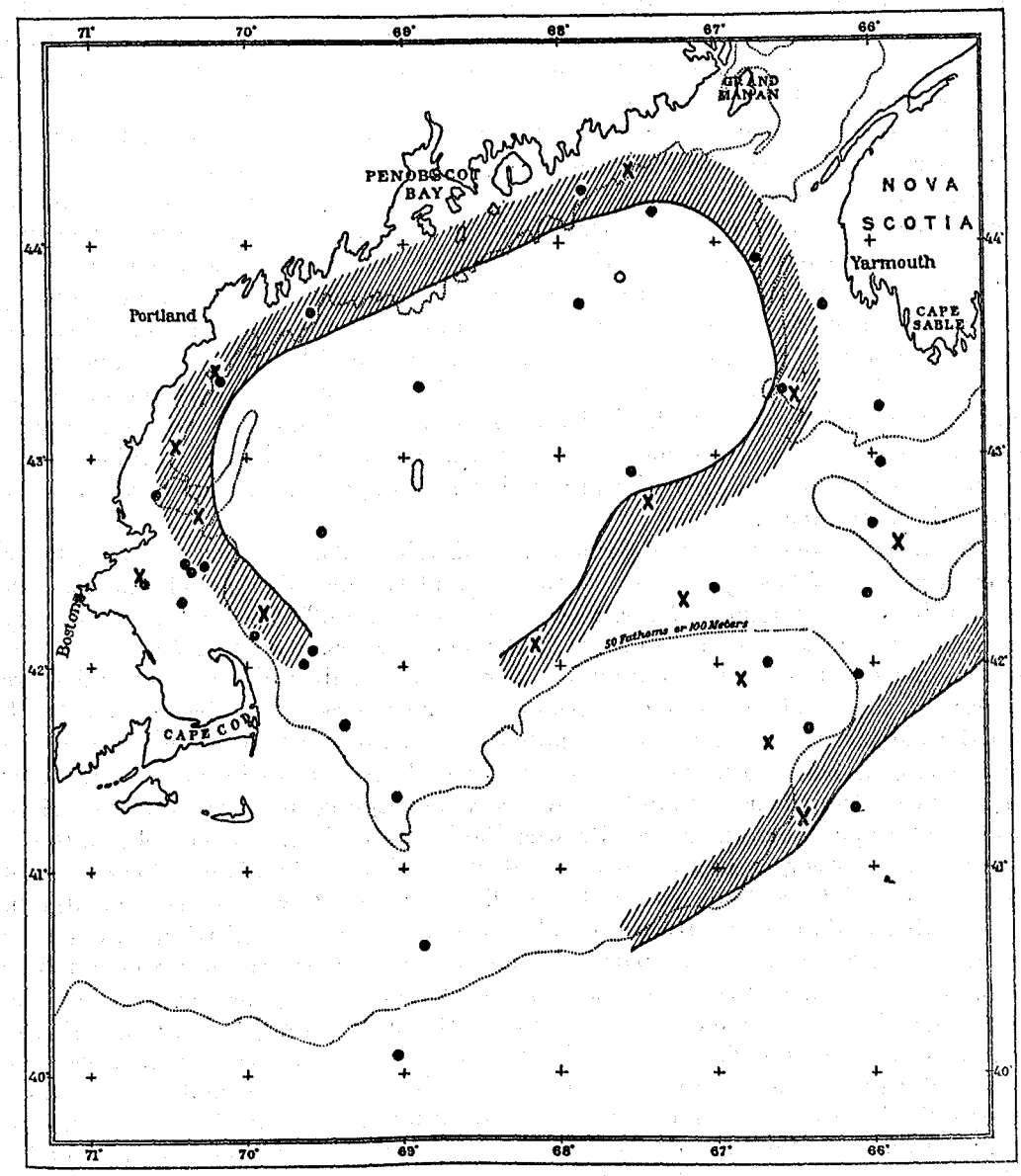


FIG. 58.—Occurrence of the copepod *Acartia clausi* during the spring of 1920. X, locality records for February and March; ●, locality records for April and May. The hatched curve incloses the area where it occurred in March

10,000 per square meter at three stations in August, but was not detected at all at sea during this month in the three previous years, which I take to mean that it passes through a summer minimum succeeding the late spring maximum. In Sep-

tember, 1915, it proved more abundant, both absolutely (on the average about 7,000 per square meter inside 100 meters and 11,000 outside) and relatively (an average of 20.5 per cent of the vertical catch of copepods), than at any time from December to August, and the average numbers per square meter rose, respectively, to 9,693 and 11,205 [92] in October of that year, when it occurred at 88 per cent of the stations, though it constituted only about 11.5 per cent of the total copepods caught in the vertical net during the month.

The two maxima suggest two breeding seasons for *A. clausi* in the gulf—one in early spring and the other in late summer—each followed by a well-marked increase in the actual abundance of the species, as measured both by the number of specimens existing per square meter of sea surface and by the percentage of the total copepod population which it constitutes. Probably it does not breed to any extent in the gulf during the autumn or winter. *A. clausi* is likewise at its minimum during winter in north European waters and most abundant during the warm months. In the southern part of the North Sea its minimum falls in February and its maximum in August (Farran, 1910). It is to be noted that the seasonal distribution of *A. clausi* in the gulf shows it to be endemic there, not an immigrant, propagating in spring in the centers where some few have persisted through the unfavorable winter season and extending its area of reproduction as its spreads far and wide with the increase in its numbers.

*Regional distribution.*—In February and March, 1920, it occurred sparingly on the eastern part of Georges Bank, on Browns and German Banks, off Machias, off the mouth of the Merrimac River, near Gloucester, and off Cape Cod, but at only 3 stations in the basin of the gulf, all in the southeastern part (fig. 58). Thus, at the season when it is at its miminum it persists in small numbers here and there throughout the shoal zone but disappears from most parts of the basin. By April, with the increase in its numbers just noted (p. 172), it had become sufficiently dispersed over the basin to be taken at most of the deep stations in one or other net; but it still continued most abundant over a zone running offshore from the neighborhood of Cape Sable out across Browns Bank to the Eastern Channel and to the eastern part of Georges Bank, with secondary centers of abundance along western Nova Scotia, off Cape Cod, and off Cape Elizabeth, just as was the case in March.

By May and June of 1915 we found *A. clausi* so generally distributed over the eastern, northern, and western parts of the gulf (in numbers ranging from 1,400 to 25,000 per square meter) that no separation into "rich" and "poor" areas is possible, except that it seems to have been scarce in the neighborhood of Mount Desert Island. Curiously enough, this was also the case on Browns Bank, which was one of its chief centers of abundance in April, 1920. Probably it is equally universal on Georges Bank during these months, judging from its presence at all the stations on the line from Cape Cod out across the western end of the bank on May 16 and 17, 1920; but there were only about 200 per square meter at the outermost station, just outside the continental edge (Station 20129), contrasted with about 14,000 at the station on the bank (Station 20128), suggesting that this was about its offshore boundary, which accords with its neritic nature.

[92] The counts of copepods for 1915, on which these calculations are based, are given in Bigelow, 1917, p. 319.

*A. clausi* continued universal over the northern and western parts of the gulf during November and October, 1915 (this, as just remarked, being its season of maximum abundance), and across the whole breadth of the continental shelf off Marthas Vineyard, varying in abundance from 6,000 to upwards of 40,000 specimens per square meter of sea area at most of the stations. Nor do our records for the midwinter cruise of 1920–1921 suggest any shrinkage in its range during the later autumn, for it occurred at nearly all the stations during that December and January. But if the picture presented by the early spring hauls of 1920 be normal, *A. clausi* must disappear from the basin of the gulf later in the winter as its numbers decline.

*A. clausi* has always averaged a larger percentage of the total copepod population in the coastwise belt of the gulf and over the offshore banks than in the deeper parts. In 1920 it formed 10 to 20 per cent of the copepod catch in the vertical hauls at most of the stations on the eastern part of Georges Bank, on Browns Bank, in the Cape Cod–Massachusetts Bay region, off Cape Elizabeth, and along western Nova Scotia from February to May, but usually less than 5 per cent at the stations in the deeper basin and channels where it occurred. From June to October in 1915, the area in which *A. clausi* usually constituted 10 per cent or more of the copepods was continuous around the whole periphery of the gulf and around Cape Cod and Nantucket to the westward (fig. 59). In December, 1920, and January, 1921, it amounted to less than 10 per cent at all but one of the stations. Thus, this species is only of minor importance in the general planktonic community in the more oceanic parts of the gulf and negligible outside the continental edge in the open Atlantic, but in shoal waters, both inshore and on the banks, it is usually an important factor and may locally equal as much as half the total catch of copepods of all kinds.

*Vertical distribution.*—The hauls have not been adapted to show the vertical distribution of *A. clausi*, and the fact that all but one of the percentages of 30 or more were in hauls shoaler than 75 meters can not be taken as meaning a concentration of this species in the upper water layers because associated with the fact that the species is most plentiful in the shoal zone. On the whole, however, *A. clausi* was a slightly larger element in the copepod community on the surface than in the vertical hauls during the spring of 1920 (March, 13 per cent; April, 15.5 per cent; and May, 14 per cent, on the average); and on two occasions—that is, Eastern Channel, March 17 (station 20073), and off the northern slope of Georges Bank, March 10 (station 20063)—we found them congregated so close to the top of the water that each of the surface hauls yielded about 1,200 specimens, whereas the vertical hauls took none in the one case and only 3 in the other. On the other hand, *A. clausi* has repeatedly proved more plentiful at some deeper level than on the surface, of which the following cases are typical:

| Locality | Date | Station | Number per square meter from vertical haul | Number taken in surface haul |
|---|---|---|---|---|
| Southeast basin | Mar. 3, 1920 | 20053 | 600 | 0 |
| Off Cape Ann | Apr. 9, 1920 | 20091 | 1,125 | 31 |
| Northeast basin | Apr. 12, 1920 | 20100 | 475 | 0 |
| Browns Bank | Apr. 16, 1920 | 20106 | 3,000 | 2 |
| Eastern part of Georges Bank | do | 20108 | 21,262 | 225 |
| Western basin | Apr. 18, 1920 | 20115 | 800 | 0 |

It is to be noted that this has been observed in the shoal water of the banks as well as in deep water. *A. clausi* has seldom been found plentiful enough in the Gulf of Maine to suggest that it is ever important there as a food supply for larger ani-

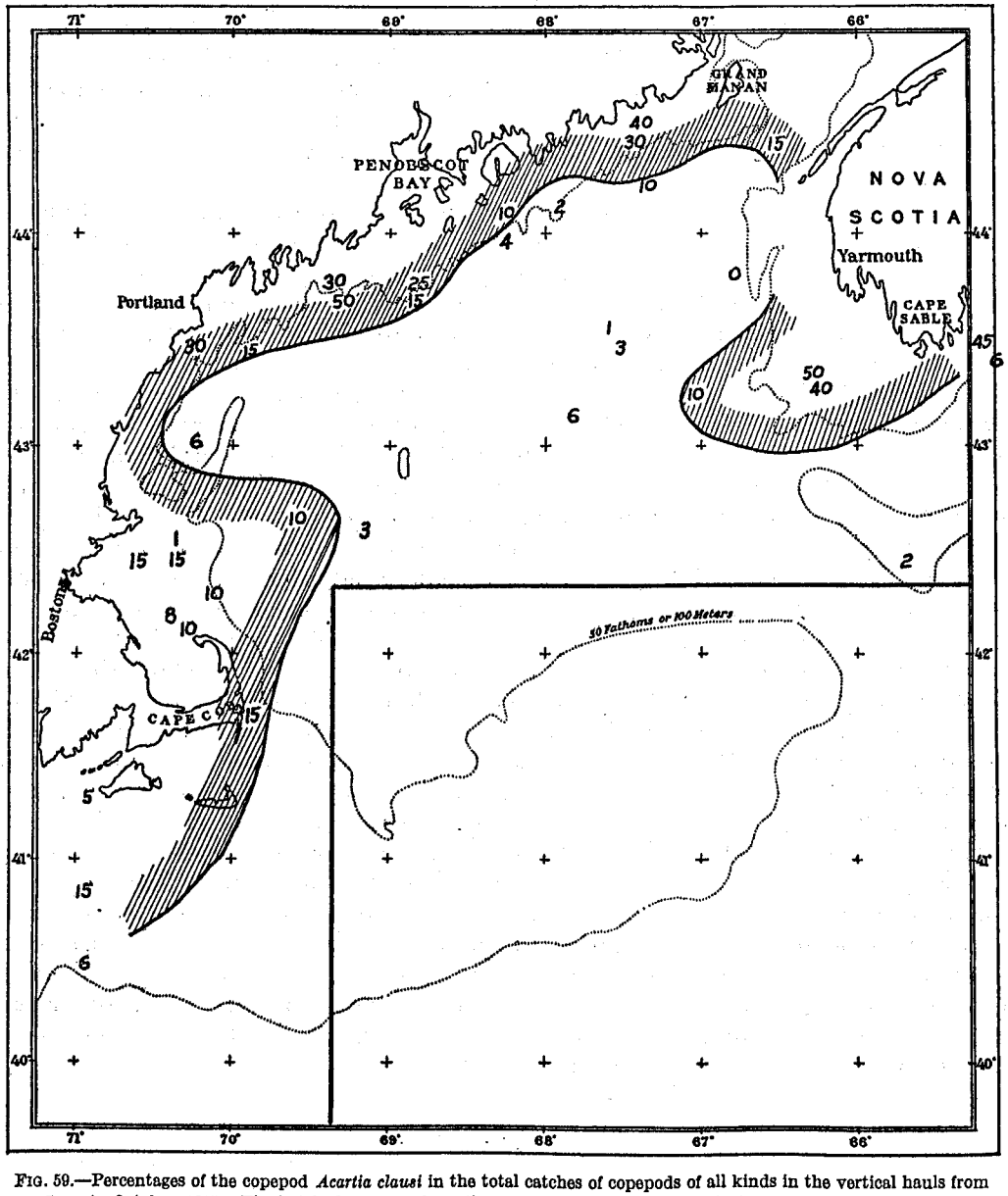


FIG. 59.—Percentages of the copepod *Acartia clausi* in the total catches of copepods of all kinds in the vertical hauls from June to October, 1915. The hatched curve incloses the area where it usually constitutes more than 10 per cent of the copepods in summer

mals. This is likewise true of it, as a rule, in north European seas, though it has been recorded there among the stomach contents of various fishes; but as Farran (1903, 1910, and 1911) reports it as taken throughout the year on the mackerel-

fishery grounds off Ireland, most commonly in autumn, it may prove a more important ingredient in the food of the European mackerel than it is ever likely to be off the seaboard of eastern North America.

### Acartia longiremis Lilljeborg

This species is of minor importance in the Gulf of Maine but is recorded sufficiently often to deserve brief mention. In the Atlantic *A. longiremis* ranges from the polar basin on the north, where it has been taken at many localities both on the European side and along the Arctic coast of Canada (Willey, 1921), to the Mediterranean on the one side and southward to Chesapeake Bay on the other. It is also reported from the Gulf of Suez. Its distribution, in general, has recently been charted by Steuer (1923).

It has usually been described as more or less neritic, though less so than *A. clausi*. According to Farran (1910 and 1911) it is mainly a littoral form in the more southern parts of its range, though often found in the open sea off Norway. Herdman, Thompson, and Scott (1898) record it regularly in the Gulf of St. Lawrence, out to the Straits of Belle Isle, and again between longitude 31° 40′ W. and the British coastal waters, but not at all in the intervening zone. It was not found at Woods Hole either by Wheeler (1901) or by Sharpe (1911), nor was it found in Rhode Island waters by Williams (1906 and 1907) or off New Jersey by Fowler (1912). Probably, however, it is to be expected all along southern New England, for Fish (1925) found it at Woods Hole from January to May, while Dr. C. B. Wilson contributes the statement that it occurs in and about Chesapeake Bay, though less abundantly than *A. clausi*.

The only previous records for *A. longiremis* in the Gulf of Maine are as follows: Station 10020 (about 4 per cent of the copepods), Gloucester Harbor, and 6 miles off Cape Porpoise (2 per cent of the copepods) during the summer of 1912; station 10251, off Cape Elizabeth, August 14, 1914 (especially interesting because upwards of 90 per cent of the hundreds of copepods taken in the surface net were adults and juveniles of *A. longiremis*)[93]; and Passamaquoddy Bay, January 16, 1920, when *A. longiremis* (adult and young) constituted 13 per cent of the copepods taken (Willey, 1921).

During the cruises of 1915 and 1920 this species proved much less plentiful and less generally distributed in the gulf than *A. clausi*, its status in the gulf differing widely from year to year. In 1920 it was not detected at all in February. In March (fig. 60) it occurred at 38 per cent of the stations, confined to four distinct regions: (1) the coastal zone from Cape Cod to Cape Elizabeth, (2) the eastern part of Georges Bank and the deep water to the north, (3) Browns Bank, and (4) the shallows off western Nova Scotia out to German Bank. In every case the number of specimens taken was trifling, the highest frequency in the vertical hauls being only 95 per square meter of sea surface. The scarcity of this species during March appears also from its percentage in the total copepod catch (0–30 per cent; average 2½ per cent).

[93] Identified by Dr. C. O. Esterly.

During April it became so scarce in the Massachusetts Bay region and over the northwestern part of the gulf generally that it did not appear there in the catches of the vertical nets, although the surface tows picked up a few at the localities marked

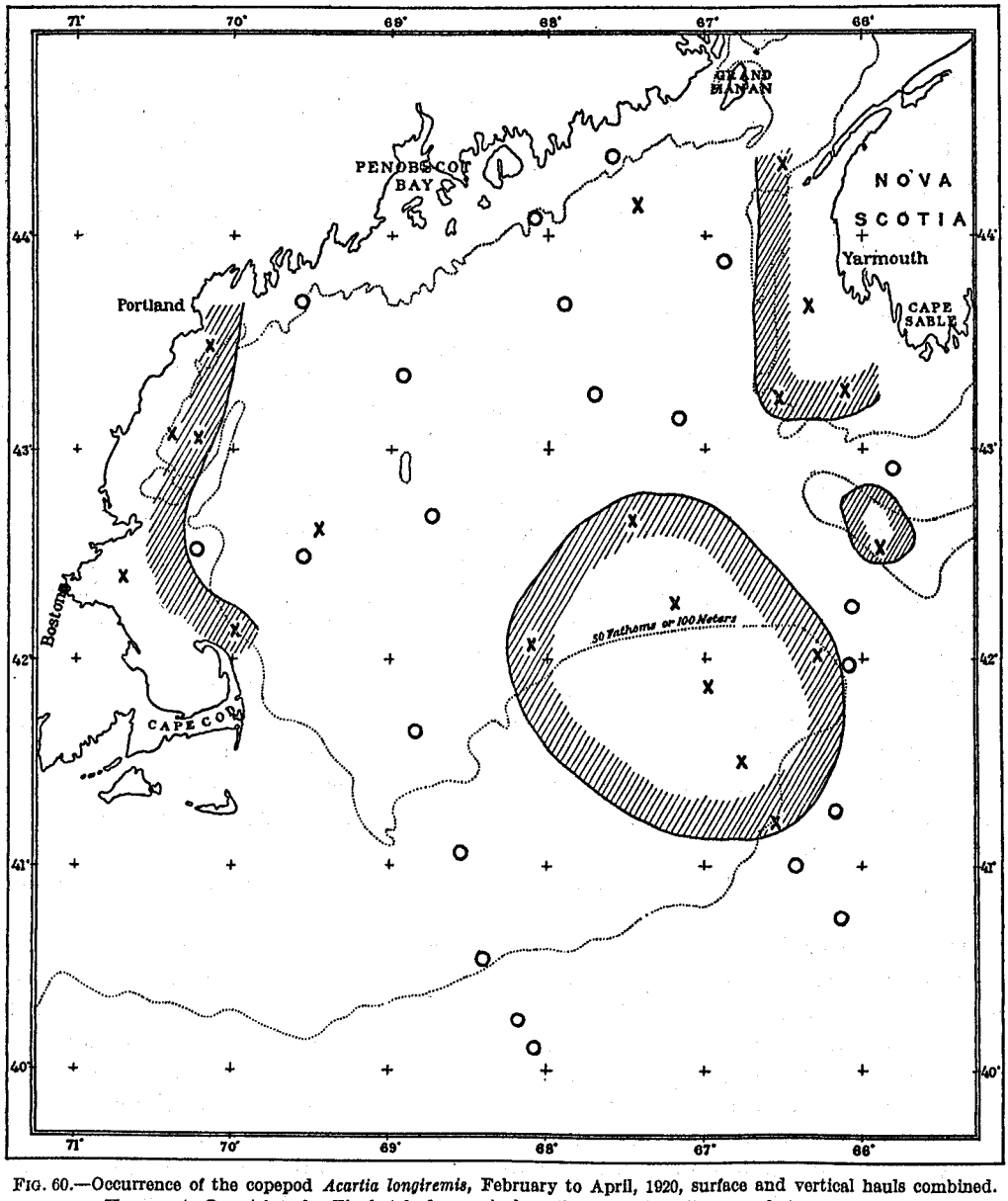


FIG. 60.—Occurrence of the copepod *Acartia longiremis*, February to April, 1920, surface and vertical hauls combined. X, present; O, not found. The hatched curve incloses the areas where it occurred at every station

on the chart (fig. 61); but, by contrast, it had spread generally over the whole eastern side of the gulf, with a rather definite line of demarcation between the areas where it did and did not occur in sufficient number for the vertical net to take it (fig. 61), but

not to the deep water off the southeastern slope of Georges Bank. The numerical frequency of *A. longiremis* likewise rose by April to a maximum of 2,800 per square meter off Cape Cod, 1,300 per square meter in the northern channel, and 863 per square

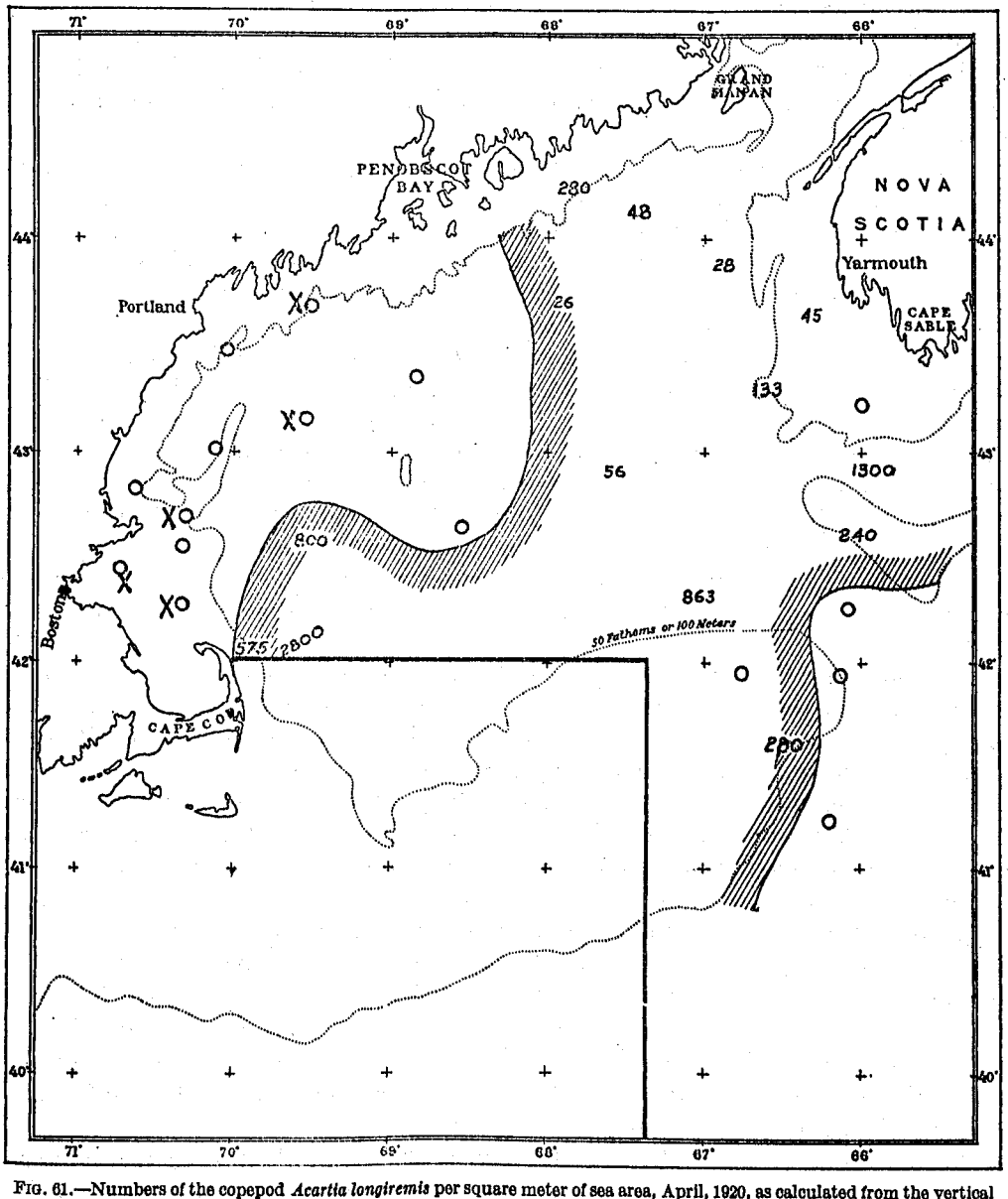


FIG. 61.—Numbers of the copepod *Acartia longiremis* per square meter of sea area, April, 1920, as calculated from the vertical hauls. O, none in vertical haul; X, taken in surface haul. The hatched curve incloses the area where it was plentiful enough to be taken regularly in the verticals

meter north of Georges Bank, though on the average it was still only about 2½ per cent of the total copepods (0–14 per cent). In 1920 it reappeared in Massachusetts Bay in May, when it occurred at all the stations there and along the line from Cape

Cod out across the western end of Georges Bank, with frequencies of from less than 10 to nearly 3,000 specimens per square meter, averaging 3½ per cent of the copepods taken in these vertical hauls. In the year 1915 it was not detected anywhere in the gulf in May or during the first three weeks of June, though vertical hauls were made at 20 stations during that period, but on June 26 (station 20099) it was taken at the rate of 430 per square meter in the western basin, and it figures in the lists (p. 298) for two August stations. In September it occurred in all the vertical hauls in the coastal zone from Cape Cod northward and eastward toward the mouth of the Bay of Fundy, as well as on German Bank (80 per cent of all the stations for the month), averaging 4,490 per square meter where the vertical net took it.

During the first half of October, 1915, it continued universal along the coastal zone from off Cape Cod to the neighborhood of Mount Desert Island (six stations), varying in abundance from 1,140 to 14,225 per square meter (average about 5,600). It also occurred in two out of three vertical hauls over the shelf south of Marthas Vineyard on the 22d (stations 10332 and 10333), frequencies of about 6,000 and 4,000 square meters. By the last week of the month it seems that it had vanished from the Massachusetts Bay region, for not a single specimen was detected at four stations there; but this can not be interpreted as a regular seasonal change, because it was taken at all the stations within 15 to 20 miles of land, from off Cape Cod to the mouth of the Bay of Fundy during December, 1920, and January, 1921, averaging about 5.5 per cent of the copepods and 10 to 15 per cent of the extremely sparse community at the mouth of Massachusetts Bay and off the Isles of Shoals (stations 10489 and 10493), though not found at any of the four stations farther out in the basin.

It is not clear from the data just outlined whether *A. longiremis* has two seasonal maxima in the gulf, one in late spring, another (much more pronounced) in early autumn, separated by a period of a month or more during which it nearly or quite disappears, as the records for the two years 1915 and 1920 suggest; or whether it followed different seasonal cycles during the two years, multiplying from April on in 1920, but not appearing at all until June in 1915. In either case it clearly attains its maximum abundance in the gulf during the warm half of the year. It is never more than a minor factor in the plankton except when all other species of copepods are very scarce, and never occurs in numbers that would be called large for other more important copepods, 14,265 per square meter being the highest frequency yet recorded for it east or north of Nantucket. *A. longiremis*, like *A. clausi*, contracts its range to the shoaler waters of the gulf during the cold half of the year, including the offshore banks as well as the coastal zone. When its numbers increase, its area of occurrence spreads out over the deep basin of the gulf, but we have not taken it outside the continental edge.

That *A. longiremis* is endemic in the gulf is proved by the presence of numerous juveniles, together with adults, at the one August station already mentioned (p. 177). This, however, does not forbid the possibility that its numbers are recruited by immigration as well as by local propagation. On the average, *A. longiremis* was relatively more important in the catches at the surface than in the vertical hauls in March and April, though not in May, as appears in the following table of its percentage in 1920, counting only the stations at which it occurred:

| Time | Surface hauls | Vertical hauls |
|---|---|---|
| | *Per cent* | *Per cent* |
| March | 14.5 | 6 |
| April | 11 | 5 |
| May | 3 | 4 |

In several instances the greater percentage on the surface was the result of a definite concentration there, proved by the capture of hundreds of specimens in the surface net at several stations where *A. longiremis* was so scarce deeper down that the vertical net missed it altogether—for instance, off the Isles of Shoals on March 5 (station 20061); off the northern edge of Georges Bank, March 11 (station 20063); on its eastern edge and southern slope, April 16 (stations 20108 and 20109); and, notably, on March 23, off Yarmouth, Nova Scotia (station 20083), where the richest surface catch of all was made (711 specimens). At a rather larger number of localities the yield of the vertical nets was considerable, where few or none were taken on the surface, as shown in the following table:

| Locality | Date | Hour | Station | Number per square meter in vertical hauls | Number taken in surface hauls |
|---|---|---|---|---|---|
| Near Mount Desert | Apr. 12, 1920 | 1 p. m | 20099 | 280 | 0 |
| Northern Channel | Apr. 15, 1920 | 10 p. m | 20105 | 1,300 | 53 |
| Browns Bank | Apr. 16, 1920 | 1 a. m | 20106 | 240 | 2 |
| Deep water north of Georges Bank | Apr. 17, 1920 | 7 a. m | 20112 | 863 | 0 |
| Western basin | Apr. 18, 1920 | 4 a. m | 20115 | 800 | 0 |
| Off Cape Cod | May 16, 1920 | 11 p. m | 20125 | 470 | 0 |
| Southwest part of basin | May 17, 1920 | 8 a. m | 20127 | 1,437 | 27 |

The most that can be said from this is that at times *A. longiremis* tends to gather at the surface, both in spring and in midsummer, but that on other occasions it keeps at least a few fathoms down. The hauls here listed give no evidence of diurnal migrations, for the richer surface catches were more often between 9 a. m. and 5 p. m. than at night, and, on the other hand, several of the hauls in which it most predominated in deeper levels were between sunset and sunrise.

*A. longiremis* has been found over a very wide range of salinity, being common in water as brackish as 6.72 per mille in the Baltic and as salt as 35.32 per mille in the English Channel. In the Gulf of Maine it occurs well within these limits. It is likewise eurythermal over a wide range of temperature, being present in the gulf indifferently in water as warm as 16° and as cold as 0.3° to 2°. The physical limits within which it reproduces locally have not been determined, but the presence of juveniles in August (p. 177) proves that reproduction takes place successfully in summer temperatures, probably upwards of 10 to 12°.

### Acartia tonsa Dana

This species was originally described from Port Jackson, Australia, and was reported by Giesbrecht (1892) from the west coast of South America, and from the Malayan Archipelago by Cleve (1901). On the one side of the North American

continent it occurs in numbers at San Diego, Calif., in the bays, but rather infrequently outside (Esterly, 1905). On the other, it is reported from the Gulf coast of Louisiana (Foster, 1904), and is a dominant copepod in sheltered inlets and brackish ponds at Woods Hole. It is abundant, also, in the open water in that neighborhood, and recorded from the Gulf Stream off Marthas Vineyard (Wheeler, 1901; Sharpe, 1911). Cape Cod seems the northerly boundary to its presence in numbers, for although Wheeler (1901) reports it from Plymouth Harbor on the southern shore of Massachusetts Bay (this is the only gulf of Maine record), none of the *Grampus*, *Albatross*, or *Halcyon* gatherings in the gulf have contained it. McMurrich did not detect it at St. Andrews, nor has it been found in Canadian waters farther east or north.

### Aetidius armatus Brady

Dr. C. B. Wilson contributes the following on the faunistic status of *Ae. armatus:*

This species is quite cosmopolitan and has a wide distribution throughout the northern Atlantic, Pacific, and Indian Oceans. It is widely distributed in the northern fauna, but nowhere occurs in any numbers. Farran (1910) has reported it as a characteristic inhabitant of the lower layers of the northeast Atlantic off the coast of Ireland and Scotland. Carl With (1915), in his report on the copepods of the Danish Ingolf expedition, said that it was found in deep water, probably as a member of the Atlantic fauna, in the Iceland-Faroe channel, Denmark, and Davis Straits. It has also been taken in the North Sea and in several of the Norwegian fjords, and was included in the list published by Esterly (1905) of copepods found in the San Diego region off the coast of southern California.

In the summer of 1915 the Canadian fisheries expedition took it in small numbers in the deep oceanic triangle off the mouth of the Laurentian channel, between the Scotian and Newfoundland Banks (two stations), and outside the continental edge off Cape Sable (Willey, 1919).

It has not been recorded previously from the Gulf of Maine, but the spring, summer, and autumn cruises of 1915 and of 1920 yielded odd specimens of it at eight stations—one for March, three for April, two for May, one for August, and one for October. It has not been reported at Woods Hole.

Although this species is evidently only a rare stray in the Gulf of Maine (at most it amounted to 1 per cent of the copepods, with a maximum frequency of 87 individuals per square meter of sea area) the locations of the captures are of interest, all being either in the peripheral belt of the gulf, with a preponderance in its eastern side, or over the continental edge. A distribution of this sort (fig. 62), which parallels the dominant counterclockwise eddy of the gulf, indicates that the species is an immigrant in the gulf from the open Atlantic and not endemic there. The fact that all but one of the records within the gulf were in hauls shallower than 100 meters suggests that it enters in the upper layers and across Browns Bank, not along the bottom of the eastern channel; but it tends to keep at some little depth, for it was not detected in any of the surface hauls from February to May, 1920, even at the stations where it occurred in the verticals.

### Anomalocera pattersoni Brady

This beautiful bluish green or Prussian blue calanoid is generally distributed over the North Atlantic between latitudes 36 and 67° N., in the Mediterranean and in the North Sea and English Channel (Giesbrecht, 1892; Brady, 1878–1880; T. Scott,

1911). It seems not to enter the Baltic, probably being barred therefrom by low salinity. It is recorded from the Indian Ocean, doubtfully from the Pacific (Giesbrecht and Schmeil, 1898), and from the Black Sea (van Breemen, 1908). Off the

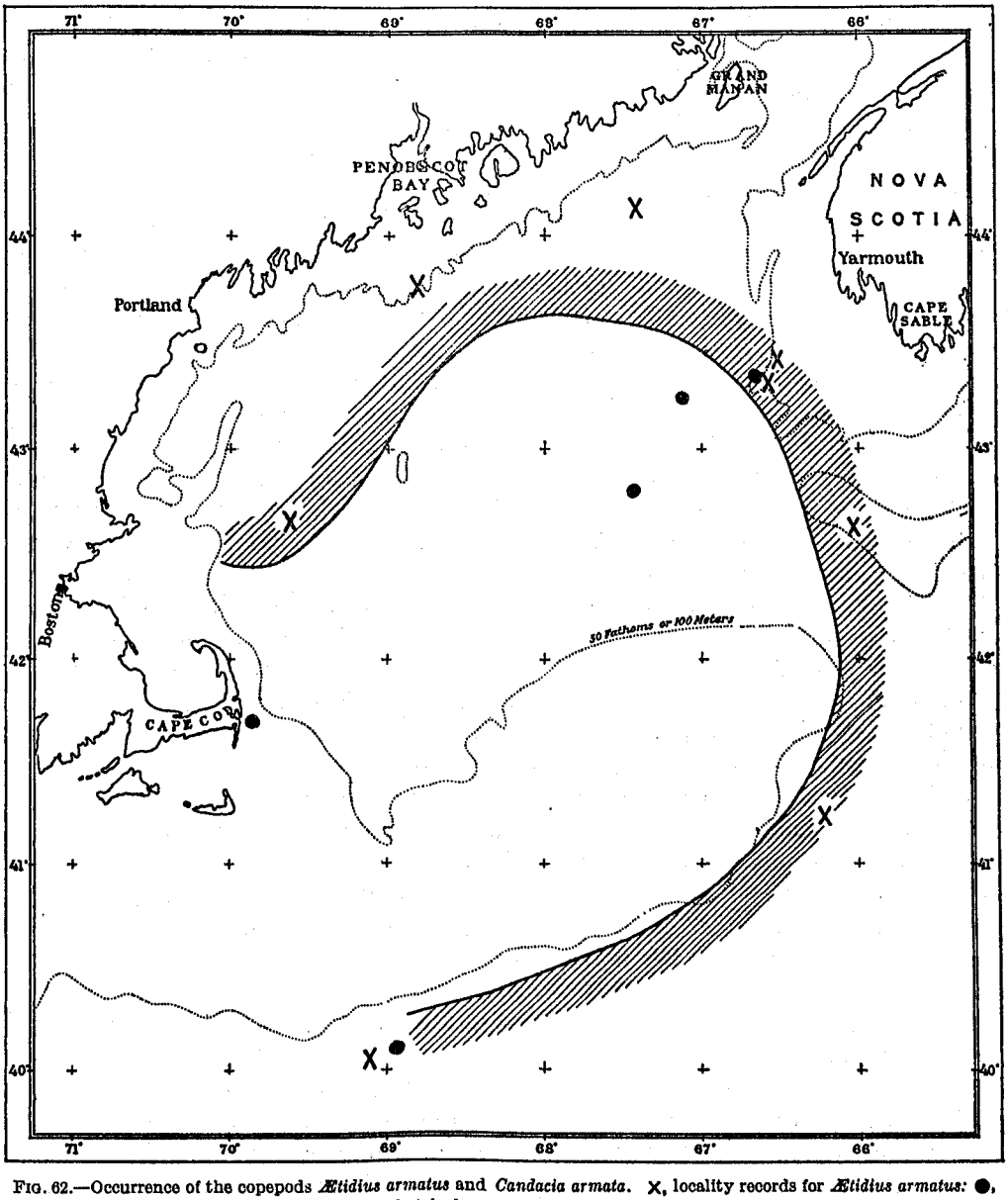


FIG. 62.—Occurrence of the copepods *Ætidius armatus* and *Candacia armata*. X, locality records for *Ætidius armatus*: ●, locality records for *Candacia armata*. The hatched curve incloses the zone where tropical-oceanic species occur most frequently

North American seaboard it has been reported from the Gulf of St. Lawrence (T. Scott, 1905; Herdman, Thompson, and Scott, 1898; and Willey, 1919); off Halifax and Shelburne, Nova Scotia (Willey, 1919); at many localities in the Gulf of Maine;

at Woods Hole and in the Gulf Stream off Marthas Vineyard (Wheeler, 1901); and likewise at several stations on the continental shelf and along the continental edge between Woods Hole and Chesapeake Bay (Bigelow, 1915 and 1922).

Because of its large size and brilliant color this is the most conspicuous of all Gulf of Maine, copepods, but is usually so scarce there that horizontal hauls must be depended upon to outline its distribution, the verticals being apt to miss it. Up to the present, time has not permitted search for it in the mass of copepods taken in the deep horizontals for the period February to May, 1920, but it did not occur at all in the surface hauls for those months (table, p. 303), and only three times and in minimal amounts (1 per cent of the catch) in the verticals, suggesting that although these captures prove its presence in the gulf in spring it is then very scarce. This is corroborated by the fact that in July it has been detected at only two of the forty-odd stations for which the copepod catches of the horizontal nets were examined by Doctor Esterly or by me (p. 10)—one of them in Massachusetts Bay and the other a few miles north of Cape Ann—but Anomalocera must either multiply in the gulf or invade it during midsummer, for it has occurred at fully 50 per cent of our stations for August and at localities generally distributed over the whole inner and northern part of the gulf north of a line Cape Cod–Cape Sable. Although no tows were made on Georges Bank in August during the period 1912 to 1921, Dr. W. C. Kendall, in his field notes (p. 12), records "green copepods" (which, from his description, can only have been Anomalocera) from enough of the surface tows on the northwestern part of the Bank and thence to Cape Cod and off Marthas Vineyard, in the last week of August, 1896 (fig. 63), to show that this copepod is as generally distributed over the offshore grounds during that month as it is in the inner parts of the gulf. The seasonal history of Anomalocera is the same in the Gulf of St. Lawrence, where the Canadian fisheries expedition did not find it at all in May or June, but widely distributed (though nowhere plentiful) in August. Similarly, it appeared in the last week of July off Halifax, where it was wanting in May (Willey, 1919).

Judging from the year 1915, Anomalocera practically vanishes from the gulf after the end of August, for it was taken in only two of the horizontal tows at the 12 September stations (on the 1st and 6th, stations 10308 and 10314), and did not appear in a collection of copepods made at St. Andrews by Dr. A. G. Huntsman on the 15th (Willey, 1919, p. 220). We have only one record of it in the gulf in October,[94] none for November, one for December (see table, p. 304), none for January, February, or until March (see table, p. 305).

Thus, Anomalocera certainly persists in the gulf throughout the greater part of the year; and it is probable that a few survive over the coldest period, though it has not actually been taken within our limits at that time. From September until July it is always very scarce, but it has a brief period of comparative abundance during the month of August, when it may become so nearly universal in all parts of the open gulf that surface tows usually pick up at least one or two. It is such a noticeable object in the catch that its presence is almost certain to be recognized. It is equally a summer copepod at Woods Hole (Fish, 1925, fig. 46).

[94] Vertical haul off Penobscot Bay, Oct. 9, 1915, station 10329.

Anomalocera is likewise least plentiful in the North Sea region generally in February, but from year to year may reach its maximum there at any time from May to November (T. Scott, 1911). Recognition of the brevity of its period of maxi-

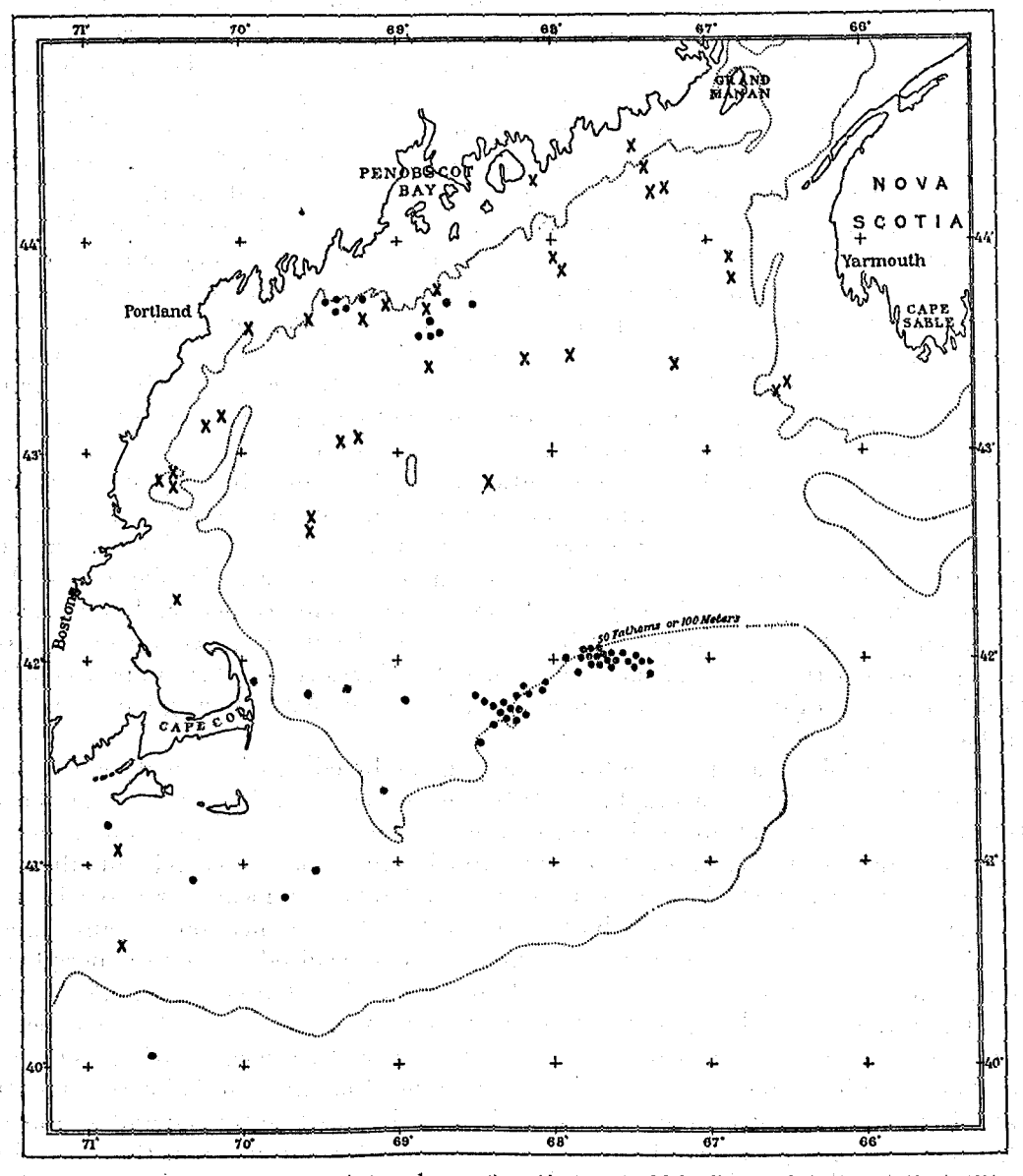


FIG. 63.—Occurrence of the blue copepod *Anomalocera pattersoni* in August. X, locality records for August, 1912 to 1914; ●, locality records for August, 1896 (from Dr. W. C. Kendall's field notes)

mum abundance (now sufficiently established as usual if not invariable) forces me to correct a previous statement that it markedly diminished in the Gulf of Maine from 1913 to 1915 (Bigelow, 1917, p. 292). Its more frequent occurrence in the

towings of 1912, 1913, and 1914 than in those of 1915 may simply have been a seasonal phenomenon associated with the fact that in the first three years the *Grampus* cruised in August, when Anomalocera is at its maximum, whereas in 1915 most of the towing was done either before July or from September on, when this copepod is scarce, with only five towing stations for August, at two of which it occurred.

Anomalocera is peculiar among Gulf of Maine copepods in being seldom, if ever, abundant even at the season when it is practically omnipresent, the catch usually amounting to less than 50 to 60 individuals (Bigelow, 1915, p. 288). In tow after tow Doctor Kendall found only one or two or "a very few." Sixty is the largest number actually counted for any of the horizontal hauls in the gulf since 1912, and 550 the greatest frequency per square meter in any of the verticals (Massachusetts Bay, station 20120, May 4, 1920). Drifting along in a dory on a day when the water is glassy calm, Anomalocera may often be seen right in the surface film, when, as Sars remarked (1903, p. 141), its movements are exceedingly rapid and energetic. On such occasions I have usually noticed one here and one there, seldom more than half a dozen or so together. Evidently it can never be important in the economy of the Gulf of Maine, where it has not been reported from the dietary of either mackerel, herring, or other plankton-eating fishes.

On the other side of the North Atlantic this copepod must be far more plentiful, for Brady (1878–1880) writes that it often occurs in immense profusion, and Sars (1903) describes it as generally congregated in great shoals, when its presence is betrayed by a disturbance of the surface like fine rain as it keeps leaping out of the water. On such occasions it may well be of economic importance, and Norwegian fishermen, who have christened it "blue bait," consider its presence a good sign of the approach of the schools of summer herring; but T. Scott's (1911) failure to find it in fish stomachs raises the question whether it is actually eaten to as great an extent as has been supposed.

No direct observations have been made on the breeding of Anomalocera in the Gulf of Maine, but the geographic distribution of the localities where it has been taken argues that local multiplication of the few that survive winter and spring—not immigration—is the cause of the augmentation that takes place in its numbers in midsummer. The fact that there is no preponderance of locality records in the eastern side of the Gulf is especially significant in this connection, because most immigrants occur there chiefly, and are more or less localized around the periphery of the gulf (p. 51) instead of as evenly and universally distributed as Anomalocera is.

Of all the Copepods occurring with any regularity in the open gulf Anomalocera is the most distinctively a surface form. This is especially the case during its period of abundance in August. In 1913, for example, most of the records for that month were from surface hauls, "only one from a haul as deep as 40 fathoms; and of course, that one specimen may have been caught at or near the surface; and this may also be true of the few specimens yielded by hauls from 20, 25, and 30 fathoms in the Gulf of Maine" (Bigelow, 1915, p. 295).

This tendency to keep close to the surface was well illustrated in August, 1914, at the following stations, in spite of the fact that the mouth area of the surface net was much less than that of the nets towed deep.

| Anomalocera | Station and depth in meters | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 10245 | | 10246 | | | 10254 | | | |
| | 0 | 100–0 | 0 | 50–0 | 150–0 | 0 | 25–0 | 75–0 | 225–0 |
| Number of specimens in sample | 1 | 0 | 6 | 0 | 0 | 10 | 0 | 0 | 0 |
| Percentage of total copepods in sample | 33 | 0 | 12 | 0 | 0 | 2½ | 0 | 0 | 0 |

There is no positive evidence that Anomalocera ever sinks more than a few meters in the Gulf of Maine in summer, and most of the Gulf of St. Lawrence records listed by Willey (1919) are likewise from the surface or from trivial depths. In winter and spring it seems to live slightly deeper, for it was not taken in any of the surface hauls from November, 1912, to April, 1913, or February to May, 1920; but it descends to only a moderate depth—probably to escape the most severe winter chilling—the vertical records for December, March, and April all being from hauls shoaler than 75 meters.

Anomalocera is similarly an inhabitant of the upper strata of water in north European seas. Sars (1903) always found it swimming close to the surface off the west and south coasts of Norway, and T. Scott (1911) describes it as most generally met with at or near the surface, very rarely in deep water, though he gives its vertical range as extending down to 700 meters.

This copepod occurs only in water of tolerably high salinity, and its preference for the surface makes it easy to establish the precise conditions under which it is living at any given station. In the Gulf of St. Lawrence it occurred regularly in water as little saline as about 30 per mille (Willey, 1919; Bjerkan, 1919). In the Gulf of Maine most of the records are from salinities of 31.55 to 33.06 per mille, and south and west of Cape Cod it occurs in water salter than 35 per mille, which is a usual salinity for it in the eastern North Atlantic. It is certainly able to survive a wide range of temperature, but in the Gulf of Maine it is most abundant when the surface water in which it lives is warmer than 10°, which may prove about the lower limit for its successful reproduction. Temperatures as high as 21° to 25°, even, seem not unfavorable for it.

Anomalocera is an inhabitant of the open sea, never yet recorded from harbors or from estuarine situations except when brought in by heavy winds or by surface currents, as occurs at times in Norway (Sars, 1903) and at Woods Hole (Wheeler, 1901). In its relationship to the North American littoral it may be described as intermediate between neritic and oceanic, maintaining itself in the Gulf of Maine and in the Atlantic basin alike.

### Asterocheres bœcki (Brady)

Doctor Wilson contributes the following note on this copepod, which is only accidental in the plankton:

This species occurred in the form of two partially mutilated specimens taken in one of the surface tows early in March, 1920. As far as could be determined, these specimens were identical with those described by Brady in his monograph on British Copepoda as *Artotragus bœcki*, but

Brady, as he himself admitted in his later writings, confused the two genera, Artotragus and Asterocheres, and should have assigned his species to the latter instead of the former. Most of the species of this genus are parasitic upon, or commensal with, some invertebrate animal, but Brady gave no information upon this point. Scott, in his "Catalogue of the Crustacea of the River Forth," reported obtaining this species in the water passages of sponges (*Chalina oculata*) growing on the walls of a pier. It was later recorded by Norman and Brady from a tidal pool on the coast of England, and it was added that this was probably a truly commensal or parasitic species, accidentally found in a free condition. This readily explains why more specimens were not found in the present collections, and it is significant that these two came from close to the coast of Maine south of Portland [station 20059].

### Calanus finmarchicus (Gunnerus)[95]

*General distribution.*—Farran (1910, p. 83), whose words I can not better, has described the distribution of *Calanus finmarchicus* as "centered in the North Atlantic. It has also been recorded from the South Atlantic off Cape Colony, the west coast of South and North America,[96] the Mediterranean, the Adriatic, and the Polar Ocean." Following the North Atlantic around from east to west, we find it occurring in dense though limited swarms off the mouth of the English Channel (Farran, 1910); on the south and west coasts of Ireland, where Farran (1903) found it the most abundant and economically important of the copepods; and on the west coast of Scotland (T. Scott, 1898, p. 182). Many authors have described the extraordinary abundance of this species in Norwegian seas. Gran (1902), Paulsen (1906), and Damas (1905), in particular, comment on the shoals of it between Norway, Iceland, and Greenland. The Ingolf expedition (With, 1915) had it at many localities off west and east Greenland. Sars (1900, p. 35) describes it as "by far the commonest of all the Copepoda in the north polar basin explored by the *Fram* expedition, forming, indeed, in all the samples the great bulk of the contents." Cleve (1900) remarked its abundance in the Labrador current. Herdman, Thompson, and Scott (1898) record it from practically every tow netting across the North Atlantic from Liverpool to the Straits of Belle Isle—largest in the Labrador current—and Farran (1910, p. 83) speaks of it as "in great abundance along the coast of North America in the path of the Labrador current, forming, in the summer months, a rich belt, which, off Newfoundland, is at least 500 miles wide." Corroborating this, the international ice patrol has taken great masses of it on the Grand Banks; Willey (1919) found it the commonest copepod between Nova Scotia and the Newfoundland Banks, in the Gulf of St. Lawrence, and along the outer coast of Nova Scotia.

It dominates the plankton of the Gulf of Maine at all seasons, as will shortly be described, and outside the immediate coastal zone is usually plentiful and often the dominant copepod over the continental shelf off southern New England to longitude about 72° W.; that is, abreast of Long Island, New York (Bigelow, 1915). South of this its occurrence along the seaboard of the United States becomes more seasonal and less regular. It is to be expected in abundance over the shelf between the latitudes of New York and Chesapeake Bay during the cold half of the year and into early summer, Rathbun (1889) having found it characterizing the plankton at many

[95] According to With (1915) the relationship of *C. helgolandicus* Sars to *C. finmarchicus* is still in doubt, but Dr. C. B. Wilson writes "Whatever may be the outcome, it seems reasonably certain that all the specimens from the Gulf of Maine are *finmarchicus*."

[96] Esterly (1905, p. 126) describes it as the commonest copepod about San Diego, Calif., and as often very predominant.

localities in this zone during April and May of 1887, while Fowler (1912) reports it in great abundance along the New Jersey coast in June, 1911, and early July, 1912. In cool summers, such as that of 1916, it continues extremely plentiful along the zone of lowest temperature on the shelf, narrowing to the southward to abreast the mouth of Chesapeake Bay until the end of summer and becoming much less plentiful in autumn, as I have described in a previous report (Bigelow, 1922), but in warm years—e. g., 1913—it practically vanishes south of New York by July (Bigelow, 1915, p, 269). So far as known, the latitude of Chesapeake Bay may be set as the southern limit to its occurrence off the east coast of the United States in numbers sufficient to color the plankton at any season. Westward and southward from abreast of Cape Sable the zone of abundance for *Calanus finmarchicus* is bounded offshore by the high temperatures and salinities of the "Gulf Stream," a boundary which fluctuates in location from season to season but which is never far outside the edge of the continent.

*Regional distribution in the Gulf of Maine.*—In the gulf *Calanus finmarchicus* is decidedly more oceanic than neritic (p. 35), but exists to some extent in estuarine situations as well as offshore. I can offer little first-hand information as to its occurrence in inclosed waters, most of our stations having been located out at sea, but it has appeared in abundance in Gloucester Harbor (p. 194), and we have likewise taken it in abundance in the harbors of Kittery, Portland (Bigelow, 1914, p. 117), Eastport, Provincetown, and in Casco Bay. Doctor McMurrich, in his manuscript list, records it regularly at St. Andrews, often in abundance, during the winter of 1915–16, from November through April, but only occasionally during the later spring, summer, or early autumn. Willey (1921) found it in abundance in the mouth of the St. Croix River during the winter of 1916–17, but decidedly rare in the winter and spring of 1919 and 1920. If these observations in the St. Andrews region apply equally to other parts of the shore line of the gulf, *Calanus finmarchicus* is to be classed as a winter copepod in estuarine waters, where it has never been found in the swarms in which it often occurs in the open sea. Williams (1906) similarly found it an abundant winter visitor to Narragansett Bay, and Fish (1925) found it in winter and early summer at Woods Hole.

Outside the estuaries and inside the continental edge, *Calanus finmarchicus* is universal in the Gulf of Maine, both in deep water and over the shoal banks, but it is consistently less abundant in the coastal zone northward and eastward from Cape Ann along Maine and Nova Scotia than off Massachusetts Bay and in the basin in general. Although the distinction between regions fertile and poor in Calanus is apparently least marked in early spring, when the species as a whole is least plentiful in the gulf, the chart for February and March, 1920 (fig. 64) shows no frequencies as great as 3,000 per square meter anywhere in the peripheral belt inside the 100-meter contour between Cape Ann and Cape Sable, with the whole of Georges Bank equally barren except for the transitory swarm of Calanus which we encountered over and off its southeastern slope on March 12, 1920, as I have described (p. 168). On the other hand, all but one of the vertical hauls in the basin and in the channels (eastern and northern) yielded more than 1,500 *Calanus finmarchicus* per square meter, and most of the hauls more than 5,000, with a maximum of 33,700 in the western basin.

In April of that year Calanus was more evenly distributed, with the coastal belt supporting about as many per square meter as the basin, but with three circumscribed centers of abundance—(1) from Cape Cod out over the western basin (sta-

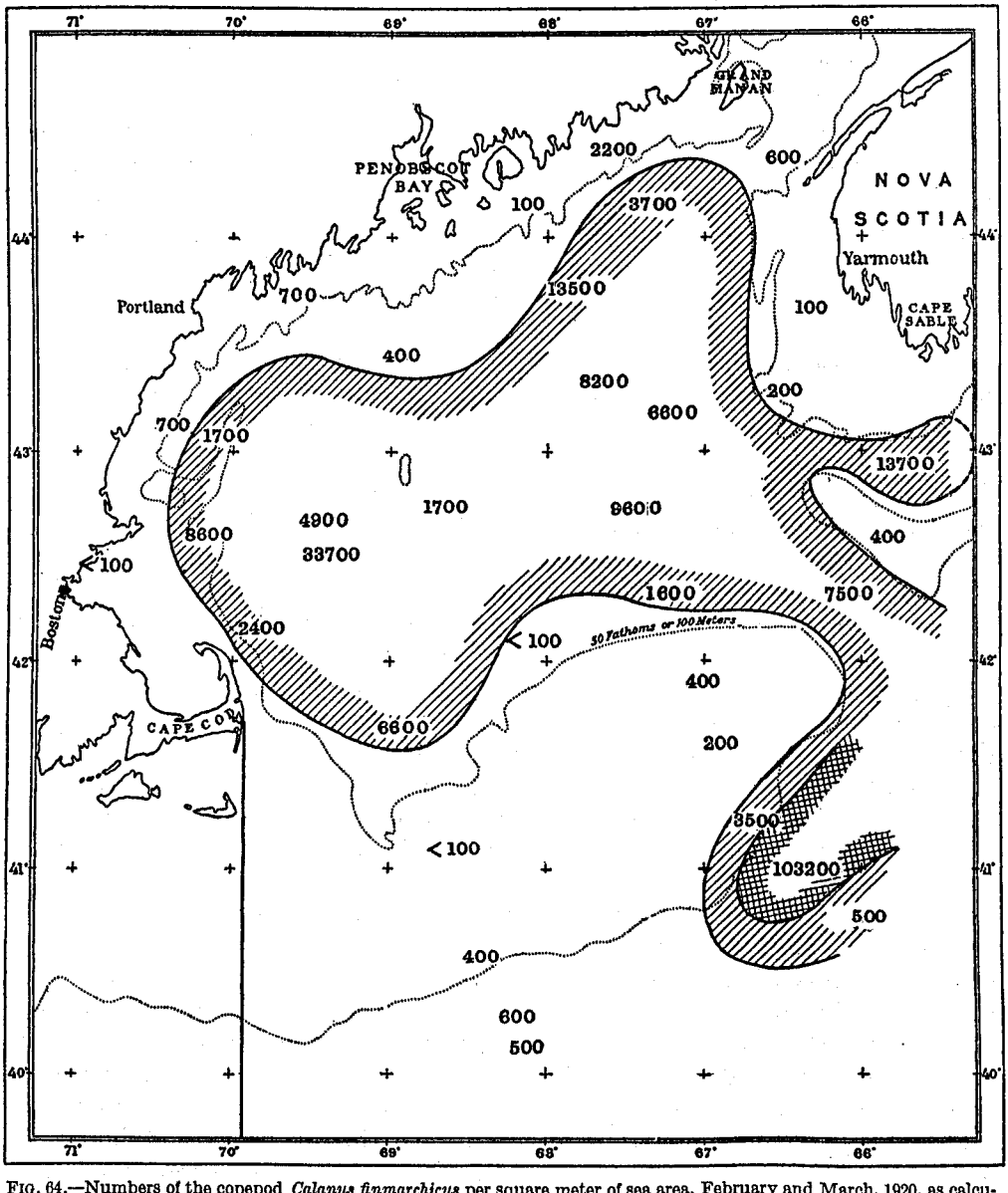


FIG. 64.—Numbers of the copepod *Calanus finmarchicus* per square meter of sea area, February and March, 1920, as calculated fron the vertical hauls. The single hatched curve incloses the area where there were usually upward of 1,000; the double hatched curve upwards of 100,000

tions 20114, 20115, 20116, and 20117), (2) in the northern channel (station 20105), and (3) on the eastern peak of Georges Bank (station 20108)—reminiscent of the local March swarm. From April on reproduction of Calanus takes place so much

more rapidly in the basin and off Massachusetts Bay than along the coasts of Maine and off western Nova Scotia that by May and June (fig. 65) we have found a marked contrast between the rich Calanus population of the former and the sparse catches of the tow net in the latter, a distinction persisting in our experience throughout the summer and into September, except that on August 11, 1914 (station 10243) there was a notable shoal of this copepod close in to Cape Sable.

We have no data on the numbers of Calanus existing in the offshore parts of the gulf later in the autumn, but in October, 1915, this copepod was far more numerous along Cape Cod, in Massachusetts Bay, and between Cape Ann and Cape

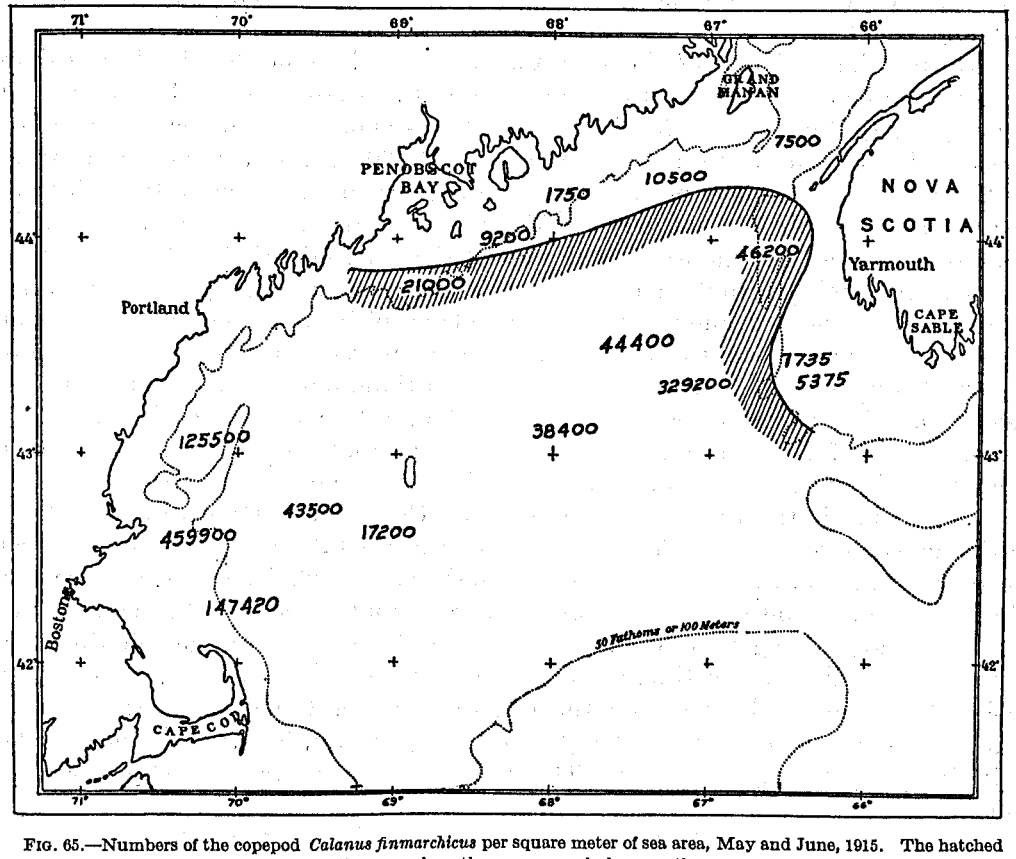


FIG. 65.—Numbers of the copepod *Calanus finmarchicus* per square meter of sea area, May and June, 1915. The hatched curve incloses the area where there were regularly more than 15,000

Elizabeth (23,000 to 122,000 per square meter) than from abreast Penobscot Bay eastward (7,700 to 14,700 per square meter)—that is, the southwestern part of the gulf was then much more prolific of Calanus than the northeastern, and probably as much so as any part of the basin, judging from the large numbers per square meter off Cape Cod (102,500) and at one station in Massachusetts Bay (122,200).

In the parts of the gulf visited by the *Halcyon* during December, 1920, and January, 1921, *Calanus finmarchicus* was most abundant in the western basin on the one side and in the Fundy deep on the other, and least so in the northeastern

part of the basin, but the data are not sufficient to show whether or not it was more plentiful in the offshore parts of the gulf than near land, as is so constantly and characteristically the case in summer (p. 189).

Our several sections across Georges Bank have shown that in summer the offshore boundary to abundant *Calanus finmarchicus*—indeed, to an abundance of copepods of all kinds—abreast the Gulf of Maine is but a few miles outside the continental edge (p. 21). Even on July 23 and 24 in the cold summer of 1916, when Calanus was reasonably plentiful over the southwestern part of Georges Bank generally, it was represented by only an occasional specimen a few miles outside the 100-meter contour, where the general aspect of the plankton was more oceanic (station 10352).

During the cold half of the year Calanus spreads somewhat farther offshore. It may even be extremely plentiful along the southeastern slope of Georges Bank in early spring (p. 189), and on May 17, 1920, it was about as numerous at the outermost station off the western end of the bank (17,000 per square meter at station 20129) as in over the latter or in the neighboring part of the basin of the gulf to the north, but it is probable that very few Calanus exist at any season more than a few miles outside the 1,000-meter contour west of the longitude of Cape Sable.

The regional distribution of Calanus is so irregular, with particular swarms often so soon dissipated, and the relative abundance of the species in different regions is in a state of such constant change, that it is not safe to postulate a typical rule for it from its quantitative distribution at any given time; but sufficient data have now been accumulated over a period of years to show (*a*) that *Calanus finmarchicus* is far more plentiful in the open waters of the gulf than in estuarine situations or among the islands, and usually most plentiful some miles offshore; (*b*) that the coastal belt inside the 100-meter contour, from Cape Ann northward and eastward to the mouth of the Bay of Fundy, is a zone of comparative scarcity for it, as contrasted with the Massachusetts Bay region, the basin as a whole, or the northern parts of Georges Bank; and (*c*) that the chief center of abundance is in the southwestern part of the gulf, along Cape Cod, off Massachusetts Bay, in the neighboring parts of the basin, and as far northward as the region of the Isles of Shoals. The eastern basin, the northern channel, and the neighborhood of Cape Sable are secondary centers, where Calanus is occasionally extremely plentiful, but we have never taken it in frequencies as great as 100,000 per square meter anywhere else within the gulf (fig. 66).

In 1920 the stock of *C. finmarchicus* increased slightly throughout the coastal zone generally between Cape Cod and Mount Desert from March to April, raising the average numbers per square meter for this region from about 1,800 to about 5,000.[97] At the head of Massachusetts Bay, off Boston Harbor, there were something like four hundred times as many Calanus on April 6 (station 20089, 1,250 per square meter) as on March 5 (station 20062, only 3 *C. finmarchicus* per square meter). On the other hand, the *Albatross* found fewer Calanus in the eastern basin of the gulf generally in April (average about 2,540 per square meter) than in March (aver-

[97] Eight stations for March and 11 for April.

age 7,320 per square meter), though the difference is perhaps not great enough to be significant in the case of a planktonic animal so usually occurring in swarms or streaks which the net may chance either to hit or to miss.

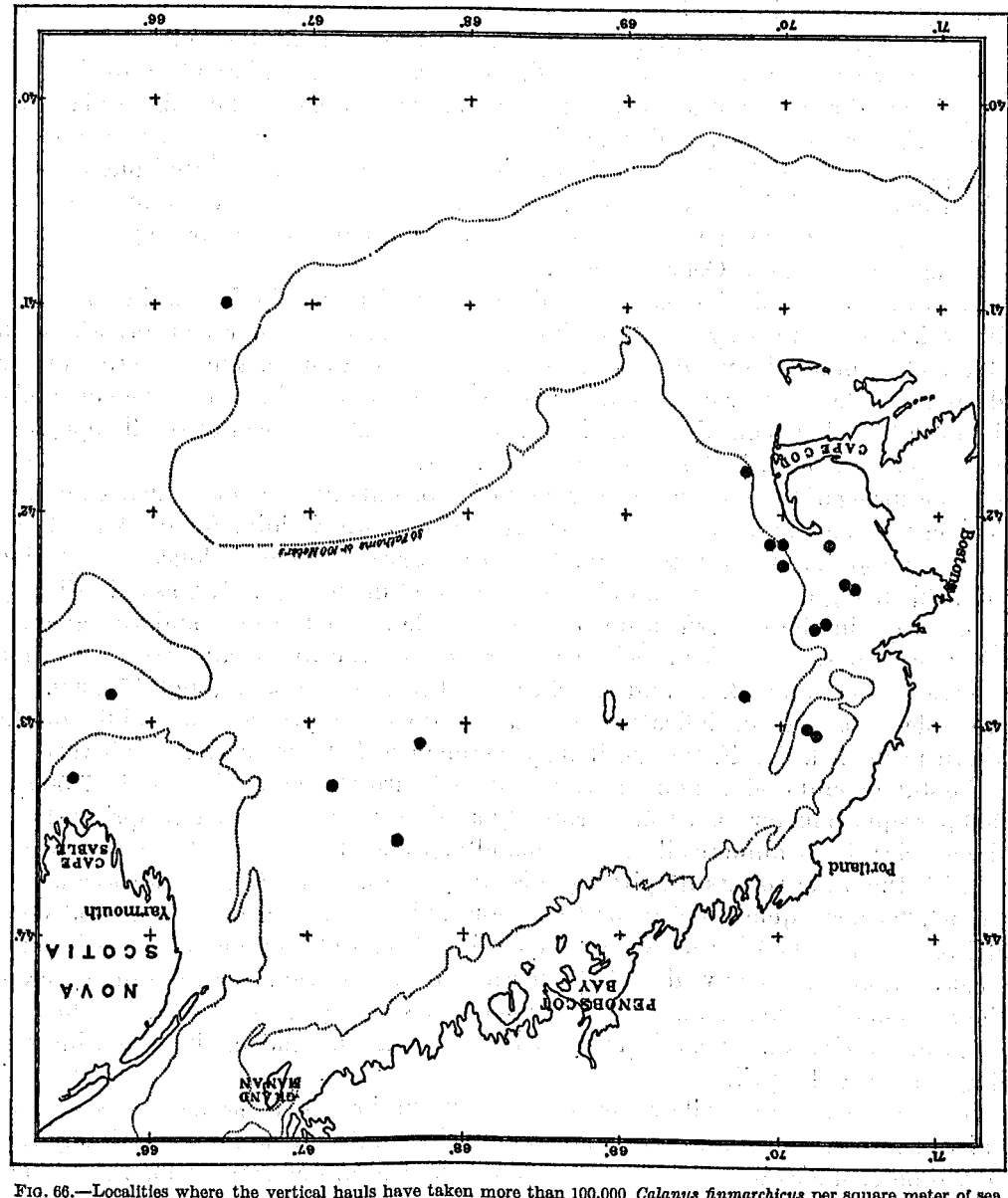


FIG. 66.—Localities where the vertical hauls have taken more than 100,000 *Calanus finmarchicus* per square meter of sea area, all years and seasons, including July stations for 1916, where an assumed percentage of 70 per cent Calanus in the vertical hauls indicated more than 100,000 per square meter

The dissipation of the swarm existing off the southeastern slope of Georges Bank in March has been noted (p. 190). Over the eastern end of the bank *Calanus finmarchicus* increased eight to ten fold from March 12 to April 16, by the evidence

of the vertical hauls, and three-fold on Browns, but decreased by about that same proportion in the eastern channel, a change probably too small to be significant. In the western basin the average number of *C. finmarchicus* at all the stations was practically the same in April (about 13,000 per square meter) as in February and March (about 12,000), but an equalization of the species had taken place.

The augmentation of the stock of *C. finmarchicus* that takes place during the later spring is the most notable event in the seasonal history of the animal plankton of the gulf. In 1920 this multiplication of Calanus began in the Massachusetts Bay-Cape Cod region by the middle of April, as I have just pointed out (p. 41), and by the first week in May it had progressed sufficiently to raise the numbers per square meter to an average of 19,000 for all the stations from near Cape Ann out across the western end of Georges Bank.

In 1913 no notable increase of Calanus was observed in Massachusetts Bay until the first week in May; this was first evidenced in Gloucester Harbor, where on the 3d Welsh found the water "reddened for areas of about a square yard, several yards apart, with what proved to be swarms of copepod nauplii and young copepods. And on the 17th, hauls off Magnolia, Mass., yielded great numbers of small copepods, chiefly *C. finmarchicus.*" (Bigelow, 1914a, p. 407.)

In the spring of 1915 the vernal augmentation of Calanus either commenced earlier in the season than in 1913 or 1920, or proceeded more rapidly, for on May 4 the vertical net took it at the rate of 459,900 per square meter off Gloucester (station 10266), this being the greatest number ever counted in the gulf. It was only slightly less numerous in the eastern basin off German Bank on the 6th, and the average number per square meter for a belt right across from the Massachusetts Bay region in the west to German Bank and Lurcher Shoal in the east was about 150,000. It is probable that the multiplication of Calanus does not proceed so rapidly in the northern parts of the gulf, though it may commence there as early as mid-April (p. 41), the June counts off Penobscot Bay and eastward [98] ranging from only 7,500 to 21,000 per square meter for 1915. Probably a fairer concept of the late spring status of the species, both numerically and regionally, would result from the union of the May with the June counts despite the disparity in date, which gives an average of about 96,000 per square meter for the whole gulf north of a line Cape Cod-Cape Sable, or about 63,000 if the vertical hauls for May, 1920, be included. Although this calculation may very well be 100 per cent out of the way, due to faults inherent in the process of estimation and to the paucity of stations, at least it shows that the stock is many times as great in late spring and early summer as it is in winter or during March and April.

It is not possible to follow the seasonal fluctuations of *C. finmarchicus* at close intervals through the summer for want of sufficient data for late June and July, nor have the percentages in which the species occurred been determined for the vertical hauls for August, 1912 or 1914. This was done for the vertical hauls for August, 1913 (Bigelow, 1915, p. 286), and for most of the horizontal hauls at various depths for stations for 1912 and 1914, when the total numbers of copepods were calculated from verticals. With Calanus so greatly preponderating over all other copepods

[98] No vertical hauls were made in this part of the gulf in May.

combined, this will at least give an idea of the general status of the species. The average numbers of *Calanus finmarchicus* per square meter for all parts of the gulf combined have been as follows: July and August, 1912, about 45,000; August, 1913, about 28,000; July and August, 1914, about 55,000—results probably not far from the truth, judging from the evenness of the frequencies from summer to summer. About 30,000 to 40,000 specimens of this copepod would then be a reasonable expectation for the average frequency below each square meter of the surface of the gulf in midsummer, though actually with extremely wide variations from station to station—that is, from hardly a trace to upward of 200,000. This is a decrease by more than one-half from the most prolific period and region of May (p. 194) and a considerable shrinkage from the stock existing generally in the gulf in May and June. Correspondingly, the richest July or August catch for the period 1912 to 1914 was less than half the richest May catch, and while we have never found less than 7,000 Calanus per square meter in May, several August catches have contained fewer than 100. In some summers, however, the stock remains very high or may even continue to increase until well into July, as exemplified by the year 1916, when vertical hauls yielded an average of about 147,000 Calanus[99] (approximately 71,000 of them being large adults) among 210,000 copepods of all kinds for six stations in Massachusetts Bay, off Cape Cod, and in the southwestern part of the basin (Bigelow, 1922, p. 136).

In September, 1915, for which month vertical hauls were made at nine stations, including the Massachusetts Bay region, the average per square meter (about 35,900), with frequencies per square meter of 4,400 to 138,400, about equaled the expectation for August; but the individual counts, station by station, show a tendency toward dispersal of the local shoals of Calanus by the general circulation of water in the gulf during early autumn, resulting in equalization of the stock, a phenomenon which often accompanies, though is not necessarily a sign of, a cessation of active reproduction.

If the counts for 1915 may be taken as typical, Calanus may be expected to increase again in numbers from September to October, the average per square meter being about 51,000 for the latter month with three of the vertical hauls more productive than 100,000 and none producing less than 7,500. This period of reproduction, if it be one, must be brief, with the stock dwindling rapidly later in autumn, for the yields of the horizontal tows taken during December, 1920, and January, 1921, were uniformly scanty. The volume of the catches, however, suggest that *C. finmarchicus* was more evenly distributed over the inner parts of the gulf at that season than we have usually found it during its period of greater abundance in spring and summer. Unfortunately, however, these stations do not afford numerical data.

*Density of aggregation.—Calanus finmarchicus*, being the most plentiful copepod in the Gulf of Maine, and, thanks to its comparatively large size coupled with its numbers, by far the most important source of crustacean food for the plankton-feeding fishes, the local abundance in which it gathers is of importance in the natural economy of the region. The numbers present per square meter are not a direct index to this, for the specimens living under that or under any other unit of the

[99] Assuming Calanus to have constituted 70 per cent of the catch, which is probably below the actual figures.

surface of the sea may be scattered sparsely through a great depth or concentrated in a shoaler stratum, depending both on the depth of water at the station in question and on whether they are more or less stratified or are evenly distributed from the surface downward.

In spring the latter state may be said to apply generally down to 175 meters; and assuming that practically the whole catch (in the case of the deeper hauls) was made above that level, as seems justified for the reasons outlined above (p. 24), we arrive at an average of about 48 Calanus per cubic meter for March, 1920, and 69 for April, with extremes of 1 to 654 and 4 to 624, respectively, for these two months. Thus it seems that a slight general increase took place from March to April, cor-

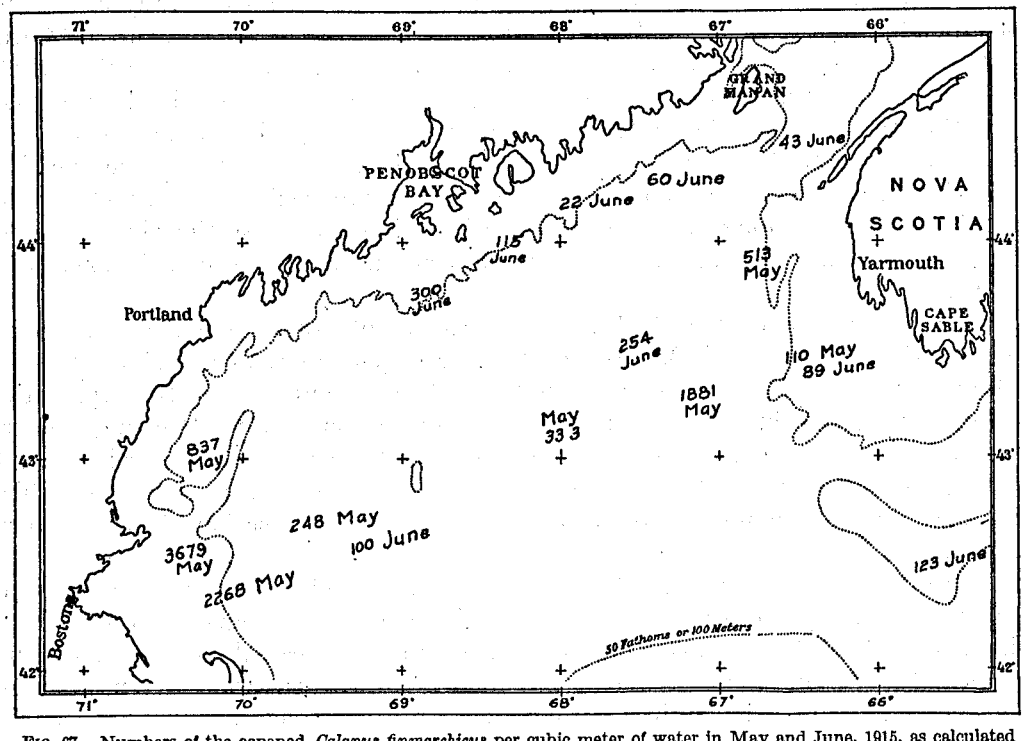


FIG. 67.—Numbers of the copepod *Calanus finmarchicus* per cubic meter of water in May and June, 1915, as calculated from the vertical hauls, assuming that all were living shoaler than 175 meters depth

responding to the beginning of the vernal wave of reproduction of the species, but irregularly from station to station and reversed at many stations, without apparent correlation between the relative density of aggregation and the depth of water or the locality in the gulf.

As might be expected, the great increase in abundance of this copepod which takes place in May is accompanied by a corresponding increase in the numbers present per cubic meter to an average of about 500 for all the May and June stations of 1915 and 1920 combined (fig. 67)—that is, to more than seven times the April average—and with a well-defined cleavage into "rich" and "poor" regions. In the western parts of the gulf and along a line toward Cape Sable Calanus then averaged

about 1,000 per cubic meter, with 2,300 and 3,700 at two stations at the mouth of Massachusetts Bay, these being among the densest aggregations of the species yet demonstrable from our vertical hauls.

In marked contrast to this rich region and to a second center of abundance in the eastern basin (1,900 per cubic meter), there was a sparse stock of Calanus along the coast of Maine east of Penobscot Bay (40 to 100 per cubic meter) in June, and it was only moderately abundant on Browns Bank (120 per cubic meter, station 10296).

In the cool year of 1916, when it is probable that the vernal cycle in the lives of planktonic animals lagged behind its normal schedule, Calanus was extremely plentiful in the Massachusetts Bay region and off Cape Cod in July, as already described (p. 195); and while the numbers per square meter fell somewhat short of the maximum for May, the numbers per cubic meter—both maximum and average—were slightly greater because of the shoalness of the localities where the vertical hauls were made.

*Numbers of copepods and Calanus finmarchicus per cubic meter, assuming the latter to average 70 per cent of the former, July 19 to 22, 1916* [1]

| Station | Depth in meters | Copepods per cubic meter | Calanus per cubic meter | Station | Depth in meters | Copepods per cubic meter | Calanus per cubic meter |
|---|---|---|---|---|---|---|---|
| 10340 | 45 | 2,066 | 1,446 | 10345 | 150 | 930 | 651 |
| 10341 | 80 | 3,312 | 2,318 | 10346 | 62 | 2,987 | 2,791 |
| 10342 | 55 | 6,145 | 4,301 | | | | |
| 10344 | 80 | 2,240 | 1,568 | Average | | 3,113 | 2,179 |

[1] The exact proportions of the several species of copepods have not been determined as yet for these hauls, but preliminary examination suggests at least 70 per cent Calanus and probably more.

The copepod population being confined largely to the deeper layers, as evidenced by the comparative poverty of the surface catches, *Calanus finmarchicus* was evidently more densely aggregated locally than even these amounts per cubic meter would suggest. For example, the haul at 40 meters (station 10344), with the 1-meter net, yielded about 6 liters in 15 minutes, chiefly copepods, and contained upward of 2,500,000 large Calanus (Bigelow, 1922, p. 136). This compares favorably with 200,000 in a five-minute haul near Iceland, listed by Paulsen (1906) as one of his richest.

In the daytime the stock of Calanus at, say, the 10 to 30 meter level, becomes to some extent enriched by the tendency of this little crustacean to sink when the sun is high; at night it is correspondingly impoverished.

The July hauls for 1916 represent the richest Calanus pasture for mackerel, herring, etc., that has come to our notice, and hence may be regarded as containing about the maximum number per cubic meter to be expected in any part of the gulf at any season, except in years for some reason unusually productive. When and where this crustacean food supply is at its best, therefore, a plankton-feeding fish finds at least 2,000 Calanus per cubic meter at some level, and probably many more at others, for this copepod has often been reported in shoals. On such occasions every few mouthfuls of water taken by an adult mackerel, herring, alewife, or shad

would contain at least one and sometimes two or three large oily adult Calanus, even without the voluntary selection of such morsels which these fishes regularly practice, and the fish may be expected to be (and often are) packed full of this "red feed."

At any time from early May until midsummer there exists a sufficient stock of Calanus, which is dense enough in some part of the gulf to afford a bountiful food supply. Our hauls point to the outer part of Massachusetts Bay, with the neighboring waters along Cape Cod to the south, offshore to the east, and probably northward to Cape Elizabeth, as on the whole the subdivision of the gulf where it appears most abundantly during the spring and early summer, both absolutely and per cubic meter of water. Secondary centers of abundance have been recorded in the eastern basin, the northern channel, and off the southeast slope of Georges Bank, but the last of these was certainly transitory, (p. 193) and the others may have been equally so.

In warm summers, when the peak of abundance for *Calanus finmarchicus* has passed before July, fewer are to be expected per cubic meter. In August, 1913, when the percentage of Calanus in the vertical hauls was determined by Dr. C. O. Esterly (Bigelow, 1915, p. 286), this copepod averaged only 244 per cubic meter at 14 stations generally distributed over the northern half of the gulf, even assuming that all of them were taken above 175 meters, the figures being as follows:

| Station | Number per cubic meter | Station | Number per cubic meter |
|---|---|---|---|
| 10087 | 293 | 10098 | 91 |
| 10089 | 94 | 10099 | 324 |
| 10090 | 229 | 10100 | 309 |
| 10092 | 503 | 10101 | 411 |
| 10095 | 104 | 10102 | 176 |
| 10096 | 330 | 10103 | 274 |
| 10097 | 160 | 10105 | 123 |

The average at the Gulf of Maine stations inside the continental edge for July and August, 1914,[100] was about 600 Calanus per cubic meter, varying from less than 100 to upward of 2,000. These calculations show that in late summer most parts of the gulf offer by no means as fertile a feeding ground for the fishes that eat Calanus as it does two or three months earlier in the season.

In the offshore parts of the gulf there is less variation in the number of Calanus per cubic meter of water, from station to station, in August than in May, with no definite contrast between "rich" and "poor" regions; but in the coastal belt the extremes, represented by very barren hauls between Mount Desert Island and the mouth of the Bay of Fundy and by upward of 2,000 at one station close to Cape Sable (station 10243), are perhaps as far apart as at any season. The fact that Calanus about tripled in number at the locality last mentioned during the interval from July 25 (station 10230) to August 11, in 1914, shows that rapid changes take place.

Nine vertical hauls for September, 1915, distributed over the eastern half of the gulf along the coast of Maine and in Massachusetts Bay give an average of approxi-

[100] A table of the number of copepods and large Calanus per square and per cubic meter for that year is given in an earlier report (Bigelow, 1917, p. 315). The present calculation for 1914 is based on an estimated average of 70 per cent Calanus, which is probably below the true figure.

mately 300 per cubic meter, paralleling the calculations for August as closely as could be expected with an animal distributed so irregularly.

*Numbers of Calanus finmarchicus per cubic meter, September and October, 1915*

| Station | Date | Depth in meters | Number | Station | Date | Depth in meters | Number |
|---|---|---|---|---|---|---|---|
| 10309 | Sept. 1 | 200–0 | 692 | 10324 | Oct. 1 | 150–0 | 225 |
| 10310 | Sept. 2 | 190–0 | 482 | 10325 | Oct. 4 | 175–0 | 634 |
| 10311 | do | 60–0 | 205 | 10326 | do | 145–0 | 325 |
| 10315 | Sept. 7 | 80–0 | 264 | 10327 | Oct. 9 | 60–0 | 126 |
| 10316 | Sept. 11 | 60–0 | 265 | 10328 | do | 60–0 | 237 |
| 10318 | Sept. 16 | 70–0 | 63 | 10329 | do | 60–0 | 245 |
| 10319 | Sept. 20 | 35–0 | 380 | 10336 | Oct. 26 | 50–0 | 2,050 |
| 10320 | Sept. 29 | 70–0 | 273 | 10338 | Oct. 27 | 80–0 | 1,528 |
| 10321 | do | 40–0 | 170 | 10339 | do | 75–0 | 343 |
| 10323 | Oct. 1 | 80–0 | 288 | | | | |

Six stations between Massachusetts Bay and the mouth of the Grand Manan channel gave about the same average (298) for the first week of October, with but little variation from station to station (see table above), evidence that, as judged by the number per cubic meter—that is, the density of aggregation and availability for fishes—*Calanus finmarchicus* was distributed with comparative uniformity over the inner parts of the gulf during the late summer and early autumn of 1915, a year probably fairly representative. Vertical hauls off Cape Cod and in Massachusetts Bay on the 26th and 27th of the month yielded it in much larger numbers, rivaling the denser communities of the species in spring and early summer.

We have no data on this subject for the months of November, December, or January, but the catches of the horizontal nets, at depths of 15 to 240 meters during the cruise of December to January, 1920–1921, were so small that Calanus must then have been distributed very sparsely, indeed, and probably in no greater numbers per cubic meter than in March (if as great), judging from the volumes of the catches of the horizontal hauls, which consisted chiefly of copepods (see table, p. 304, for percentages of Calanus). Thus the whole Gulf of Maine supports a much sparser community of Calanus in winter and until May than it does from late spring to October, with the maximum density of aggregation for this copepod falling from May to July, the seasonal fluctuations in this respect paralleling those of the actual numerical strength of the local stock.

*Percentage of occurrence.*—The degree to which *Calanus finmarchicus* predominates over all other copepods in the Gulf of Maine basin may best be illustrated by the percentages of this species in the total catches of copepods. The vertical hauls of 1915 1920, and 1921, combined, averaged about 55 per cent *C. finmarchicus*, inclusion of the surface hauls for the spring of 1920 and the horizontals made during the summers of 1912 and 1914 bringing theprecentage up to about 60. Furthermore, *C. finmarchicus* is the only copepod that has occurred at every tow-net station in all parts of the gulf at all seasons and in almost every haul, vertical or horizontal, and the only one that we have ever taken in 100 per cent purity. The three instances of this among the surface tows for 1920 (stations 20100, 20111, and 20112, see table, p. 303) are not especially significant, the total catch being so small in each case that other less common species occurring side by side with Calanus might easily have been missed by the net.

Among 246 hauls, vertical and horizontal, for which the proportionate representation of different copepod species has been determined, 51 have contained 90 per cent or more of *C. finmarchicus*. At 12 of our 42 tow-net stations for July and August, 1912, this was the only copepod detected by Doctor Esterly in the subsurface hauls. Its dominating rôle in the copepod community of the gulf may be further emphasized by the statements that it has been an unusual event for any other species to form as much as 50 per cent of the catch, and that we have never found as many as 50,000 of any other copepod per square meter, though there are often upward of 100,000 Calanus.

The frequent dominance by *C. finmarchicus*, especially in spring and early summer, not only over other copepods but of the entire community of planktonic animals, is commented on in an earlier chapter (p. 37). If the seasons of 1920 and 1921 can be taken as representative, *C. finmarchicus* is at its lowest ebb (compared with other copepods, as well as absolutely) during January and February, when it constituted 30 to 90 per cent (average about 55 per cent for the two months) of the copepods caught in horizontal and vertical hauls in the inner parts of the gulf (tables, pp. 299 and 304), but only 2 to 10 per cent over the western end of Georges Bank or outside the continental edge to the southward. The average percentages for March (58 per cent) and April, 1920 (57 per cent), were about equal, but experience in 1915, 1916, and 1920 proves that the percentage of Calanus among the total copepods increases notably as the spring advances, consequent on the active vernal multiplication of this species (p. 194), which no other local copepod rivals. In 1920 the relative augmentation of *C. finmarchicus* far outstripped the general augmentation of the copepod community as a whole[1] in the southwestern part of the gulf and on the western portion of Georges Bank. The percentage of Calanus in the vertical hauls at the May stations for the two years combined averaged about 80 per cent for the more prolific parts of the gulf.

Direct comparison can not be made between the percentages for May and for June (average 56 per cent), because most of the stations for the latter month were located in the northern corner of the gulf, where we have not towed in May. Consequently, the difference may be a regional phenomenon, not seasonal.

The vertical hauls for August, 1913—14 in number—give an extreme range of from 87 per cent to 12 per cent Calanus, averaging 50 per cent, and 4 August hauls for 1915 average 46 per cent Calanus, suggesting that this species is proportionately less dominant in the general copepod population of the gulf in late summer than in spring. Forty-five horizontal hauls at various depths generally distributed over the gulf, including Georges Bank and out to the continental shelf, for July and August, 1914, averaged 71 per cent Calanus, with 100 per cent on several occasions, in both surface and deep hauls—that is, about the same percentage that resulted from the vertical hauls for May, 1920 (table, p. 302), and only slightly less than for that month in 1915 (table, p. 297). It is therefore doubtful whether any decided diminution in the percentage of Calanus, relative to other copepods, is a regular phase in its annual cycle in the gulf during the period June to August, though there may be a considerable variation in the percentage of Calanus from summer to

[1] Compare stations 20044 to 20047 with stations 20127 to 20129, table, p. 299.

summer, consequent on fluctuations in its actual abundance, and in the abundance of the other species of copepods. Twenty-one vertical hauls at as many stations for September and October, 1915, give an average of only 38 per cent and 42 per cent of Calanus, respectively—that is, little more than half of the May percentage.

The percentage of Calanus averaged somewhat higher in the horizontal hauls of December, 1920 (about 58 per cent; table, p. 304). However, this does not reflect an increase in the actual abundance of the species (which, on the contrary, decreases markedly in numbers during the late autumn and early winter), but a still more pronounced decrease in the local stock of other species of copepods. Thus, while curves for the actual and for the relative abundance (percentage) of *C. finmarchicus* would be similar for the spring, they would be contradictory for the September–December quarter, and to this extent the percentages taken by themselves would give a totally false picture of the seasonal fluctuations of the species in the Gulf of Maine.

From the economic standpoint this means that any copepod-eating fish in the Gulf of Maine is likely to make Calanus its chief diet from May until August and in October, but to depend less on it and more on other copepods during the early autumn and again in late winter and early spring.

The average percentages need further qualification to bring out the great irregularity in the relative abundance of the species which we have encountered from station to station on most of the cruises and from month to month at individual stations, irregularities connected with the streaky way in which *C. finmarchicus* often occurs, and with the formation and dissipation of its shoals. In Massachusetts Bay, for example, the percentage fell from 80 to 45 at one locality off Gloucester between March 1 and April 9, 1920, but increased from 6 per cent to 50 per cent off Boston Harbor, near by, during approximately the same interval. In the western basin, at three successive stations, the percentage of *C. finmarchicus* was 90 on February 23, 25 on March 24, 75 on April 18, and at three stations along a line running out from Ipswich Bay toward Platts Bank, on April 9 and 10, the percentages were alternately 75, 25, and 80. Seventy-five per cent of Calanus in the southwestern part of the basin on February 23, but only 2 per cent on the neighboring part of Georges Bank the same day, was evidence of a corresponding difference in the actual number of *C. finmarchicus* per square meter—respectively, 6,562 and 25—but on the southeastern slope of the bank the percentage fell only from an average of about 75 per cent on March 12 to 60 per cent on April 15, although this interval saw the dissipation of a very dense swarm of Calanus, occasioning a shrinking in the number per square meter from 103,000 to about 600.

Apart from the question of vertical stratification (p. 24), the percentages of Calanus have proved more nearly uniform over considerable areas in the later spring and summer. In early May, 1920, for example, it constituted 60 to 80 per cent of the copepods at most of the stations in the southwestern part of the gulf and on the western end of Georges Bank (table, p. 302). In July and August, 1914, its percentages in the horizontal hauls at most of the stations inside the continental edge approximated the average (71 per cent) for all the stations, irrespective of regional variations in the actual abundance of the species. In September and the

first half of October, 1915, considerable differences were noted in the percentages from station to station, but during the last week of the latter month the percentage of Calanus (50 per cent) was nearly uniform at the several stations off Cape Cod and in Massachusetts Bay. In December, 1920, and January, 1921, considerable regional differences obtained in the horizontal hauls, with extremes of 90 per cent of *C. finmarchicus* in the western basin (station 10490, table, p. 304) but only 10 per cent in the eastern basin (station 10502).

The only definite regional subdivision that can be drawn in summer, from the standpoint of the percentages of *C. finmarchicus*, is between the gulf proper (including its offshore banks) and the waters outside the continental edge. Calanus is usually dominant in the copepod community of the former, but is only a very minor element in that of the latter. Experience suggests that the farther out in the Atlantic basin abreast the gulf, the less important relatively and the less plentiful absolutely is this copepod. It is probable that this is equally true throughout the year, but it is certain that the line of demarcation lies farther out from the continental edge in late winter and spring than in the warm season, when the high salinities and temperatures of the inner edge of the Gulf Stream are closest in to the banks—witness the notable dominance of Calanus off the southeastern slope of Georges Bank in March and April, 1920, and the increase in its percentage in the catches off the western end of the bank from February (5 and 6 per cent) to May (80 per cent, station 20129; table, p. 303).

The data so far gathered show that this species may attain a very high percentage anywhere in the inner parts of the gulf. When the local copepod plankton is more intensively studied, characteristic regional differences may be developed there, too.

*Vertical distribution.*—The vertical distribution of *C. finmarchicus* in the Gulf of Maine varies somewhat with the season of the year. In spring, as exemplified by the February to May cruises of 1920, it was taken in all but one of the surface hauls, irrespective of the time of day. The numbers of specimens per haul do not suggest any diurnal migration upward by day and downward by night, such as this copepod carries out in summer (p. 204), the average being somewhat greater for hauls made between 7 a. m. and 6 p. m. (average, 521 Calanus per haul in February and March; 1,458 in April and May) than for those made between 6 p. m. and 7 a. m. (average 263 for February and March; 838 for April and May). Whether Calanus actually is as plentiful at the surface during the spring months as it is at the lower levels can hardly be determined from the data available.

Further evidence that the surface stratum is as productive of Calanus in spring as are the underlying waters is afforded by the average percentages of occurrence, which for the surface hauls [2] are about the same as for the verticals for the several months, and show a corresponding increase with the advance of the season (p. 201), as follows. Note, also, that the only spring hauls yielding 100 per cent Calanus in 1920 were at the surface (stations 20100, 20112, and 20113).

[2] Taken in hauls uniform in duration and in the diameter of the net employed.

| Date | Percentage in surface hauls | Percentage in vertical hauls |
|---|---|---|
| March | 53 | 58 |
| April | 63 | 57 |
| May | 76 | 80 |

It is probable that a certain number of *C. finmarchicus* exist right down to the bottom of the trough of the gulf in spring, as they do in summer, though no direct proof of this is yet at hand. However, were it as plentiful below, say, 175 meters as it is above that level, the deepest vertical hauls—that is, those filtering the longest columns of water—would on the average have yielded the largest catches of Calanus, which was not the case. Actually, the average numbers (about 11,000 per square meter) taken in 15 vertical hauls from depths of 200 to 340 meters in the basin, and in one off the southeastern face of Georges Bank from 1,000 meters,[3] during February, March, and April, 1920, were less than the yields of 20 shoaler vertical hauls from depths of 100 to 175 meters (average approximately 18,000 *C. finmarchicus* per square meter)—evidence that there were not enough Calanus below 175 to 200 meters to add appreciably to the catches. The two richest catches for March and April [4] were in hauls from depths of only 150 and 125 meters, respectively.

With the increasing intensity of the sunlight and progressive warming of the water which accompany the advance of the season, the surface stratum evidently becomes less favorable for Calanus, for in summer it is usually decidedly scarce or even wanting in the surface hauls, even at localities where it swarms a few meters down; but at other summer stations it has been taken in abundance at the surface. I have already pointed out (Bigelow, 1915, p. 290) that its absence on the surface in the regions where it swarms in deeper water is not caused altogether by sunlight, for while it probably does tend to descend during the most brilliantly illuminated hours, on several occasions we have made rich catches on the surface when the sun was high in the sky. Such was the case off the entrance to Gloucester harbor on July 22, 1912 (station 10012), when nearly a liter was taken in the 4-foot net on the surface at about 3 p. m. Again, on August 14, 1914 (station 10251), we made a rich surface catch of Calanus at about 2 p. m. off Cape Elizabeth; in July, 1916, a month when *C. finmarchicus* was notably abundant, surface hauls yielded considerable numbers off Cape Cod at 4 p. m. (station 10345), and off Marthas Vineyard at 5 p. m. (station 10351). Willey (1919, p. 181) records the presence of this copepod in abundance on the surface in the Bay of Fundy between 3 and 4 p. m. under a bright sun; but, as he further remarks, this is unusual. Willey suggests that in the Bay of Fundy the active stirring of the water by tidal currents may be instrumental in bringing the Calanus up at an hour when they ordinarily shun the surface, an explanation that may apply to the particular case in point but not to the other instances just mentioned, which were in regions of weak vertical circulation and certainly not of upwelling.

[3] This station touched the swarm of Calanus already described for that location.

[4] 103,300 and 78,000 per square meter, stations 20068 (southeast slope of Georges Bank, Mar. 12) and 20105 (Northern Channel Apr. 15, 1920, station 20078).

Most of the other surface catches of Calanus in the gulf that can be classed as "rich" have been made during the hours after the sun has declined below an altitude of about 8 to 10°, or before it has risen that high in the morning. More specifically, five of these rich surface catches were at 6 to 7 p. m., two at 8 to 10 p. m., five at 10.30 p. m. to midnight, two at 1 to 2 a. m., and two at 6 a. m. Cases in point are stations 10024, 10027, 10038, and 10042 in July and August, 1912; a swarm off Gloucester on July 7, 1913; stations 10093, 10097, and 10100 in August, 1913; and stations 10246, 10247, and 10254 during August, 1914. Thus in the Gulf of Maine Calanus shows some tendency in summer to diurnal migration upward toward the surface at the approach of sunset, which it deserts after sunrise in the morning. Esterly (1911a, p. 142), in his study of the diurnal migrations of *C. finmarchicus* at San Diego, Calif., where the surface was practically barren of it during the day, found it "overwhelmingly more abundant at the surface about twilight or immediately after" than at any other hour, with its plurimum at about 7 to 8 o'clock in the evening; but the fact that we made as many rich catches about midnight as about sunset suggests that in the Gulf of Maine it is as likely to swim upward at one hour of night as another. It has been as scarce at the surface at most of our night stations, even when plentiful deeper down, as it usually is in the daytime, evidence that the vertical movement is only carried out at particular times and places, or that it usually fails to bring any large percentage of the Calanus right up to the top of the water. For example, "Calanus certainly did not come to the surface off Cape Cod during the night of August 5 [1913], for surface hauls taken at 2 a. m. and at practically the same locality at 8 a. m. (station 10086) yielded very few Calanus, although the deep haul caught thousands" (Bigelow, 1915, p. 290). Other instances of the same sort for other hours between sunset and sunrise might be mentioned.

Our few stations (10399 to 10404) in the western part of the gulf for October 31 to November 8, 1916, indicate a similar tendency on the part of Calanus to shun the surface by day but to ascend by night during the autumn as during the summer, for the one surface haul moderately productive of large Calanus was at 4 a. m. (station 10402), while juveniles were taken in numbers on the surface at 6 a. m. (station 10400). At the other stations (10 a. m., 2 p. m., and 3 p. m.) the surface hauls yielded few, though it was moderately plentiful at 50 to 180 meters.

During the winter, as the water continues to cool and the sun is low, the surface must gradually offer a more favorable environment to Calanus, resulting in its occurring as regularly and probably as plentifully there by March as deeper down, irrespective of the time of day. How early in the winter this takes place remains to be learned, however.

These observations corroborate Esterly's conclusion that when Calanus does carry out a vertical diurnal migration it is not induced thereto solely by the time of day, but that the direction of its vertical swimming (or sinking) is governed by geotropism, which changes with physiological changes in the animal itself. Esterly's experiments pointed to varying degrees of solar illumination as governing these changes, thus bringing its reactions into line with those of other copepods. (See, for example, Parker, 1902, on Labidocera.) This explanation, however, does

not cover its constant presence on the surface in the gulf at all hours of the day in spring, contrasted with its absence from the surface by day in autumn (p. 204), the illumination being about as bright at the one season as at the other.

It is possible that temperature, combined with light, may be a factor in the case—that is, Calanus may tend to sink in warm, brightly illuminated water, but to rise in pale illumination, irrespective of its temperature—but until this interesting subject has been studied more thoroughly I need only emphasize that the reactions of Calanus in their local application to the gulf result in its being far less plentiful in the surface stratum than below 10 meters or so by day, and often by night, during the half of the year when the temperature is highest and the solar illumination brightest.

Horizontal hauls locate the zone of chief abundance for this copepod in the gulf at 25 down to about 100 meters depth during the months of July, August, and September, showing that it tends to avoid the deepest waters of the gulf in summer as well as in winter and to congregate in the mid depths. I have pointed out elsewhere (Bigelow, 1915, p. 290) that in the summer of 1913 much larger catches of Calanus usually were made in hauls from 30 to 40 meters than from 100 to 170 meters at stations where we towed at three levels—surface, intermediate, and deep—with the shallower catches "usually two to four times as large in bulk as the deep ones, a difference too great to be charged to the difference in mouth area between the 4-foot and the Helgoland nets. And this source of error was further checked by occasionally alternating the two nets." The only exceptions to this rule during that cruise were at three stations in the eastern half of the gulf (10093, 10097, and 10100), where Calanus was about equally abundant in the deep and shallow hauls and plentiful right up to the surface. Again, on July 19, 1916, a much larger quantity of *C. finmarchicus* (upward of 1½ liters) was taken in Massachusetts Bay in the 30–0 meter haul than at 83–0 meters. The next day a 40–0 meter haul off Cape Cod (station 10344) yielded upward of 2,500,000 large Calanus (Bigelow, 1922, p. 136),[6] not to mention smaller ones, while the 88–0 meter haul took not over one-twelfth as many, estimated by their bulk (6 liters in the one case and less than one-half liter in the other).

The catches of Calanus in the open horizontal nets likewise averaged from two to three times larger from above 100 meters than from greater depths during the cruise of July and August, 1914; and though stations 10246, 10248, and 10254 were exceptions, with several times as many Calanus and other copepods taken in tows at 150 to 225 meters as at 50 to 75, it was only above 100 meters that notably large catches were made (Bigelow, 1917, p. 312).

The chief zone of abundance for *C. finmarchicus* in the Norwegian Sea also lies above 200 meters (Damas, 1905, p. 11), with about 400 meters as its lower limit. Around Iceland Paulsen (1909) found it in great abundance down to 500 meters; Nordgaard and Jørgensen (1905) record it as most plentiful at 200 to 300 meters in the Norwegian fjords in winter; and Damas and Koefoed (1907) found it down to at least 1,200 meters depth between Norway, Spitzbergen, and Greenland.

[6] Our largest catch of large Calanus.

In the San Diego region Esterly (1911) took it in abundance as deep as 400 to 500 meters, to which depth diurnal migration was effective.

Physical factors offer no apparent explanation for the comparative scarcity of Calanus in the deepest water of the gulf as compared with the intermediate levels, both temperature and salinity being well within the optimum for it; and it is more likely that the cause lies in the distribution of the food supply, Calanus tending to congregate at the levels where the microscopic plants on which it feeds are most abundant.

*Reproduction.*—It is now well known that *Calanus finmarchicus* deposits its eggs singly in the water, where they float until the young copepod hatches in the "nauplius" stage. Being of characteristic appearance (Damas, 1905), Calanus eggs are easily recognized in the plankton. The larval stages are distinguishable by the number of thoracic and abdominal segments and developed legs, as well as by their size. The stages are described by Lebour (1916). Damas's (1905) notation of them, now generally adopted, is as follows:

| Stage | Thoracic segments | Abdominal segments | Fully developed legs |
|---|---|---|---|
| I | 2 | 2 | 2 |
| II | 3 | 2 | 3 |
| III | 4 | 2 | 4 |
| IV | 5 | 3 | 5 |
| V | 5 | 4 | 5 |
| VI, adult female | 5 | 4 | 5 |
| VI, adult male | 5 | 5 | 5 |

The proportionate numbers in which the different stages in development have occurred in the many samples, American and European, which have now been studied by various authors, indicate that *C. finmarchicus* passes most of its existence in the late postlarval stages, living only for a short time as an adult, to perish shortly after breeding; but much is yet to be learned of its breeding habits in detail.

Only a few scattered observations have been made on the occurrence of eggs or juveniles of *C. finmarchicus* in the Gulf of Maine; enough, however, to show that it is regularly endemic there and that the local stock is chiefly the product of reproduction in the Gulf, though more or less recruited by immigration from colder waters to the east and north.

As previously remarked (p. 194), swarms of copepod nauplii and young copepods appeared off Gloucester during the first week of May, 1915, a decided increase in juvenile Calanus took place in the neighborhood of the Isles of Shoals during the first half of the month, and there were great numbers of young Calanus in Massachusetts Bay off Magnolia on the 17th. In 1920, again, copepod nauplii newly hatched swarmed in the surface waters of the bay on May 4 (stations 20120 and 20121, fig. 27 and 28), and on the 16th juveniles of *C. finmarchicus* were identified among a rich catch of young copepods off Gloucester (station 20124).[6] The fact that the Calanus that swarmed off Cape Ann on May 4, 1915 (p. 297), were mostly in the younger, intermediate stages of growth is sufficient evidence that a production

[6] These juvenile stages were taken chiefly on the surface and in some abundance in the vertical hauls as well (see table, p. 297).

of nauplii such as that just mentioned does actually presage the great augmentation of *C. finmarchicus* that takes place in that side of the gulf during the late spring and early summer. In other words, the Massachusetts Bay region and neighboring waters are actually important centers of reproduction for the species, and of growth, leading to a dominance of adults in July. Willey (1921) has remarked that this part of the Gulf of Maine would seem to be the southern headquarters for the production of *C. finmarchicus* in the northwestern Atlantic, and it is not unlikely that the Calanus population of the gulf as a whole originates chiefly in the area bounded by Cape Elizabeth on the north, Cape Cod on the south, and the western basin offshore.

Judging from the data for 1915 and 1920, the production in this region must be very large to account for the local abundance of this copepod in May and July, but it is probably not to be compared with the tremendous production that takes place in the Norwegian sea, for Calanus eggs have not occurred in notable numbers in any of the samples in question,[7] whereas Damas (1905, p. 12) describes them as locally so abundant between Norway and Iceland that in certain regions they are one of the principal elements in the plankton, even to the exclusion of everything else.

No attempt has yet been made to determine the presence or absence of the early stages of *C. finmarchicus* in the samples from other parts of the gulf. Probably it breeds to some extent over the whole of it (Willey (1921) mentions juveniles in Passamaquoddy Bay in April), but the preliminary study of the tow nettings points to the region just outlined as by far the most productive center of local production. It is also safe to say that spring, from late April on, is the chief breeding season for Calanus in the gulf, and that breeding probably continues actively through June to account for the abundance of juveniles in various stages which we found off Cape Cod on July 9, 1913 (station 10057; Bigelow, 1915, p. 291),[8] and in Provincetown Harbor on July 20, 1916 (station 10343). It is certain that no production comparable with the vernal wave takes place later in the summer, though positive evidence (in the form of eggs and juveniles) as to whether Calanus spawns at all in the gulf during July, August, or September is yet to be sought among the masses of copepods collected on our cruises. Doctor Esterly's [9] report of many juveniles at two stations off southern Nova Scotia on July 29 and August 6, 1914 (stations 10235 and 10237), shows that Calanus breeds well into the summer east of Cape Sable.

In 1915 the increase in the numbers of *C. finmarchicus* in the gulf during early autumn was preceded during the first half of September by an abundance of development stages of copepods in the tow. (See table, p. 298.) If these larval stages actually were *C. finmarchicus*, as seems probable from the constant dominance of the copepod fauna by that species, this points to a second but less productive breeding season in autumn, an interpretation corroborated by the presence of a large proportion of juveniles of this species in the surface tows near the Isles of Shoals and in the western basin on November 1, 1916 (stations 10400 and 10401). Development stages of some copepod were likewise recorded in comparative abundance for January, 1921,

[7] No special attention has yet been paid to the eggs in the Gulf of Maine tow nettings—a task for the future.
[8] These were identified by Dr. C. O. Esterly.
[9] In a letter.

by Dr. C. B. Wilson (table, p. 305), but the fact that no decided multiplication of the later stages of Calanus takes place during late winter (p. 39) suggests that these belonged to some other species of copepod and that *C. finmarchicus* breeds little, if at all, in the gulf from September or October until the following April.

In north European seas generally, where the biology of this copepod has attracted the attention it deserves, it is primarily a spring or summer breeder, the spawning season commencing soon after vernal warming of the water is appreciable and consequently varying with latitude and with oceanic conditions. Thus Gran (1902) found it in full breeding condition on the northwestern coast of Norway (latitude about 67° N.) in April and May; Damas (1905) in June in the Norwegian sea, where the Arctic and Atlantic currents meet, and in May and June around the Faroes. Paulsen (1906) states that the reproductive season south of Iceland lasts from March into June; Damas and Koefoed (1907) describe this copepod as spawning in late June along Norway and in the fjords of Spitzbergen; while With (1915) found it in breeding condition in June in Denmark Strait, in May south of Iceland, in June and July off West Greenland, and as late as the last days of July off eastern Greenland. Thus With justly interprets the term "spring," as descriptive of the chief breeding period of *C. finmarchicus*, to mean the period at which the waters reach a certain temperature and salinity, and which varies according to the latitude from March (February?) to August (east Greenland). The April to June spawning in the Gulf of Maine thus parallels the breeding period of this copepod in the southern parts of the northeastern Atlantic area.

Although most European authors have credited *C. finmarchicus* with one comparatively brief period of reproduction annually, Paulsen (1906), with whom With (1915) agrees, has pointed out that it probably breeds to some extent at other seasons also in Norwegian and Icelandic waters, just as it certainly does in the Gulf of Maine, because adults of both sexes have been found at other times of year almost everywhere in northern seas where towing has been carried out at appropriate depths.

If it proves characteristic of *C. finmarchicus* to have two distinct periods of active reproduction in the Gulf of Maine—a major in spring and a minor in autumn—as a preliminary study of our samples suggests, and only one in north European and Arctic seas, the difference may simply be one of latitude, the first spawning occurring so early in the year in the gulf and autumnal cooling commencing so late that there is opportunity for a part of the product of the spring hatch to mature and breed before the temperature of the water falls too low for sexual development. Thus, it is probable that for most of the stock breeding is an annual event and the individuals survive for a year; for others it is biennial, with the autumn hatch passing the winter in the late postlarval stages, as Paulsen (1906) suggests, and enough irregular reproduction taking place at any time from early spring until well into the autumn to maintain the variety of stages in development that have been seen throughout the year. More intensive study of the Gulf of Maine samples may be expected to throw light on this question that would be important not only as bearing on the life history of the species but with regard to the natural economy of the gulf, of which *C. finmarchicus* is the most important planktonic inhabitant.

The chief value of the foregoing notes on the reproduction of Calanus is their demonstration that this copepod is regularly endemic in the gulf just as it is in the Gulf of St. Lawrence (Willey, 1919). How far west of Cape Cod Calanus breeds in any abundance is still to be determined. Judging from its constant presence off southern New England (p. 188) and from the fact that juveniles were numerous over the inner part of the shelf off Long Island and off New York on August 1 and 26, 1916 (stations 10362 and 10396; Bigelow, 1922, p. 143), it is probable that considerable production takes place that far west. The rich catches of Calanus made farther south during that summer consisted in the main of very large individuals, which apparently did not succeed in reproducing to any extent because young stages were scarce or absent west and south of Cape Cod in the following November.

There is reason to believe that the Calanus stock of the eastern part of the Gulf of Maine is recruited to some extent by immigration around Cape Sable from more northerly breeding centers. Thus, a swarm of large Calanus with comparatively few young stages, in the eastern basin on May 6, 1915 (station 10270), might (so far as internal evidence goes) as well have represented an immigration as a late stage in a local reproduction cycle, the unmistakable westward extension of the Nova Scotian current at the time giving the first alternative an *a priori* probability which our failure to find any great production of young Calanus in this region in April, 1920, tends to corroborate. The swarm off the southeast slope of Georges Bank in March, 1920, had probably drifted thither from the east or northeast.

At present it is impossible to state how regularly such immigrations into the gulf take place, or their precise source, but it is probable that in the maintenance of the stock of this copepod existing in the Gulf they are of far less importance than local production.

Such data as are available suggest, furthermore, that the northern and eastern parts of the gulf are kept supplied with Calanus chiefly by the dispersal of the swarms of young produced in the southwestern side, the general circulation of the gulf indicating a general anticlockwise drift eastward along the northward side of Georges Bank and thence northward and westward around the gulf. Nor is a drift of this sort inherently improbable, for Calanus regularly carries out far more extensive involuntary migrations from its chief breeding centers in north European and sub-Arctic seas.

*Relationship to temperature and salinity.*—Most authors have described *C. finmarchicus* as eurythermal, which is certainly true within very wide limits. In the Gulf of Maine it occurs regularly over a range of from fractionally above 0° to 20° (station 10254, surface, Calanus plentiful). I do not know the highest range in which it has ever been found, but on August 30 and 31, 1913, the *Grampus* took occasional specimens (living) in 24.44° on the surface off Delaware Bay, where by sinking 20 meters or so it could have found much cooler water of 11 to 12° (Bigelow, 1915, p. 290). Although apparently it is able to exist in such high temperatures, much evidence has been accumulated to the effect that somewhat cooler water offers a more favorable environment for it, whether as it effects the growth of the Calanus itself, its reproduction, or its food supply. This was unmistakably the case in the

southern extremity of its range during the summer of 1916, when there was a very close correspondence between the limits occupied by abundant Calanus on the shelf south of New York, vertically as well as horizontally, and water of 4 to 7°. With one exception it swarmed only in water of 6° or colder (Bigelow, 1922, p. 143, figs. 45 to 47).

In general it may be said that along the North American seaboard *C. finmarchicus* is abundant and dominates the plankton only in temperatures lower than 12 to 15°, or where it can have ready recourse to water as cool as this by sinking or by swimming downward a few fathoms. The fact that in 1916 Calanus was not as definitely concentrated in the deeper water between Marthas Vineyard and Delaware Bay in November as in August, is in line with this general thesis, for the equalization in its vertical distribution corresponds to the vertical equalization of temperature (and of salinity) which takes place there in autumn; and it suggested that "the failure of the southern Calanus swarm to migrate to the surface during the midsummer nights, as it so often does in the Gulf of Maine and elsewhere, was due either to the very high surface temperature, or possibly to the very low surface density" (Bigelow, 1922, p. 145). With the advance of autumn both these barriers are weakened by surface cooling, until in winter, thanks to the vertical uniformity of the water, the only physical factors governing vertical migration are sunlight and geotropism.

At the other extreme, while *C. finmarchicus* probably can survive in the very lowest temperatures obtaining anywhere at sea, the isotherm of 2° has been found to mark approximately the lower level to its regular occurrence in the northern part of the Norwegian Sea (Damas, 1905). Damas and Koefoed (1907) found it more plentiful in the intermediate strata in the seas between Spitzbergen and Greenland at temperatures of 1 to 2° and upward than in the colder water below.

It is probable that *C. finmarchicus* requires a somewhat higher temperature for its successful reproduction. Thus the abundance of early postlarval stages in the Gulf of St. Lawrence during June, July, and August (Willey, 1919) suggests that breeding takes place there chiefly after the end of May, by which season the upper 20 meters or so have warmed by several degrees from the winter minimum. This is certainly the case in the Massachusetts Bay region, where nauplii did not appear in any abundance in 1920 until the whole column of water, down to 70 meters, was warmer than 2.7° and the upper 25 meters warmer than 4.5°.

The relationship between the breeding range of this copepod and temperature is similar around Iceland, for in spring it spawns abundantly to the south of the island in water of 4° and upward; but apparently it does not do so at all to the north, where the temperature remains as low as 1 to 3° throughout May, though enough Calanus drift westward around Iceland to make this copepod extremely abundant along the northern coast in summer (Paulsen, 1906). As Damas and Koefoed (1907) have pointed out, *C. finmarchicus* is therefore less Arctic in its relationship to temperature than is *C. hyperboreus*, probably finding the lower limit to its active reproduction at about 2 to 3°; and the same for its rapid growth, though it is able to survive through long periods of lower temperature, growing slowly if at all.

*C. finmarchicus* is likewise indifferent to changes in salinity within wide limits, but I have been unable to learn that it is regularly abundant anywhere in water more saline than about 35.3 per mille[10] (Farran, 1910). Thus high salinity is probably a more effective barrier to its dispersal seaward abreast of the Gulf of Maine and thence southward along the continental edge of North America than is high temperature, though, to quote from an eminent student of this group (Willey, 1919, p. 176), "the factor which determines the limit of southern dispersion of *C. finmarchicus* is clearly neither a simple physical constant nor a single organic tropism," but "includes the biological factors of food-supply and propagation."

*C. finmarchicus* is regularly and abundantly present in considerably less saline water (31 to 33 per mille) in the western side of the North Atlantic than Farran (1910) set as the lower limit to its plentiful occurrence in the North Sea region (33.5 per mille), and apparently it was spawning actively in a salinity of only 29 to 30 per mille in Massachusetts Bay in May, 1920. Judging from its status in the entrances to the Baltic, however, and from its rarity within the latter, probably it can not exist long in water much fresher than this, though it may reach brackish situations as driftage.

*Economic importance.*—The importance of *C. finmarchicus* in the general economy of the Gulf of Maine and of all other seas where it abounds can hardly be overestimated. Certainly it is no exaggeration to call it the most important single planktonic animal, probably more important in the gulf in its relation to both larger and smaller organisms than all other copepods combined. It is the basic food for the local mackerel, and is certainly a major article in the diet of the herring, alewife, and shad while these are at sea. All the other fishes of the offshore waters of the gulf that eat plankton at all may be expected to feed on Calanus more than on any other single item. Through the medium of the herrings, which are nourished on it, Calanus helps support the finback and humpback whales, *Balænoptera physalus* and *Megaptera nodosa* (the only whalebone whales now common in the gulf), though neither of these feeds directly on copepods, their whalebone being too coarse (p. 97). On the other hand, it is probable that Calanus makes greater inroads on the planktonic plants on which it preys than do all other copepods combined, and conceivably it may practically exterminate them locally and temporarily.

### Calanus gracilis Dana

Dr. C. B. Wilson contributes the following note:

This species has been reported from the western part of the Mediterranean and from the Indian and Pacific Oceans as well as the Atlantic. Cleve (1900), in discussing the distribution of Atlantic Copepoda, gave the northern and southern limits of this species as from the 44th parallel north to the 35th parallel south. The Gulf of Maine, therefore, is about its northern limit, and it would not be expected to appear in large numbers. Neither would it be widely distributed. It is worthy of note that Pesta has reported it from a depth of 1,200 meters in the Adriatic, while Giesbrecht gave 1,500 meters as the maximum depth limit. The few specimens found in the present plankton were obtained in October from shallow water rather close to the shore [at two stations off Marthas Vineyard and at one in Massachusetts Bay (see table, p. 298)].

[10] Willey (1919, p. 176) records abundant Calanus at a salinity of 35 per mille in the edge of the Gulf Stream between the Scotian and Newfoundland Banks on June 1, 1915.

This species was not found in the Woods Hole region by Wheeler (1901), nor did Dr. C. O. Esterly detect it among the tow nettings of the *Grampus* made between the Gulf of Maine and Chesapeake Bay during the summer of 1913 (Bigelow, 1915, p. 287), but Willey (1919, p. 218) reports it from two stations outside the continental edge off Cape Sable, July 22, 1915. It has no regular place in the fauna of the Gulf of Maine, where it is only a stray.

### Calanus hyperboreus Krøyer

This is an Arctic species with its chief center of distribution in polar seas, where it is probably circumpolar and universal, having been taken at many localities off the northern coasts of Europe, Asia (to longitude 136° E.), and America (north coast of Alaska, Dolphin, and Union Strait; Willey, 1920). It is described by Damas and Koefoed (1907) as the commonest surface copepod in the Greenland sea. It drifts southward past Iceland with the east Icelandic current over a well-defined tongue (Farran, 1910), spreading thence in small numbers over the southern part of the Norwegian sea to the Skager—Rak and the southern Norwegian fjords, where Sars (1903) regards it as a "relict" species. A few are also carried southward in the cold bottom current across the Wyville Thomson ridge into the North Atlantic, where it has been recorded southward to latitude 51° N., longitude 11° 43′ W., off the mouth of the English Channel.[11] On the American side it occurs generally and abundantly over Davis Strait (With, 1915) and Baffins Bay (Aurivillius, 1896). Curiously enough, Herdman seems not to have had it on his two traverses of the Labrador current abreast the Straits of Belle Isle during the summer of 1897,[12] but the Canadian fisheries expedition of 1915 found it generally distributed over the Gulf of St. Lawrence as well as between Nova Scotia and the Newfoundland Banks and over the continental shelf along the Nova Scotian coast to abreast of Cape Sable. On their summer cruise, however, it was not found at the stations outside the continental edge west of Sable Island (Willey, 1919). It has been taken at many localities in the Gulf of Maine, shortly to be discussed, but Georges Bank and Cape Cod mark the limit to its occurrence as anything more than an accidental stray in this direction. South of this our only record for it is one specimen off Delaware Bay on August 12, 1916, in a haul from 70 meters (Bigelow, 1922, p. 148).

*Regional and seasonal occurrence in the Gulf of Maine.*—Judging from our experience in 1915 and 1920, *Calanus hyperboreus* is, to all intents, universally distributed over the gulf during the late winter, early spring, and early summer. Thus it appears at about 80 per cent of the stations in Doctor Wilson's lists for February to May, 1920, at localities covering all parts of the gulf from the immediate coastal zone, on the one hand, out to the continental edge, on the other, and indifferently from the eastern side to the western, irrespective of the depth of water (fig. 68); and since a species as comparatively rare as *C. hyperboreus* might easily be missed by the vertical hauls, probably it was actually present at every station. Similarly,

[11] For further details see Gran (1902), Paulsen (1906), Damas and Koefoed (1907), and Farran (1910).

[12] Unless possibly some of the Calani listed by Herdman, Thompson, and Scott (1898) as *C. propinquus* were actually *C. hyperboreus*.

it occurred in the vertical hauls at all but one of the May and June stations for 1915 (table, p. 297), covering the basin and coastwise waters of the gulf and Browns Bank as well.

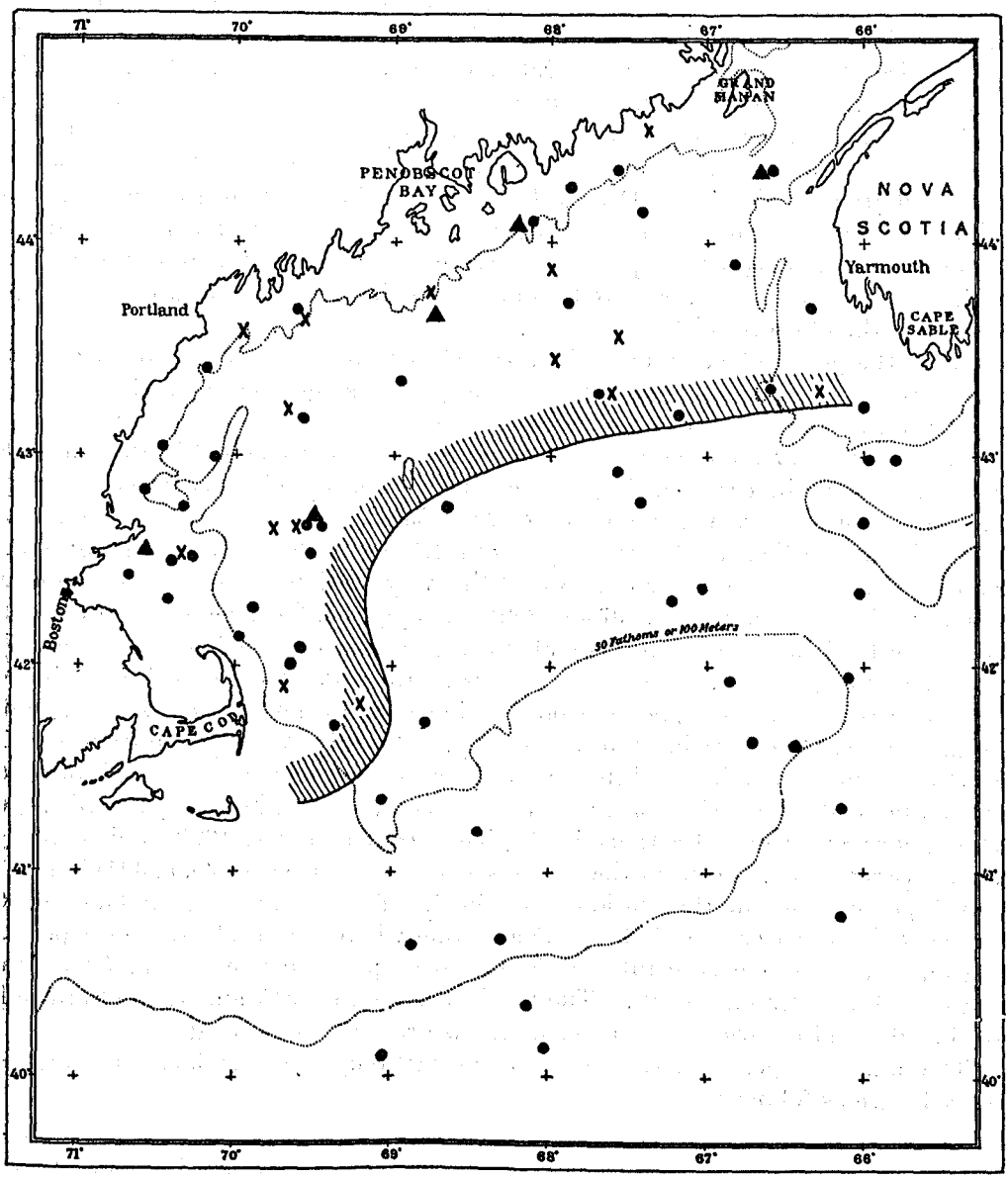


FIG. 68.—*Occurrence of the copepod Calanus hyperboreus at different seasons.* ●, locality records, February to May; X, July to November; ▲, December and January. The hatched curve marks the offshore limit to the occurrence of this species in summer

During the summer and early autumn it continues widespread in the northern and western parts of the gulf [13] over a belt some 60 to 70 miles wide paralleling the

[13] In addition to the localities marked (fig. 68), Willey (1921) found it forming about 8 per cent of a sample of copepods collected in a 10-fathom tow off Eastport, Me., Aug. 2 1916.

coast; but during the July and August cruise of 1914 we failed to find it at any station in the southeastern part of the basin, in the eastern and northern channels, on Georges or Browns banks, or near Cape Sable, indicating that at this season the *C. hyperboreus* of the Gulf of Maine are entirely cut off from the more northerly centers of abundance along the outer coast of Nova Scotia, though continuous with them and drawing from them by immigration earlier in the year (p. 217). During December and January it occurred in the horizontal hauls in the western basin, off Penobscot Bay, off Mount Desert Island, and in the Fundy Deep in 1920 and 1921 (table, p. 304); also at three stations off Gloucester in the winter of 1912–1913 (Bigelow, 1914a, p. 409); and Willey (1921) records it in some abundance in the mouth of the St. Croix River from November to February during the winter of 1916–17, but not in January, 1920, though two specimens were noted in a tow taken on the 25th of March in that year. Unfortunately our November–January cruises have not extended to the offshore banks.

Thus, the geographical range of *C. hyperboreus* in the gulf narrows from the sea shoreward in summer and expands offshore again at some time (just when remains to be discovered) during autumn or winter.

Numerically *C. hyperboreus* is never more than a minor element in the plankton of the gulf, though its economic importance may be considerable because of its large size. Thus the average percentage of *C. hyperboreus* at the stations where it was detected in the vertical hauls was only about 4.5 per cent for March, 1920; 7 per cent for April, 1920; 2 to 3 per cent for all the May stations; and 7 per cent for all the June stations (see tables, pp. 297 and 299). In July, 1915, it averaged 2½ per cent of three vertical hauls, and in 1913 about 1 per cent of two hauls (80 and 270 *hyperboreus* to 8,800 and 5,400 *finmarchicus*). In 1912 there was 1 *hyperboreus* to 50 *finmarchicus* in a sample from one station (10023), and 6 *hyperboreus* among thousands of *finmarchicus* in another (10040). On July 22, 1916 (station 10345) only one specimen was detected in a preliminary survey of some thousands of copepods and none at all at neighboring stations. Willey (1919), however, records 8 per cent of *hyperboreus* near Eastport in August. In December, 1920, and January, 1921, it averaged 3.5 per cent at the stations where it occurred (table, p. 304) but only about 1 per cent at all the stations combined. The maximum abundance of *C. hyperboreus* is 45 per cent, but this is at a station where the total catch of copepods of all kinds was extremely scanty (7,500 copepods per square meter off Gloucester on April 9, 1920, station 20090). The vertical hauls for 1915 and 1920 afford only eight instances of *hyperboreus* in percentages as great as 15 per cent.

The numbers per square meter—counting only the stations at which it occurred—are as follows:

| Date | Average | Maximum | Minimum |
|---|---|---|---|
| February, 1920 | 583 | 1,125 | 25 |
| March, 1920 | 403 | 4,162 | 0 |
| April, 1920 | 804 | 9,100 | 0 |
| May, 1915, and May, 1920 | 2,561 | 20,575 | 0 |
| June, 1915 | 1,634 | 6,450 | 25 |

Evidently the numbers of *C. hyperboreus* existing in the gulf increase considerably from February to May and then decrease during June,[14] and later in the summer the species becomes so scarce that we have never found as many as 3,000 per square meter at any station [15] for July, August, September, or October, while none at all have been detected at most of the midsummer and autumn stations. The fact that *C. hyperboreus* has been detected at only about 10 per cent of the towing stations for July and August, notwithstanding its wide distribution at that season, contrasting with its presence at 80 to 100 per cent of the stations during March, April, May, and June (p. 212), is further evidence of its scarcity in the Gulf of Maine in summer. In 1915 it occurred at 10 per cent of the September stations and at one out of eleven stations east and north of Nantucket in October, while in December, 1920, and January, 1921, Dr. C. B. Wilson detected it at about one-third of the stations.

The regional distribution of the richer and scantier catches of *C. hyperboreus* proves interesting from the standpoint of the source of the local stock, whether endemic or immigrant. When the stations are plotted, where appreciably more than the average number per square meter for the respective months were taken, (fig. 69), it appears that during the season of maximum abundance for the species (March to June) it is usually most plentiful in three distinct localities—(1) in the Massachusetts Bay region and thence out to the western basin; (2) in the eastern side of the gulf from the northern channel (but not on Browns Bank) westward over the neighboring basin; and (3) along the southeast face of Georges Bank. In all other parts of the gulf, including the waters intervening between these "rich" centers—that is, all along the coasts of Maine, in the northeastern corner off the Bay of Fundy, in the central and southern parts of the basin, and over Georges and Browns Banks—*C. hyperboreus* has been uniformly much scarcer. Unfortunately the stages in development of the specimens taken in the vertical hauls, on which this chart is based, have not yet been determined; but such a distribution, coupled with the seasonal increase in the numbers of *C. hyperboreus* during the spring, would be presumptive evidence that the western center is a region of local production, drawing little from immigration but contributing to the stock in other parts of the gulf.

If such be actually the case, this would be by far the most southerly spawning ground for this species. Until Willey's (1919) account of the copepods of the Canadian fisheries expedition appeared, such a suggestion might have seemed highly improbable, *C. hyperboreus* having previously been known to breed only in the polar sea; but his discovery of young stages, besides adult females (but no adult males), in the gatherings at many localities in the Gulf of St. Lawrence, southeast of Nova Scotia, and along the continental shelf westward nearly to the longitude of Cape Sable, proved that the regular breeding range of this copepod extends much farther south along the American coast than it does off Europe. Willey has more recently reported adult males—previously known only from the far north—as well as adult females and younger stages at the mouth of the St. Croix River near St. Andrews,

[14] This statement is justified by the fact that the cruises for April, May, and June have covered the parts of the gulf most prolific in this species.

[15] Maximum for summer, 2,700 per square meter off Mount Desert Rock, Aug. 13, 1913, station 10100.

February 23, 1917 (Willey, 1921). He maintains that these individuals would not reproduce where found, but the presence of adults of both sexes of breeding age in

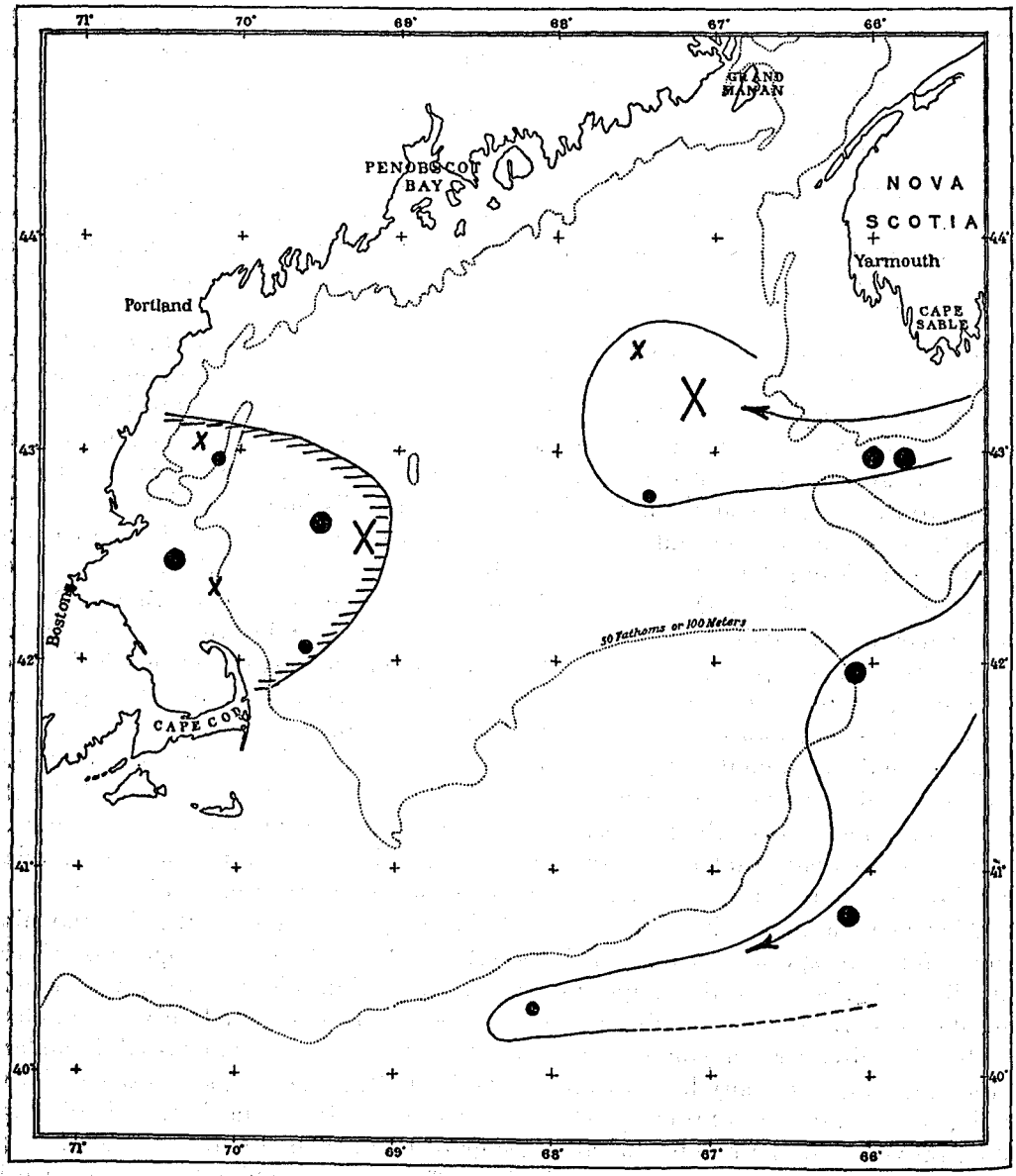


FIG. 69.—*Calanus hyperboreus.* ●, February to April stations with 50 per cent more than the average number per square meter for the respective months; X, May and June. The large symbols mark three times the average catch or more. The plain curves and arrows indicate the chief lines of migration; the hatched curve the probable site of local reproduction within the Gulf.

the Bay of Fundy becomes more suggestive of local breeding if taken in conjunction with the existence of a more or less isolated center of abundance for the species off

Massachusetts Bay, and makes the hypothesis that the latter is actually a center of local production worthy of consideration.

The two eastern centers are indicative of immigration, being continuous with the more abundant occurrence of the species to the eastward along the outer coast of Nova Scotia. More direct evidence that the comparatively rich gathering made off the slope of Georges Bank on March 12, 1920 (station 20069), was such a wave from the northeast is the fact that it was no more plentiful there a month later (station 20109), though at most localities its numbers had about doubled in the interim (p. 214).

It is, furthermore, entirely consistent with the probable flow of the currents in this region in spring that there should be a drift of *C. hyperboreus* from northeast to southwest along the continental edge and perhaps over the southern edge of Georges Bank during March and April, continuing into June in some years, but the evidence at hand suggests that few pass west of longitude 70° at any season. The large catches in the northern channel and the eastern basin in March, April, and May, contrasted with the scarcity of the species at all our Browns Bank stations irrespective of season, point to the former as the chief route by which *C. hyperboreus* enters the Gulf of Maine. If the data for the two years, 1915 and 1920, can fairly be combined, it would seem that there is comparatively little movement in this direction before the end of April; but with *C. hyperboreus* relatively much more plentiful in the northern channel on March 20 (station 20078), and again on April 15 (station 20105), than in the neighboring parts of the gulf, invasion only awaited the first considerable movement of water westward past Cape Sable, which occurs by the first half of May, for the richest catch of the species yet recorded in the gulf was made in the eastern side of the basin on May 6 (station 10270).[16] A comparatively large catch (about twice the average for the month) in this general region six weeks later (station 10288, June 19) may have been evidence of continued immigration throughout May and into June.

There is nothing in the records of the distribution of the species for summer or autumn to suggest that *C. hyperboreus* rounds Cape Sable in appreciable numbers later in the summer; but to find it doing so would not be surprising, for the stock existing along the outer Nova Scotian coast during the warm months fluctuates so widely from year to year that Esterly did not detect it at all in the *Grampus* tows between the cape and Halifax during the last week of July and first week of August in 1914, whereas Willey (1919) records a moderate representation of the species over the shelf generally nearly to the cape in August, 1915. Willey (1921) has explained the presence of *C. hyperboreus* at St. Andrews in the winter of 1917 as an invasion.

*Vertical distribution.*—*C. hyperboreus* occurs to some extent on the surface in the gulf in spring (table, p. 303), but more regularly deeper down, appearing in the lists for about 80 per cent of all the vertical hauls during this period but in only about 50 per cent of the surface hauls, though the latter filtered much larger volumes of water. Counting all the stations at which surface hauls were made in 1920 (table, p. 303),

[16] Doctor Wilson's analysis of the catch made in the vertical net at this station proves my earlier statement (Bigelow 1917, p. 292) that *C. hyperboreus* was rare or absent in this general region at the time, to have been incorrect.

there were only about 2 per cent of *C. hyperboreus*, less than half its percentage in the verticals. In the two instances when the percentage rose to 25 and 30 per cent, 500 and 150 copepods of all kinds were taken—that is, only 125 and 45 *C. hyperboreus*, respectively. It has been detected in only one surface haul in the gulf for July, August, or September—that is, off Cape Elizabeth on August 14, 1913 (station 10103; see Bigelow, 1915, p. 293), a locality where the surface temperature was comparatively high (16.11°) and where it was probably brought up to the top of the water by vertical currents. The date when it abandons the uppermost stratum can not be stated, no data being available on this for the May and June cruises of 1915, but probably its sinking is induced by the vernal warming of the surface water.

*Relationship to temperature and salinity.*—As might be expected from its polar origin, *C. hyperboreus* occurs in greatest number and is most regularly distributed in the gulf in comparatively low temperatures, the great majority of the spring (February to May) records being from temperatures of 1 to 5°. It is doubtful whether any of the specimens taken in June were actually living in water warmer than 7°, and most of the few captures in the later summer have been in horizontal hauls at depths where the temperature ranged from 4.8 to 8°, only one of them in the much warmer surface stratum. The highest temperatures in which the presence of *C. hyperboreus* is definitely established, apart from the one capture on the surface just mentioned (p. 217), are 9 to 10°,[17] a temperature in which probably it could not long survive.

If *C. hyperboreus* actually does succeed in breeding in the western side of the gulf in spring and early summer, probably it does so exclusively in temperatures lower than 3 to 4°, the range of temperature at the rich March and April stations (stations 20087 and 20090, fig. 69) being from 2.25 to 5.09°, and the comparatively large numbers taken there on June 26, 1915 (station 10299), may be explicable as resulting from spawning some weeks or months previous when the temperature was no higher than that. The richest immigrations of *C. hyperboreus* into the gulf so far encountered have been in temperatures falling between 1.9 and 4.6°. It is not probable that the distribution of *C. hyperboreus* is influenced by variations in salinity within the limits prevailing in the open waters of the Gulf of Maine.

### Candacia armata Bœck

This large and powerful species may be recognized by the asymmetry of the posterior part of the body, the genital segment being irregularly dilated in the middle, and the first segment of the abdomen having a sac-shaped dilatation turned toward the right side. The frontal margin between the bases of the antennæ is squarely truncated, also. It has been recorded from the coast of Norway, the British Isles, the Mediterranean, the North Atlantic, and the Indian Ocean (Scott, 1911), while Esterly[18] (1905, p. 194) described it as "rather common" at San Diego, Calif. The

[17] Off Penobscot Bay, Aug. 4, 1913, station 10101, temperature at 50 meters about 9.3°; off Seal Island, Nova Scotia, Sept. 2, 1915, station 10311, whole column of water, surface to bottom, 9.4 to 10.1°; off Machias, Me., Oct., 9, 1915, station 10327, whole column 9.4 to 9.8°.

[18] As *C. pectinata* Brady.

*Grampus* had it in fair numbers at three stations along the outer edge of the continental shelf south of Delaware Bay and off Delaware Bay in July and August, 1913, in hauls from about 40 meters' depth (Bigelow 1915, p. 287). Wheeler (1901) reported a considerable number of specimens of both sexes (as *C. pectinata* Brady) from the "Gulf Stream," 70 miles south of Marthas Vineyard, on July 25 and 29, 1899, and Willey (1919) counted two specimens among 100 copepods off the mouth of the Laurentian channel between the Scotian and Newfoundland banks on June 1, 1915, at a temperature of 10.2 to 13.75° and salinity of upward of 35 per mille. It did not appear in any of the collections made by the Canadian fisheries expedition on the banks or in the Gulf of St. Lawrence, nor did Herdman, Thompson, and Scott (1898) report it between the Straits of Belle Isle and Liverpool.

*Candacia armata* has not been reported from the Gulf of Maine previously, but Doctor Wilson lists it at two stations outside the continental edge on March 14 and May 17, 1920 (stations 20077 and 20129); also in the eastern part of the basin of the gulf on March 3 (station 20053) and on German Bank on April 15 (station 20103), from vertical hauls (table, p. 299). It likewise appears in one vertical haul in the eastern part of the basin for May, 1915 (station 10270), one off Cape Elizabeth for September (station 10319), and one off Cape Cod for October of that year (station 10336; table, p. 297), but not in any of the surface hauls.

The general geographic range of the species, as summarized above, and its distribution in British waters, where it is most plentiful in the English Channel and penetrates the northern part of the North Sea from the north around Scotland, point to an oceanic origin for the occasional specimens taken in the Gulf of Maine. The localities of record bear this out, being grouped in the eastern side and near shore in the western (fig. 62), like other visitors from the open basin, with no records in the western basin or from Georges Bank. It is a decidedly rare species in the gulf, usually amounting to 1 per cent or less of the copepods, only once reaching 4 per cent, and it is not likely that it is endemic there.

### Centropages bradyi (Wheeler)[20]

Dr. C. B. Wilson, in a letter, describes it as "fairly common on the Atlantic coast off the mouth of Chesapeake Bay." Wheeler (1901) obtained both sexes in the Gulf Stream, 70 miles south of Marthas Vineyard, in July. Willey (1919) lists it at three stations outside the continental edge, along the inner edge of the Gulf Stream, off Cape Sable, and off Sable Island in July, 1915, and Esterly (1905) records it from San Diego, Calif.

This species has not been recognized previously in the Gulf of Maine, where it is to be expected only as a straggler from warmer waters offshore. In 1920 it was noted in one vertical haul off Cape Cod for March and one off Gloucester in May (table, p. 299); in 1915 occasional specimens were noted in the eastern basin on June 14 and near Cape Elizabeth on September 20 in vertical hauls. The numbers of specimens concerned are in each case minimal, 1 per cent being the maximum frequency.

[20] This name was given by Wheeler (1901, p. 174) to the species figured by Brady (1883) as *C. violaceus* Claus, but which, as Giesbrecht (1892) pointed out, is quite distinct. It is readily distinguished from the other two species of the genus mentioned here by lacking spines at the posterior corners of the thorax.

**Centropages hamatus (Lilljeborg)**

This species is so far known from the North Atlantic area between the latitudes of 40° N. and 70° N. (Scott, 1911), including the North Sea and the Baltic—most commonly within a moderate distance of the coast. Sars (1903) describes it as common along the whole west and south coasts of Norway, and, according to Scott (1911, p. 106), it is "one of the more common of the Calanoida met with in the North Sea."

On the American side it did not appear in the towings made south of New York during the summer of 1913 (Bigelow, 1915, p. 287) or 1916, but was taken off that port on August 26, 1916 (station 10394; Bigelow, 1922, p. 146), and near the Long Island shore on August 1, 1913 (station 10083), which, so far as I can learn, are the most southerly records for it along the United States coast. Northward it becomes more plentiful. Williams (1906) found it in Narragansett Bay in January and February, and it is "nearly always present in the tow at Woods Hole, in Vineyard Sound, and in the Gulf Stream south of Marthas Vineyard," writes Dr. C. B. Wilson.[21] Wheeler (1901) also records it as nearly always present in considerable numbers at Woods Hole. Its range includes the Gulf of Maine, as described below. Willey (1919) found it at many localities on the banks and over the deep intervening channel between Nova Scotia and Newfoundland in May, 1915, but not at the more oceanic stations, and restricted to the immediate vicinity of the Nova Scotian coast in July. It is widespread and plentiful in the shoaler parts of the Gulf of St. Lawrence (T. Scott, 1905; Willey, 1919), and Herdman, Thompson, and Scott (1898) report it from the Labrador current off the Straits of Belle Isle out to longitude about 53° W., and again between longitude 28° 24′ W. and the coasts of Great Britain, but not over the intervening stretch of ocean.

*Gulf of Maine.*—*C. hamatus* appears only twice in the published lists of Gulf of Maine copepods from the *Grampus* cruises—viz, occasional specimens off Boothbay on July 26, 1912 (station 10016), and off Cape Porpoise on August 18 of the same year (Bigelow, 1914, pp. 115, 116). It was not taken in the vertical hauls during June, 1915, and at only two of the four August stations (table, p. 298), proving it decidedly uncommon in the open waters of the Gulf during the summer, though it may be more plentiful in estuarine situations, where we have made few hauls. It appeared in about 60 per cent of the September verticals for 1915 (Willey (1919) lists it for 3 out of 10 stations near St. Andrews during that month), and it occurred at about half the October stations in the gulf east and north of Nantucket that year, off Gloucester on October 31 (station 10399) and off Cape Cod on November 8 in 1916 (station 10404; Bigelow, 1922, p. 135). No information is available as to its local status in November; but the fact that it occurred at about 50 per cent of the midwinter stations for 1920 and 1921 (table, p. 304) points to its constant and widespread presence throughout autumn and early winter. It was detected in only 2 of the 80 vertical hauls made in various parts of the gulf during the spring season of 1920 (table, p. 299), and there were less than 100 per square meter in every case.

During the month of October in 1915, *C. hamatus* averaged about 9,000 per square meter at the several stations where it occurred to the eastward and northward of

[21] In a letter.

Nantucket, and 7 per cent of the total catch of copepods; but it was much more plentiful, relatively as well as absolutely, in the shoal water south of Marthas Vineyard on October 21 and 22 (stations 10331 to 10333), with 12,240 to 58,500 per square meter (constituting 6 to 25 per cent of the total copepods), and was most numerous at the station closest to the land.

Numerical data as to the occurrence of *C. hamatus* are not available for the early winter, but it formed about the same proportion of the catches in the inner parts of the gulf (2 to 16 per cent, averaging 6 to 7 per cent), at the stations where it occurred in December, 1920, and January, 1921, as in autumn. It has never amounted to more than 1 to 2 per cent of the copepods at any station from February to the middle of September, nor has it been more numerous than about 4,000 per square meter. Obviously this suggests that *C. hamatus* is definitely seasonal in the gulf, occurring with some regularity from September until January but only very sparsely from February until August. Thus, even at the season and in the zone of its greatest abundance, *C. hamatus* is but a minor element in the copepod population of the gulf.

The regional distribution of the captures (fig. 70) is interesting, nearly all being near shore and the majority within a few miles of land, with not a single record anywhere in the central and southern parts of the basin or on Georges or Browns Banks. Although *C. hamatus* occurs across the whole breadth of the continental shelf off southern New England, on the one hand, and from Cape Sable eastward, on the other, its geographic range within the Gulf of Maine[22] has so far proved neritic, as contrasted with oceanic, and closely parallels that of the neritic medusæ (p. 33).

No observations have been made on the breeding of *C. hamatus* in the gulf, but the abundance of developmental stages of copepods of some sort during August and the first half of September, preceding the increase that takes place in the number of adults of this species and of its ally, *C. typicus*, during the last half of September, suggest that both of these species are regularly endemic in the gulf. If this be the case it breeds in comparatively high temperatures, stated tentatively as upwards of 7° in the gulf because of its neritic distribution, chiefly in salinities lower than 32.5 per mille.

### Centropages typicus Krøyer

This species is described by T. Scott (1911) as a true Atlantic form, estuarine as well as oceanic. In the eastern Atlantic it occurs from the Mediterranean to northern Norway, being one of the common species in the North Sea region generally, where it often occurs side by side with *C. hamatus;* but it has not been reported from Arctic seas. In the western North Atlantic it has been found on the Louisiana coast of the Gulf of Mexico (Foster, 1904) and occurred commonly over the continental shelf as far south as the mouth of Chesapeake Bay during the summers of 1913 and 1916—was, in fact, the commonest copepod at many of the stations but chiefly in the uppermost stratum of water, as I have described in earlier reports (Bigelow, 1915, p. 293, and 1922, p. 146).

In July, 1913, the *Grampus* took it abundantly off New York, and although Williams (1906) does not list it from Narragansett Bay, Wheeler (1901, p. 173)

[22] Also plentiful in the eastern side of the basin on August 20, 1926.

describes it as "nearly always present in small numbers in the tow taken from the Fish Commission's wharf at Woods Hole and in the neighboring Vineyard Sound."

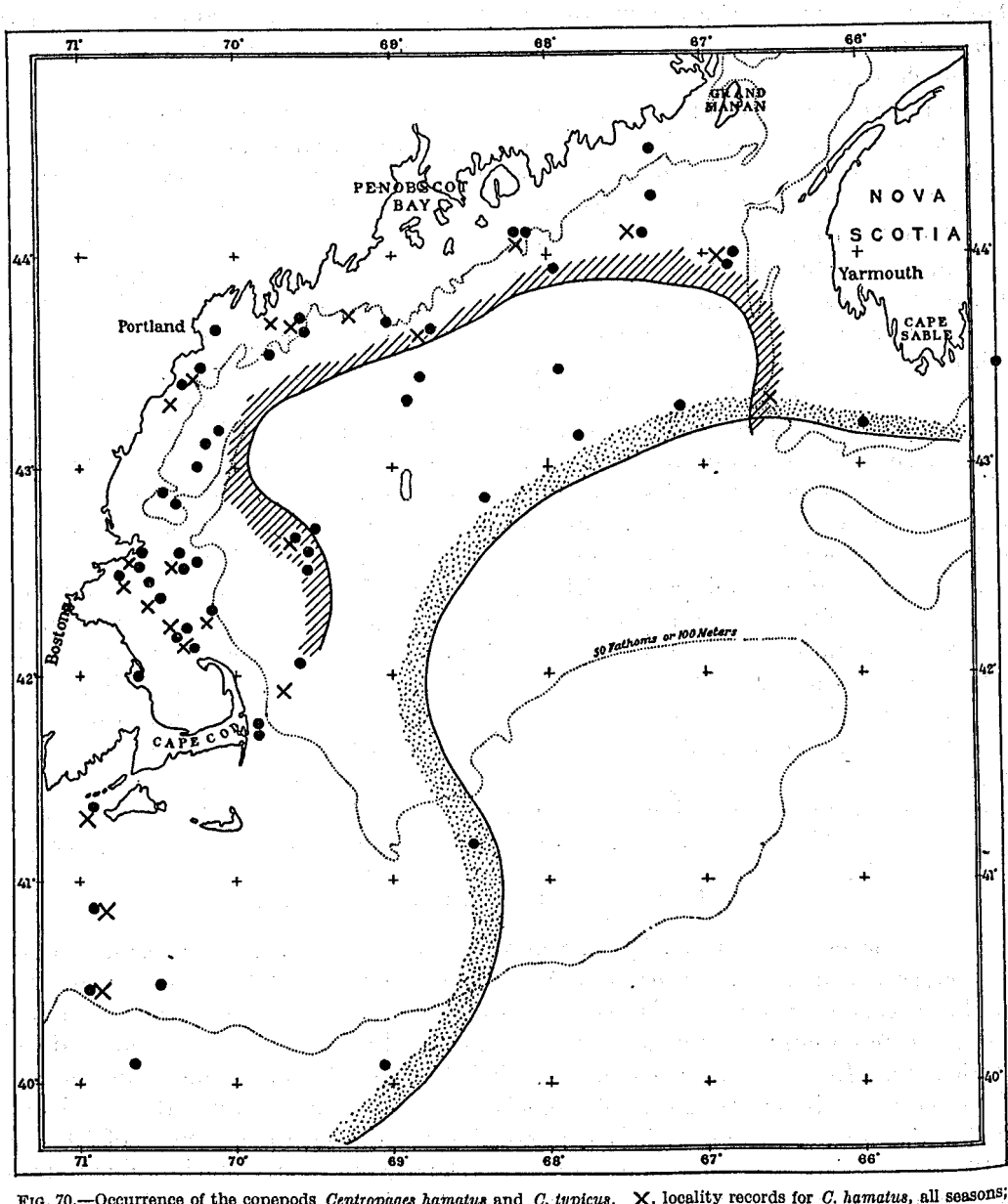


FIG. 70.—Occurrence of the copepods *Centropages hamatus* and *C. typicus*. ×, locality records for *C. hamatus*, all seasons; ●, locality records for *C. typicus*, all seasons. The hatched curve incloses the chief zone of occurrence for *C. hamatus* within the Gulf; the stippled curve for *C. typicus*

It occurred abundantly also in the Gulf Stream 70 miles south of Marthas Vineyard. Fish (1925) also took it regularly at Woods Hole.

On July 10, 1913 (station 10062), it swarmed near the 100-meter contour off Marthas Vineyard, and again on October 21 and 22, 1915, it occurred right across the whole breadth of the continental shelf off Marthas Vineyard, most abundantly near shore (see table, p. 298, stations 10331 to 10333), all of which proves it as widespread out to the continental edge off southern New England as it is farther south.

*C. typicus* has proved to be a decidedly more important member of the plankton of the Gulf of Maine than is its relative, *C. hamatus*, as is described below; but Cape Sable evidently marks the most northerly and easterly limit to its regular occurrence along the North American coast line, for it does not appear in Willey's (1919) lists of copepods collected on and along the slopes of the Nova Scotian and Newfoundland Banks and in the intervening deeps. The *Grampus* did not find it between Cape Sable and Halifax that same summer. It has not been reported from the Gulf of St. Lawrence, nor did Herdman take it west of longitude about 28° W. on his two traverses of the North Atlantic between Liverpool and the St. Lawrence River. Comparison with the known range of *C. hamatus* shows *C. typicus* to be the more southerly of the pair by about 7° of latitude, in terms of its northern boundary.

*Gulf of Maine.*—When the locality records for *C. typicus* in the Gulf of Maine are expanded to include Georges Bank [23] (fig. 70) there is no evident concentration in the western side or in the eastern.

It is reported from Plymouth Harbor by Wheeler (1901) and from St. Andrews by Willey (1919); hence it would no doubt be found in similar estuarine situations all along the intervening coastline. Apparently it is never plentiful as far east as the shallows west of Nova Scotia and perhaps never reaches Browns Bank or the eastern part of Georges, and one record close to land off Shelburne, Nova Scotia, September 6, 1915 (station 10313), is, so far as I can learn, the most easterly known outpost of the species on the Atlantic coast of North America. The preponderance of records in the inner parts of the gulf, as contrasted with the basin, accords with a nature more neritic than oceanic (p. 35). In fact, its distribution east and north of Cape Cod closely parallels that of the hydromedusa *Phialidium languidum* p. 350); but this applies only to the most northerly part of its range, for off southern New England and thence southward it occurs generally right out to the continental edge.

*Seasonal fluctuations.*—In its seasonal ebb and flow in the gulf, *C. typicus* closely parallels *C. hamatus*. Thus it was so rare during the spring quarter, as exemplified by the February to May cruises of 1920, that it was detected in only 6 out of 81 vertical hauls (about 7 per cent); it appeared in but one May haul in 1915 and not at all in June. Furthermore, the numbers of specimens concerned have invariably been small on the few occasions when *C. typicus* has figured in the spring lists. On the western part of Georges Bank (February 23, 1920) it constituted 18 per cent of the copepods, but the total number was so small that this percentage amounts to only about 325 *C. typicus* per square meter. The maxima during the February to June period are 2,625 per square meter in the western basin on February 24, 1920 (station 20049), and 4,115 in the eastern basin on May 6, 1915 (station 10270, see tables, pp. 297 and 299), with less than 300 per square meter at the few other stations of record for these months.

[23] Also dominant over northern and eastern parts of Georges Bank, at the surface, August 7, 1926.

There are only two records of *C. typicus* in the gulf in July—one off Cape Elizabeth on the 29th (station 10019) and the other in Casco Bay on the 31st (station 10020)—both in 1912. The records point to a notable increase in August, when it occurred at 23 per cent of the stations (7 out of 31) in 1912, 40 per cent (8 out of 20) in 1913, and at 2 out of 11 in 1914. It is most regularly distributed in the gulf during autumn and early winter, occurring at 60 per cent of the September stations and 66 per cent of the October stations in 1915 and at about 60 per cent of the stations for December, 1920, and January, 1921. The local abundance of the species, as well as the generality of its distribution, likewise increases during late summer and autumn, mounting to an average of about 1,000 per square meter for August, 1913 (counting only the stations where it is actually recorded east and north of Nantucket), about 5,300 for September, 1915 (maximum 18,200 in Massachusetts Bay on the 29th), and to about 8,637 during that October (maximum 24,450 in Massachusetts Bay on the 27th). Off Marthas Vineyard on October 22, 1915, the numbers per square meter ranged from about 58,400 near shore (station 10331) to slightly more than 12,000 on the outer part of the continental shelf (station 10333). Even at its season of maximum abundance, *C. typicus* is usually a minor element in the plankton of the gulf, averaging only 7 to 9 per cent of the total copepod population at the stations where it occurred in September and October, 1915 (table, p. 298). Occasionally, however, it may dominate locally near shore—witness 40 per cent of this species in Massachusetts Bay on September 21 of that year (station 10321)—but probably this never happens out at sea in the gulf.

*C. typicus* constituted so small a percentage (1 to 8 per cent) of the scanty catches of copepods made during the December and January cruise of 1920 and 1921 as to suggest a shrinkage in its numbers during the late autumn.

The numbers of *C. typicus* present per square meter are further interesting as proving the Massachusetts Bay region generally and the waters off Cape Cod its chief centers of abundance in the gulf during the late summer and autumn. In late winter and spring the largest catches have been made in the western and eastern sides of the basin—2,600 per square meter at the former locality on February 23, 1920 (station 20049), and 41,100 per square meter near German Bank on May 6, 1915 (station 10270). It is also worth noting that this last was the richest catch of *C. typicus* that has ever been recorded east of Nantucket, though at a time of year when the species occurs only irregularly in the gulf and usually in very small numbers.

*Breeding.*—No observations have been made on the breeding of this species in the gulf, but the fact that its chief center of local abundance lies off Massachusetts Bay, whereas summer immigrants, whether of northern or of Tropic origin, enter chiefly via the eastern side, is strong evidence that the stock is maintained by local reproduction, aided little, if at all, by immigration. The presence of this species within the gulf throughout the year tends to corroborate this. Seasonal fluctuations point to summer as the chief breeding season, as does the fact that in 1915 the autumnal multiplication of *C. typicus* and *C. hamatus* was preceded by an abundance of larval copepods of some sort (see table, p. 298). With only one period of abundance annually, and that well-marked in contrast to the scarcity of the species during the other months, it is safe to assume one chief breeding period for it yearly.

*Vertical distribution.*—In an earlier report (Bigelow, 1915, p. 293) I have noted that west and south of Cape Cod, *Centropages typicus* is most abundant near the surface, citing as noteworthy examples of this one station (10088) where the surface haul yielded ten times as many specimens as the haul from 80 fathoms, though made with a net of only one-sixth the mouth area, and another (10083) where the surface haul brought in several hundred *C. typicus* and the haul from 20 fathoms only one specimen. Our largest catches of the species have also been on the surface, where it swarmed off Marthas Vineyard on July 10, 1913 (station 10062), and at 15 fathoms off New York on July 12 (station 10066).

Observations of this same tenor were made in the Gulf of Maine during August, 1912, *C. typicus* amounting to about 40 per cent of the copepods at the surface at station 10041 but not over 2 per cent at 40 meters; about 60 per cent at the surface and not found at all at 30 meters at station 10042. At a third station for that month (in Massachusetts Bay, station 10044) it and *C. finmarchicus* each constituted 50 per cent of the copepods on the surface. Our few records for it north of Cape Cod in August, 1914, are also from surface hauls; and while it has figured in a considerable number of hauls at various depths in one year or another, it has never been more than a trifling percentage of the copepod catch in the deeper horizontals, and rarely in the verticals (p. 225). Failure to take it in the surface hauls during the spring of 1920 (table, p. 303) is not necessarily significant in this connection, the species being so rare at that season that it might have been missed by the nets. Consequently it may be classed as typically a surface form in the gulf, most plentiful above 20 meters and perhaps never sinking as deep as 100 meters. It is likewise most numerous near the surface in north European seas.

*Relation to physical conditions.*—In different seas *C. typicus* occurs over a wide range of temperature and salinity. Along the Atlantic seaboard of North America its presence is established in water as warm as 24.4° (Bigelow, 1915, p. 293) and as cold as 3.05° (station 20104, April 15, 1920). It did not occur in the coldest waters of the gulf, for example in the inner part of Massachusetts Bay, at the season of minimum temperature, and the locations of the few early spring records suggest either that it tends to withdraw from the coastal waters as the latter chill or that the specimens living there perish, leaving only those that are in the parts of the gulf less subject to winter cooling to survive the cold season. The fact that the species did not appear in the surface hauls for March or April suggests that *C. typicus* may sink in the deeper parts of the gulf as the surface chills. In the western basin, for instance, where this copepod was comparatively numerous on February 23, 1920 (station 20049), it might have been in temperatures anywhere between 5.6° and 2.8°, according to the precise depth at which it was living.

However this may be, *C. typicus* increases notably in abundance about when the upper 20 meters or so have warmed to the maximum annual temperature, and the tendency of the species to keep near the surface makes it safe to set 8° to 10° as the lower limit to its active multiplication in the gulf. In autumn it is probable that its numbers fall off after the upper 20 meters have chilled appreciably below this figure, which, speaking broadly and for the gulf as a whole, takes place some time during November.

The salinities of the open waters of the Gulf of Maine lie so far inside the limits within which *C. typicus* has been found abundantly in other seas that this is probably not an important factor in its local distribution horizontally or vertically. Certainly no part of the gulf can ever be too salt for an animal occurring regularly in salinities of upwards of 35 per mille in European seas. Toward the other extreme, *C. typicus* is common in salinities of 31 to 32 per mille at Woods Hole, and one of our largest catches was in water of about 31.5 per mille (on the surface off New York, July 12, 1913, station 10066); but the fact that this species is apparently absent from the Baltic makes it probable that it is more susceptible to low salinity than its relative, *C. hamatus*, which is generally distributed there, and thus suggests that the very lowest salinities of the surface along shore in the gulf (below 30 per mille) at the time of the spring freshets may be unfavorable for it.

### Dactylopusia thisboides (Claus)

The known distribution of this harpacticoid [24] includes Franz Josef Land, Bear Island (south of Spitzbergen), the north and west coasts of Norway, the British and French coasts, Mediterranean, Red Sea, and Woods Hole, Mass., where Sharpe (1911) collected it among algæ on sandy bottom in about 2 fathoms of water in July, the latter being the only previous American record. It is also reported from Kerguelen in the southern Indian Ocean, from the collections of the German South Polar Expedition (Brady, 1910), but until these southern specimens are described it remains doubtful whether they are actually identical with the northern form. Brady (1878–1880) dredged this species in all kinds of situations, from brackish water, on the one hand, out to depths of 40 fathoms, on the other, among weeds on bottom; but it has been found only close to land and is not usually planktonic.

At St. Andrews, where the stirring of the water by violent tides is probably responsible for bringing it up to the top, Doctor McMurrich lists a few specimens on one occasion only—a tow at 7 fathoms on April 5. This record is interesting as extending its known range to the littoral zone of the Gulf of Maine, but it is hardly to be expected in the plankton of the open sea there.

### Dwightia [25] gracilis (Dana)

This species is widespread in the warmer parts of all three great oceans. In the Atlantic it has been taken at various localities from latitude 36° 44′ S. to latitude 52°27′ N. (west of Ireland) in the east, and northward to the Gulf of Maine in the west, most frequently in the tropical zone between latitudes 10° S. and 30° N. It also occurs far and wide in the Mediterranean (Thompson and Scott, 1903). In the Red Sea, Arabian Sea, Indian Ocean down to the latitude of the Cape of Good Hope, and among the Malay Archipelago it has been reported from so large a proportion of tow nettings that it can be described as universal (Thompson and Scott, 1903; Cleve, 1901, 1903; and A. Scott, 1902, 1909); and the German South Polar Expedition had it at Kerguelen and even farther south (Brady, 1910; Wolfenden, 1911).

[24] This has been summarized, with quotation of authorities, by Sars (1903–1911) and Sharpe (1911).

[25] C. B. Wilson (1924), finding that the generic name Setella, by which this species has long been known, was preoccupied by Schrank in 1902 for a genus of Lepidoptera, has proposed Dwightia in its place.

In the Pacific it has been described from north of Papua, the Philippines, Straits of Sunda, the China Sea, north of the Hawaiian Islands, and other localities between latitudes 32° S. and 30° 22′ N. (see Giesbrecht, 1892, and Brady, 1883, for lists of Pacific records), but it does not appear in Esterly's (1905 and 1911) lists of the copepods of the San Diego region.

The geographic distribution of this species is thus tropical and warm temperate. The only previous records of *Dwightia gracilis* off the North American coast are from the "Gulf Stream," 70 miles south of Marthas Vineyard, where many were taken on July 25, 1899 (Wheeler, 1901, p. 188), and Woods Hole (Fish, 1925). Dr. C. B. Wilson's lists add seven records for the Gulf of Maine (table, p. 297) and one near Shelburne, Nova Scotia (station 10291). In the gulf, *D. gracilis* is to be regarded as an immigrant of southern-oceanic affinity, and, correspondingly, most of the locality records for it, like those for the two species of Rhincalanus and for Scolecithricella, are in the peripheral belt near the eastern, northern, and western shores. Being for the months of March, April, June, October, and December, they show that it is to be expected in the gulf at any time of the year; but since all five of the records from within the gulf have been based on odd specimens (three at station 20063 were the most specimens noted in any one haul inside of Georges Bank), either the immigrations into the gulf are in very small numbers and at rare intervals or such as do enter survive only for a brief period in the low temperatures to which they are subjected there. A somewhat larger catch (about 140 per square meter) was made on the southeastern part of Georges Bank on March 12, 1920 (station 20063). It may be taken as certain that this copepod appears in the gulf only as an immigrant, never breeding there.

In tropical seas this species has been taken repeatedly on or close to the surface, and the Gulf Stream specimens described by Wheeler (1901) were also, presumably, from the surface; but it has not been found in any surface haul in the Gulf of Maine, all the records there being from open-net hauls, vertical and horizontal, from depths ranging from 30–0 to 190–0 meters. Apparently it is more apt to enter the gulf at least some few meters down and to remain there as long as it survives in its journeyings in the gulf. But for it, as for Scolecithricella (p. 285) and for the two species of Rhincalanus (p. 283), the preponderance of captures near the coast of the gulf points to the upper 50 to 100 meters, where the counterclockwise Gulf of Maine eddy is most active, as the stratum in which it chiefly drifts. The chart for Rhincalanus, Scolecithricella, and Dwightia (fig. 72) is a graphic illustration of the tendency of natural flotsam of any kind, entering the eastern side of the gulf from the oceanic basin offshore, above, say, 100 meters, and keeping at or above that level, to circle its periphery, leaving its central basin bare.

### Ectinosoma neglectum G. O. Sars

This harpacticoid is described by Sars (1903–1911) as abundant along the southern and western coasts of Norway, usually in 10 to 20 fathoms on muddy bottom. He also records it from polar islands north of Grinnell Land, and Willey (1920) mentions it from the Arctic coast of Canada. Apparently it is strictly a boreal–Arctic species. I find no previous record of it on the east coast of North America, but

Doctor McMurrich (in his plankton lists, see p. 12) lists a few at St. Andrews on January 23 and again on January 26, 1916. Probably it becomes pelagic only by accident in tide-swept situations.

### Eucalanus attenuatus Dana

This species is widely distributed in the warmer parts of the Atlantic, Pacific, and Indian Oceans, and in the Mediterranean. In the northeastern Atlantic it has been taken as far north as the Faroe Channel. Wheeler (1901) records one specimen from the Gulf Stream off Woods Hole; our outermost station (10218) off the continental edge south of Georges Bank yielded a few in hauls from 60–0 and 300–0 meters on July 21, 1914; and Willey (1919) records it in equally small numbers from about the same position, relative to the continental slope, off Cape Sable on July 22, 1915.

In the Gulf of Maine it occurs very rarely, only as a stray from the oceanic waters of the Atlantic Basin. Its name does not appear at all in the summer lists for the years 1912 to 1914, or during the months of February and March, 1920, or May, 1915; but there is record of it in small numbers (1 to 2 per cent of the copepods) in Massachusetts Bay on April 6 (station 20089) and on May 4 (station 20121), and on German Bank on April 15 (station 20103), all in 1920. In 1915 odd specimens appeared in the vertical hauls in the Fundy Deep on June 10 (station 10282), in and off Massachusetts on September 29 and October 1 (stations 10321 and 10323), and finally off Penobscot Bay on January 1, 1921 (station 10496). When these locality records are plotted in connection with those of its genus mate, *E. elongatus* (fig. 71), they point to immigration into the eastern side of the gulf and around its northern shore to the Massachusetts Bay region, which is the route followed by most of the planktonic immigrants. It is evident from the dates just given that *E. attenuatus* may stray into the gulf at any time of the year, but it is not likely that it is ever able to establish more than a temporary footing there.

### Eucalanus elongatus Dana

This species, described by Farran (1911, p. 93) as "characteristic of the warm seas of the open ocean," has been recorded from sundry widely separated localities in the tropical parts of the Pacific and Indian Oceans, in the Mediterranean, and in the south and north Atlantic. According to Farran (1911) it occurs the year round in the Atlantic as far north as the coasts of Ireland, while Wolfenden (1904) describes it as abundant in the Faroe Channel and not uncommon in the fjords of Shetland, and the plankton lists of the International Committee for the Exploration of the Sea show that it is frequently carried round the north of Scotland into the North Sea and even to the Skager-Rak. Not being known from the Norwegian sea farther north, its northern limit, as Wolfenden remarks, is well defined. Wheeler (1901) did not find it in the Gulf Stream gatherings taken off Marthas Vineyard, but more recently we have taken it at three stations over and seaward from the southwestern part of Georges Bank (July 21, 1914, station 10218, and February 23, 1920, stations 20044 and 20045); also off the southeast face of the same bank on March 12 (Station 20069) and in the eastern channel on April 16 (station 20107),

proving it to be of general occurrence in the oceanic water outside the continental edge abreast of the gulf in winter as well as in summer. It was in sufficient numbers at the three spring stations (approximately 500, 1,000, and 3,800 per square meter) to show that it may locally attain a fair degree of abundance at that season. Willey (1919) also reports it in small numbers from one station outside the continental edge off Cape Sable on July 22, 1915.

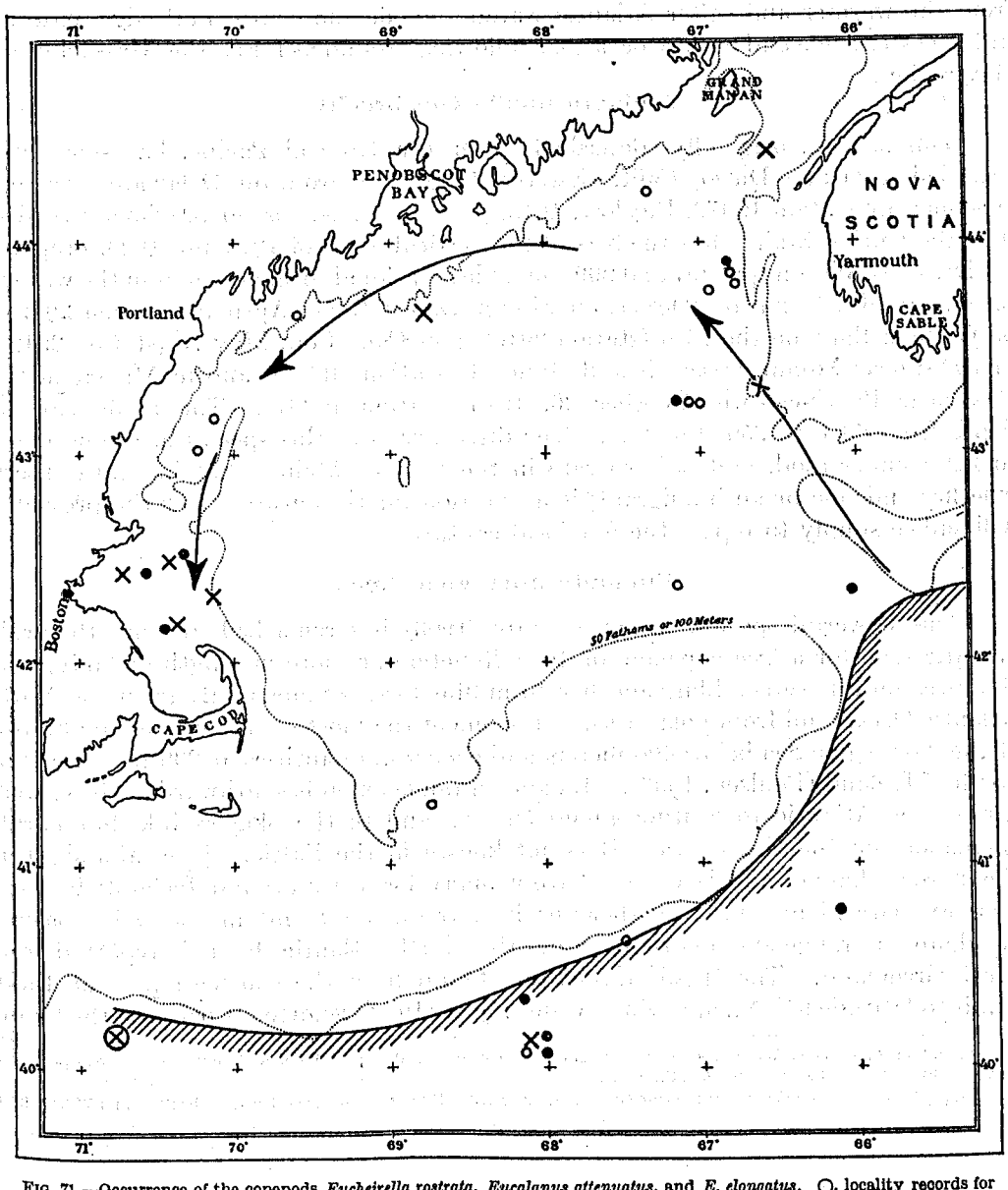


FIG. 71.—Occurrence of the copepods *Eucheirella rostrata*, *Eucalanus attenuatus*, and *E. elongatus*. ○, locality records for *Eucheirella rostrata*: ×, locality records for *Eucalanus attenuatus* (⊕, approximate location of Wheeler's record); ●, locality record for *E. elongatus*. The arrows mark the chief route of immigration into and around the Gulf; the hatched curve, the inshore boundary to the area of regular occurrence for all three of these copepods.

Only five captures of this species are recorded from the inner parts of the gulf (fig. 71), as follows: Massachusetts Bay region, August 22, 1914 (station 10253), and September 29, 1915 (stations 10320 and 10321); eastern basin, May 6, 1915 (station 10270); and off Lurcher Shoal, April 12, 1920 (station 20101). In each case the record is based on occasional specimens only.[26]

*Eucalanus elongatus*, like *E. attenuatus*, is only a rare stray in the Gulf of Maine from the warmer and salter Atlantic waters outside the continental edge, entering in the eastern side and on rare occasions following around as far as the Massachusetts Bay region.

### Euchæta media Giesbrecht

This species, originally described from the tropical Pacific, has since been recorded from San Diego, Calif. (Esterly, 1905), and from off Delaware Bay (one specimen at station 10072, Bigelow, 1915, p. 287). There is no previous record of it in the Gulf of Maine, but the lists of the vertical hauls of 1915 and 1920, prepared by Dr. C. B. Wilson (pp. 297 and 299), include occasional specimens of it in the western basin, March 24 (station 20087); off Mount Desert Rock, April 10 (station 20098); on German Bank on the 15th (station 20103); off Cape Cod, May 16 (station 20125) in 1920; near Mount Desert Island, June 11 (station 10284); and in Massachusetts Bay near Provincetown, October 26, 1915 (station 10337). The hauls vary in depth from 60–0 to 250–0 meters. The distribution of this species in the oceans is so little understood, and it is so rare in the Gulf of Maine, that its status there, whether endemic or an immigrant, is a question for the future. For the present it will suffice simply to report the few local captures.

### Euchæta norvegica Bœck

This powerful species, which, as Sars (1903) has remarked, reaches the truly gigantic size, for a free copepod, of 10 millimeters or more in length of body, with the furca and its setæ adding another 10 millimeters, is known only from the North Atlantic Ocean and from polar seas. It is one of the most characteristic inhabitants of the Norwegian Sea below 400 meters and occurs in quantities at 200 to 400 meters north of Iceland (Paulsen, 1906). Its known range extends southward in the eastern side of the Atlantic to latitude about 50° N., and to the Skager-Rak, but hardly encroaches on the North Sea. It is not known in the Baltic. It is abundant in the Faroe Channel and is recorded from many localities around Iceland; between Norway, Greenland, and Spitzbergen; in Barents Sea; and in the polar basin.[27] No doubt its range extends right across the North Atlantic, for it is reported from West Greenland. The Ingolf Expedition found it in the southern part of Davis Strait to latitude 65° N., and Murray and Hjort (1912) reported it between the Grand

[26] At station 20101 Doctor Wilson lists it as 1 per cent of the copepods (table, p. 301), but with only about 550 copepods of all kinds caught in the net there were but 6 of this species.

[27] For further details and references see Farran (1911), Sars (1900, 1903), Damas and Koefoed (1907), With (1915), and Willey (1920).

Banks of Newfoundland and Flemish Cap.[28] *E. norvegica* is widespread in the Gulf of St. Lawrence, in the deep oceanic triangle between the Scotian and New-

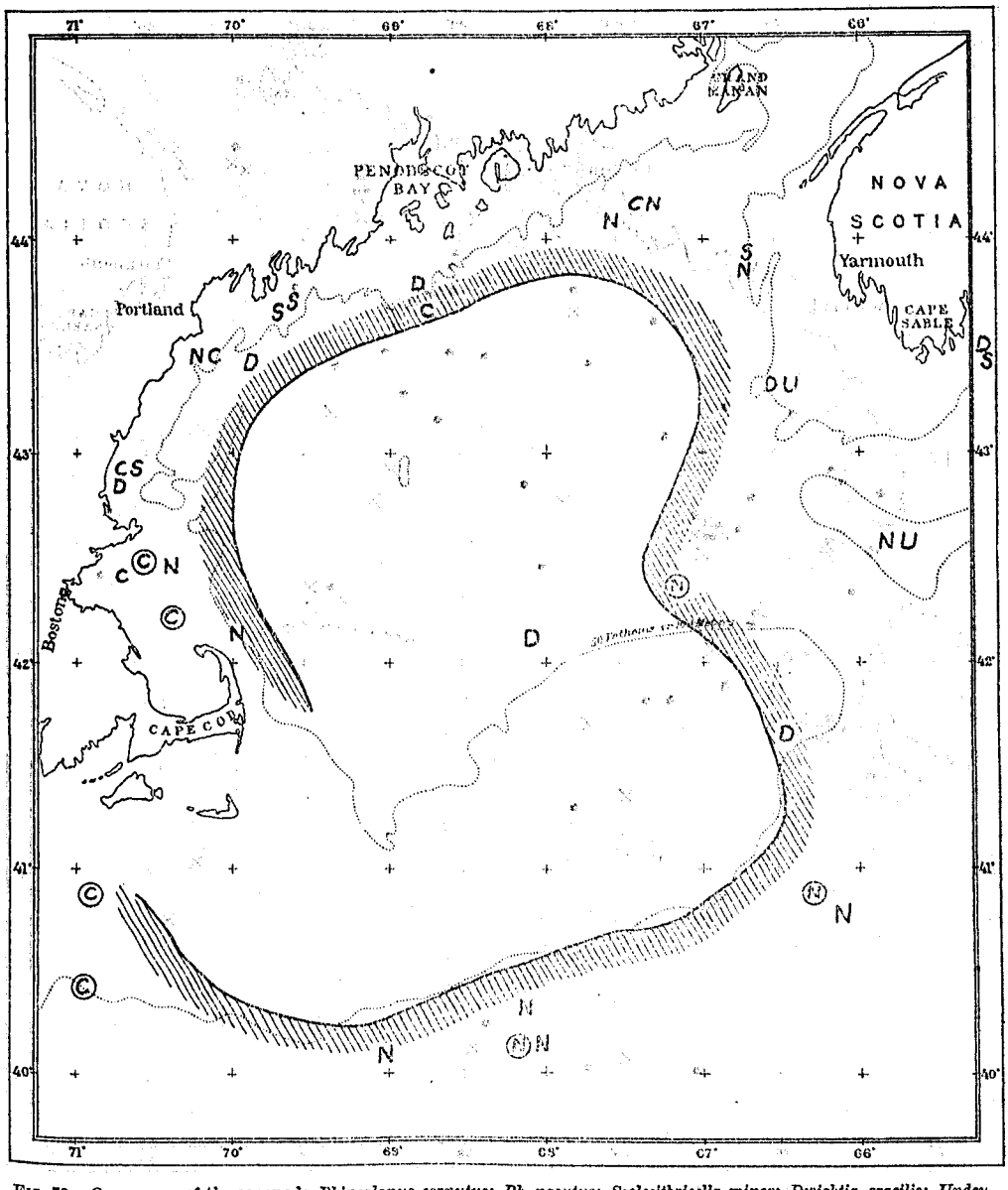


FIG. 72.—Occurrence of the copepods *Rhincalanus cornutus; Rh. nasutus; Scolecithricella minor; Dwightia gracilis; Undeuchæta major*, and *U. minor*. C, locality records for *Rhincalanus cornutus:* D, for Dwightia; N, for *Rhincalanus nasutus:* S, for Scolecithricella; U, for Undeuchæta. The hatched curve incloses the area where these oceanic species have been taken most frequently

foundland Banks, and over the deeper parts of the continental shelf along Nova Scotia (Willey, 1919, tables; Bigelow, 1917, fig. 88). It is one of the most charac-

[28] Listed sim a Euchæta, but probably this species.

teristic planktonic animals in the deeper strata of the Gulf of Maine and abreast its mouth along the continental slope. The most southerly record of it off the American

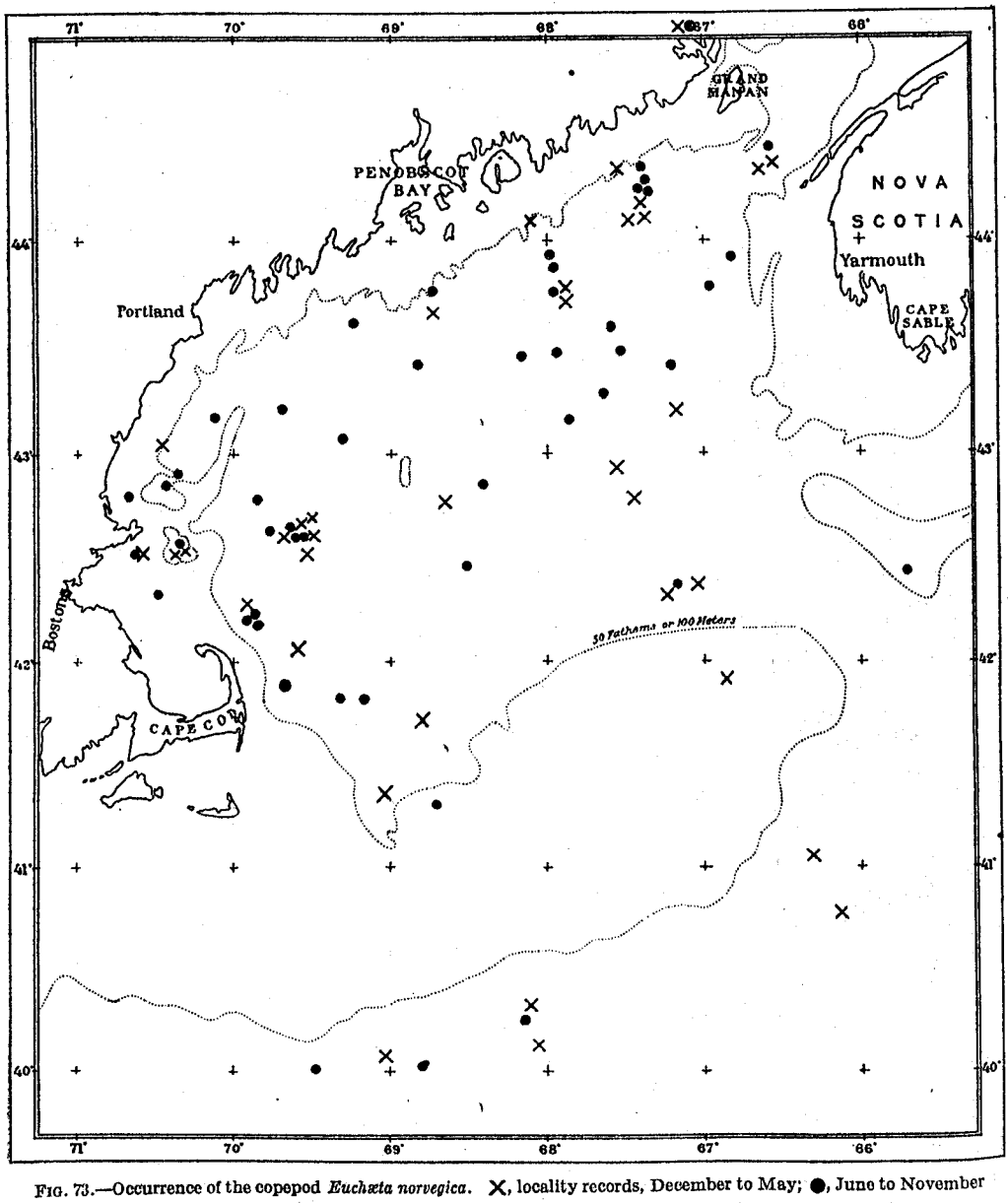


FIG. 73.—Occurrence of the copepod *Euchæta norvegica*. X, locality records, December to May; ●, June to November

coast is in latitude 37° 46′ N. (Bigelow, 1922, p. 148; station 10384, August 12, 1916) in a haul from 500–0 meters.

The locality records for *E. norvegica* prove it generally distributed over the basin of the Gulf of Maine at all times of the year (fig. 73), and so nearly universal there that it has been taken in about 80 per cent of all the horizontal hauls below 100

meters, irrespective of the season. In August, 1913, for example, every such haul captured it, and in the spring of 1920, 80 per cent of the deep hauls took it. In fact, we have learned to expect it in every deep haul (it is made very conspicuous in the catch by its large size and by the brilliant blue egg clusters borne by the adult females) and to regard it as almost as typical of the bottom waters of the gulf below, say, 150 meters as *Calanus finmarchicus* is of the upper 100 meters. The plotted positions (fig. 73) do not suggest that its area of regular occurrence in the gulf undergoes any expansion or contraction with the change of the seasons.

Although so nearly universal in appropriate depths, *E. norvegica* "is never abundant in the Gulf of Maine in the sense that Calanus or any of the other small copepods can be so described" (Bigelow, 1915, p. 292), the richest horizontal hauls yielding a few thousands at most, as is described in detail below. Since the passage of even the deeper vertical hauls through the stratum regularly inhabited by Euchæta is necessarily brief everywhere in the gulf,[29] the result has been that the vertical hauls have often missed it at stations where it has been taken in the horizontals, and consequently do not give a true picture of its distribution. For example, it does not appear in the list of copepods for the vertical haul in the eastern basin on June 10, 1915 (station 10283), though considerable numbers were taken in the horizontal haul as they had been a month previous also (station 10273).

Contrasted with its universal distribution in the basin of the gulf and its constant occurrence there, we have few records of this species inside the general 100-meter contour, whether in the coastwise zone or over the offshore banks—Georges and Browns. Records of it in Massachusetts Bay (fig. 73)—apparent exceptions—are all located in the deep sinks off Gloucester where Euchæta is apparently a permanent inhabitant of the deepest water below, say, 60 to 70 meters.

Present knowledge suggests that *E. norvegica* regularly ranges closer in to the land—and in shoaler water—off the Eastport-St. Andrews region, just within the entrance to the Bay of Fundy, than elsewhere in the gulf, Willey (1921) having reported 7 per cent of this species in a 10-fathom tow off Eastport on August 2, 1916, and having found a quantity of Euchæta in the stomachs of pollock caught about Campobello Island, New Brunswick. *E. norvegica* also entered the mouth of the St. Croix River to abreast of St. Andrews on February 23, 1917 (Willey, 1921), this being the only record of its presence in any estuarine situation tributary to the Gulf of Maine. Our failure to take this species at any of the stations in the deep eastern and northern channels is instructive in connection with the possibility of its immigration into the gulf.

Although the geographic range of *E. norvegica* follows the continental edge as far as the longitude of Delaware Bay (p. 232), it has been found at only about 50 per cent of our deep stations abreast the mouth of the Gulf of Maine, and only once (the station noted, p. 232) beyond the longitude of Nantucket in this direction, although a number of hauls were made along the slope southward to the latitude of Chesapeake Bay in the summers of 1913 and 1916. Longitude 70° may therefore be set as about the western boundary to its regular presence along the North American coast.

[29] In explanation I may point out that only the deepest half of a vertical haul from 200 meters is likely to take Euchæta.

Records of *E. norvegica* along the slope westward and southward from the eastern channel have all been from deeper than 100 meters, and this southward extension of its range is probably only a narrow zone above the 500-meter level—perhaps not more than 20 to 30 miles wide—sandwiched in between the continental slope on the one side and the high temperatures offshore on the other. The recent discovery of this copepod living at 1,000 to 1,250 meters at two *Michael Sars* stations in the Sargasso Sea west of the Azores, however, between the fortieth and fiftieth meridians of longitude (Murray and Hjort, 1912, p. 657), makes it probable that it will be found widely distributed over the whole Atlantic basin in the deeps, like the chætognath *Eukrohnia hamata*, with which it is often taken.

The presence of *E. norvegica* at six out of our seven deep stations off the slopes of Georges Bank and off Shelburne, Nova Scotia, during the spring of 1920 (not found at station 20109), but at only three of our five summer stations outside the continental edge abreast the gulf, and at none of our July, August, or October stations off Marthas Vineyard, indicates a distinct seasonal periodicity in this part of its range, with its maximum abundance in the cold months; but one of these spring stations (20069, March 12, 1920) yielded it in greater numbers per square meter (about 7,750) than any vertical haul yet made within the Gulf of Maine.

*Actual numbers.*—Although *E. norvegica* often gives character to the catches of the deepest horizontal hauls because of the scarcity of other copepods, it has averaged only about 930 per square meter for all seasons and at all the stations where it figures in the lists for the vertical hauls, with maxima of 4,690 in the eastern basin on August 6, 1915 (station 10304), and 7,750 off the southeast slope of Georges Bank on March 12, 1920, as just noted (station 20069). The average for June to September within the gulf (about 1,200 per square meter) has been slightly above the annual average, and that for February to May slightly below it (about 800), but so small a difference can not safely be interpreted as evidence of any notable seasonal fluctuation in the numerical strength of the species.

The density of aggregation, as measured by number per cubic meter, is likewise invariably small. Assuming that all the specimens taken in hauls deeper than 100 meters came from below that level, as most of them certainly did, the maximum per cubic meter would be less than 50 and the average something like 10; but this is probably an overstatement, because some few Euchæta were shoaler—that is, scattered through a longer column of water.

In terms of percentage *E. norvegica* has invariably ranked low in the vertical hauls, its maximum being 20 per cent off the southwest slope of Georges Bank, February 22, 1920 (station 20044), and 10 per cent on several occasions within the gulf (tables, p. 297), where its average for all the verticals has been about 4 per cent. But it occasionally dominates the catch in the deepest horizontal hauls at or below 150 meters (e.g., closing-net haul at 85 to 60 fathoms, August 29, 1912, station 10043), and on several occasions it has amounted to 30 to 50 per cent of the copepods taken. At times, however, we have found only 2 per cent or less of Euchæta in hauls as deep as 175 to 250 meters (table, p. 304).

*Vertical distribution.*—Perhaps the most interesting phase of the status of *E. norvegica* in the gulf is its vertical distribution, for, unlike most of the other common

local copepods, it is most characteristic of the deepest water there. As just pointed out, it has been taken in the great majority of the horizontal hauls below 100 meters, and as a general rule it may be stated that the deeper the haul the more certain it is to yield Euchæta, and in the greatest numbers, both absolutely and relative to other copepods. During the July and August cruises of 1913, for example, it was taken more abundantly at "90–0 fathoms at station 10100, 80–0 fathoms at stations 10088 and 10097, 75–0 fathoms at station 10090, 70–0 fathoms at station 10061" (Bigelow, 1915, p. 292) than in any of the shoaler tows. The use of closing nets is requisite for more definite information on this point, because the open tow nets often pick up such large amounts of Calanus and other copepods in their journeys up and down that it is impossible to estimate the relative abundance of Euchæta and Calanus at the towing level.

In contrast with the frequency with which *E. norvegica* occurs in the deepest Gulf of Maine hauls, it is usually wanting in tows shoaler than 100 meters, which establishes that level as roughly the upper limit to its regular range. Among the several hundred hauls at lesser depths with various nets it has been detected in only 20 of the horizontals[30] and 7 verticals (tables, pp. 297 and 299) and only twice shoaler than 40 meters; and the fact that on at least two of these occasions it was about equally abundant at 60 meters and in considerably deeper hauls is evidence that *E. norvegica* reaches the upper strata of water as the result of temporary dispersals and not by a general ascent on the part of the whole local stock. On six occasions it has been taken on the surface in various parts of the gulf, as follows: (1) 12 miles off Mount Desert Rock, August 16, 1912, at 3 a. m. (station 10032); (2) in the northeastern part of the basin off the mouth of the Bay of Fundy, August 13, 1913, 2 a. m. (station 10097); (3) near the same locality, August 12, 1914, 10 p. m. (station 10247); (4) western basin, August 22, 1914, 8 p. m. (station 10254); (5) in the southwestern part of the basin, the following night, 11 p. m. (station 10256); and (6) Fundy Deep, March 22, 1920, 2 p. m. (station 20079). It will be noted that these localities extend right across the gulf from northeast to southwest—that is, they do not suggest that Euchæta comes more often to the surface in the northeastern corner of the gulf, where vertical mixing by tidal currents is most active, than in the more stagnant and stratified and vertically stable waters off Massachusetts Bay and Cape Cod. More extensive data may prove that a local difference of this sort does actually obtain; indeed, it is to be expected. Neither does the evidence available suggest that Euchæta rises to the surface more frequently during the winter or spring than in summer, for it appeared in only one of the 55 surface tows for February–May, 1920 (table, p. 303). The times of day for the several surface captures of *E. norvegica*, if corroborated, would indicate that in summer it makes its rare visits to the surface only at night, but that in early spring (probably also in winter) it may do so at any hour.

Damas and Koefoed's (1907) characterization of *E. norvegica* as a form living mostly in midwater but occasionally appearing at the surface applies as well to it in the Gulf of Maine as in the Greenland seas. *E. norvegica* has been found in small numbers at the surface in most other regions where it occurs regularly. This, for

[30] Willey (1921) also reports Euchæta at about 20 meters off Eastport and near the surface at St. Andrews.

instance, is the case in the fjords and along the coast of Norway (Sars, 1903; Farran, 1910), between Iceland and the Faroes (Wolfenden, 1904), in the Faroe channel, in the Gulf of St. Lawrence, and along the outer coast of Nova Scotia (Willey, 1919). In the northeastern Atlantic reports of it at the surface have usually been based on immature specimens; but this rule does not apply to the Gulf of Maine, Willey (1922) having found it in the breeding state close to the surface near St. Andrews. Euchæta necessarily inhabits a somewhat shoaler zone in the gulf (with its lower limit set at about 300 meters by the topography of the bottom) than in the Norwegian sea and between Iceland and the Faroes, where it occurs chiefly below 200 to 300 meters, and down to 1,000 meters.

*Breeding.*—Our failure to find *E. norvegica* at any time in the eastern or northern channels (we have one record of it on Browns Bank, June 24, 1915, station 10296) and the fact that its seasonal fluctuations in abundance along the continental shelf are not reflected within the gulf are evidence that the maintenance of the Gulf of Maine stock depends more on local reproduction than on immigration. Were the opposite true, we would expect to find it in the two channels, these being the entrances for visitors from the mid-depths offshore, or from the east and north, and most plentiful within the gulf at the season when it is most plentiful outside. Adult females with egg clusters attached are familiar objects in the deeper Gulf of Maine tows, while Willey (1921) has found adult males with spermatophores as well as egg-bearing females and immatures of both sexes at St. Andrews.

Willey's specimens were taken in February, and since females with egg sacs were noted in the *Albatross* tows on March 3, 1920 (station 20055), and outside the continental edge off Shelburne, Nova Scotia, on the 19th (Station 20077), while most of the summer catches of the species have contained them, *E. norvegica* evidently spawns throughout the year in the Gulf of Maine. The vertical distribution of the species proves that reproduction takes place almost entirely below 100 meters, though occasional individuals in breeding condition may occur at the surface.

*Relationship to temperature and salinity.*—The tendency of this species to keep to deep water makes it easy to establish the physical conditions under which it lives in the gulf.

The great majority of the captures have been in comparatively high salinities (33 to 34 per mille) and from temperatures lower than 10°, the quantitative occurrence of the species pointing to the higher salinity and to a temperature lower than 8° as its optimum. Such of the Gulf of Maine stock as lives below 150 meters inhabits a zone in which the yearly range of temperature is narrow—for the most part between 6 and 4°. However, its presence at the surface proves that it can survive a brief visit in water as warm as 19 to 20° (stations 10254 and 10256, western basin, August 22 and 23, 1914). On the other hand, the wide Arctic distribution of *E. norvegica* makes it unlikely that the temperature is ever unfavorably low for it in the Gulf of Maine, which is corroborated by its presence near the surface at St. Andrews during the coldest season (Willey, 1921). The failure of this species to work farther inward toward the Baltic [31] than the Skager-Rak makes it probable that salinities lower than

[31] One record from the Kattegat is mentioned by Farran (1910).

32 to 33 per mille are an effective bar to its wanderings, and its distribution in the Gulf of Maine is consistent with this.

*Economic importance.*—*E. norvegica* has been considered as of comparatively little economic importance in the northeastern Atlantic because of the considerable depth of its habitat. But it occurs regularly within reach of at least one of the important plankton-eating fishes in the Gulf of Maine, for Willey (1921) found the stomach of an American pollock (*Pollachius virens*) densely packed with a mass of Euchæta and euphausiid remnants in about equal amounts, the percentages of different copepods which he tabulates—84 per cent Euchæta, 3 per cent *Calanus finmarchicus*, 2 per cent *C. hyperboreus*, and 1 per cent *Metridia longa*—suggesting that the fish had voluntarily selected the Euchætæ in preference to the smaller *C. finmarchicus*, which was probably far the more plentiful of the two. Another pollock opened by him had also eaten Euchæta. To what extent mackerel and the several species of herring feed upon it in the gulf is not known, but it is likely to be an important article in their diet when it rises toward the surface.

### Euchæta spinosa Giesbrecht

This species, known from localities in the North Atlantic, Mediterranean, Indian Ocean, and Pacific (Giesbrecht, 1892; van Breemen, 1908; Thompson and Scott, 1903; Esterly, 1905), has been reported from surface collections off Nausett Beach, Cape Cod, and off the northern extremity of the cape by Sharpe (1911, p. 410), but it has not appeared in any of the more recent towings in the gulf or in Canadian Atlantic waters.

### Eucheirella rostrata (Claus)

This is an oceanic species, widespread in the temperate Atlantic (Cleve, 1900; T. Scott, 1911) and common on the Pacific coast of the United States at San Diego, Calif. (Esterly, 1905 and 1911). It has been recorded at several stations along and outside of the continental edge off Chesapeake and Delaware Bays and off New York (Bigelow, 1915, p. 296; 1922, p. 147), abreast of Georges Bank (stations 10218 and 10219), and thence eastward and northward along the slope of the Nova Scotian shelf and in the Laurentian channel (Willey, 1919, p. 189, fig. 9). Although this copepod is not typically tropical, it enters the Gulf of Maine as a visitor from the mid-depths along the inner edge of the "Gulf Stream," and its locality records, like those for other planktonic organisms of that category, are localized in the eastern side of the gulf and around its periphery (fig. 71). The station records number 13, all but 4 of them being for July and August—2 for May, 1 for June, and 1 for September. Evidently the species is most apt to enter the gulf during the warm months, and apparently it does not do so at all in the low temperatures of late autumn, winter, and early spring.

All records of the species off the east coast of America have been from depths of 50 meters or deeper, and the Gulf of Maine records are all based on occasional specimens.

### Eurytemora herdmani Thompson and Scott

This species is known only from the coasts of North America. It was originally described from the lower reaches of the St. Lawrence River below Quebec (Thompson and Scott, 1898), and has since been found in the Gulf of St. Lawrence (T. Scott, 1905; Willey, 1919), on the Bering Sea shore of Alaska and Arctic shores of Canada (Willey, 1920), in the Gulf of Maine, at Woods Hole (Sharpe, 1911; Fish, 1925), and in Narragansett Bay (Williams, 1906 and 1907).

In the Gulf of Maine it probably occurs in all harbors, having been taken at Gloucester, Rockport, Kittery (Esterly, in Bigelow, 1914, p. 116), and at St. Andrews, where Doctor McMurrich[32] found it regularly throughout June, July, August, September, and October, occasionally in February, April, and May, but not at all in November, December, or March. Willey (1919 and 1921) also records it from one station in Passamaquoddy Bay in September, 1915, and again on November 2, 1916. Altogether we have eight records of this species in the open Gulf—off Boston Harbor and off Boothbay Harbor on July 13 and 26, 1912 (stations 10006 and 10016); in the western and eastern basins on August 31 and September 1, 1915 (stations 10307 and 10309); off the Isles of Shoals on October 4, 1915 (station 10325); western basin and southeast slope of Georges Bank on March 24 and April 16, 1920 (stations 20087 and 20109); and off Boston Harbor on December 29, 1920 (station 10488). Never more than a few specimens have been taken at any offshore station.

Judging from these records, it seems that *Eurytemora herdmani* is characteristic of estuarine situations and perhaps also of brackish water all around the coast line of the gulf, but that such specimens as drift offshore are equally able to survive in the open sea, and so are as apt to be met with in one part of the gulf as another and even out to the continental edge. But being so scarce everywhere in the gulf away from the close vicinity of the coast, it is not likely that this species breeds successfully there outside the outer headlands. McMurrich's observations point to the summer and early autumn as its season of maximum abundance, and winter and early spring as its minimum abundance in Gulf of Maine harbors and river mouths, but at Woods Hole Fish (1925) found it regularly in winter as well as summer.

### Gaidius tenuispinis Sars

This is an Arctic and North Atlantic species recorded from many stations in the polar basin (under the ice, Sars, 1900), from the seas between northern Norway and Jan Mayen, Spitzbergen and Greenland; around Iceland; along east and west Greenland and in Davis Strait;[33] and Esterly (1911) had one specimen in a vertical tow from 325 fathoms at San Diego, Calif. In the eastern side of the Atlantic it occurs southward regularly to the Iceland–Faroe and Faroe–Shetland channels. There are a few records from the Norwegian sea, from north and east of Scotland, and from deep water southwest of Ireland (Murray and Hjort, 1912, p. 655). In the polar sea it has been taken at the surface in latitude 85° N. (Sars, 1900). All other records of it have been from considerable depths, varying from 100 to 1,000 meters.

[32] In his unpublished plankton lists.

[33] For more detailed statements of its occurrence in northern seas see Sars (1900), Mrázek (1902), Damas and Koefoed (1907), Farran (1910), and especially With (1915).

On the American side Willey (1919) lists it at one station in the Gulf of St. Lawrence and one just outside the continental edge of Le Have Bank off Nova Scotia, and the *Michael Sars* had it near Flemish Cap, east of the Grand Banks. Wolfenden (1911) has described as this species a Gaidius from the Antarctic and off the Cape of Good Hope, but differences which he mentions, though slight, may prove sufficient to differentiate the northern from the southern form when larger series are compared; hence the bi-polarity of the species can not be accepted yet as definitely established (With, 1915). *G. tenuispinis* has not been found in the Pacific, where a closely allied form, *G. pungens* (Giesbrecht), occurs in lower latitudes.

There are no previous records of *G. tenuispinis* in the Gulf of Maine or farther south in the western Atlantic, but odd specimens were taken in the vertical hauls off Penobscot Bay on April 10, 1920 (station 20097), and again on January 1, 1921 (station 10496)—about 6 specimens on the first occasion and 15 on the second. It also figures (1 per cent) in the list of copepods taken at the outermost station outside the continental edge off Shelburne, Nova Scotia, on March 19, 1920 (station 20077, table, p. 300). Evidently *G. tenuispinis* reaches the gulf, which is its extreme southern limit on the American coast, only as an accidental stray from the north, and is more apt to do so during the cold half of the year than in summer.

### Halithalestris croni (Krøyer)

This is one of the largest of harpacticoid copepods and one of the few representatives of the group recognized in the plankton of the open Gulf of Maine by Doctor Esterly (in Bigelow, 1914, p. 115; 1915, p. 287; 1917, p. 290) or by Dr. C. B. Wilson (tables, p. 207), and at Woods Hole by Fish (1925, p. 146). It is widely distributed in the North Atlantic, being known on the European side from the Bay of Biscay northward to the Faroe Channel, Iceland, Spitzbergen, and north of Norway, including the English Channel and the northern part of the North Sea. On the American side it has been reported at several stations in the Gulf of St. Lawrence (Herdman, Thompson, and Scott, 1898; Willey, 1919), in the Straits of Belle Isle (Herdman, Thompson, and Scott, 1898), in the Gulf of Maine, and at Woods Hole, but as yet not farther south.

*Gulf of Maine.*—Previous records for the Gulf are two hauls in the central basin in July, 1894;[34] St. Andrews, September, 1915 (Willey, 1919); and occasional specimens mentioned for that locality during the months of November, January, and April in Doctor McMurrich's lists of the local plankton (p. 12). *H. croni* was not detected in the numerous horizontal hauls for the years 1912 to 1914, reported on by Doctor Esterly, probably because entirely overshadowed by the masses of Calanus and other calanoids; but the vertical and surface hauls for 1915, 1920, and 1921 (tables, pp. 297, 299 and 304) extend its range over the Gulf of Maine generally, including the coastal zone and the basin indifferently, to the eastern part of Georges Bank and to the continental slope off its southwestern face (fig. 74). It has not yet been found on the western part of the bank or off Nantucket, but judging from its widespread distribution in the gulf it is to be expected there. The records cover the months of March, April, May, June, August, September, and January, proving that it is present in the gulf the year

[34] Listed by Sharpe (1911) from latitude 42° 55′, longitude 68° 49′, and latitude 42° 07′, longitude 70° 08′, and collected by the *Grampus*.

round, with 12 station records for March, 7 for April, 3 for May, and only 1 or 2 for each of the remaining months. On its face this seasonal distribution of the records would suggest that *H. croni* is most widespread during the spring, and so scarce during

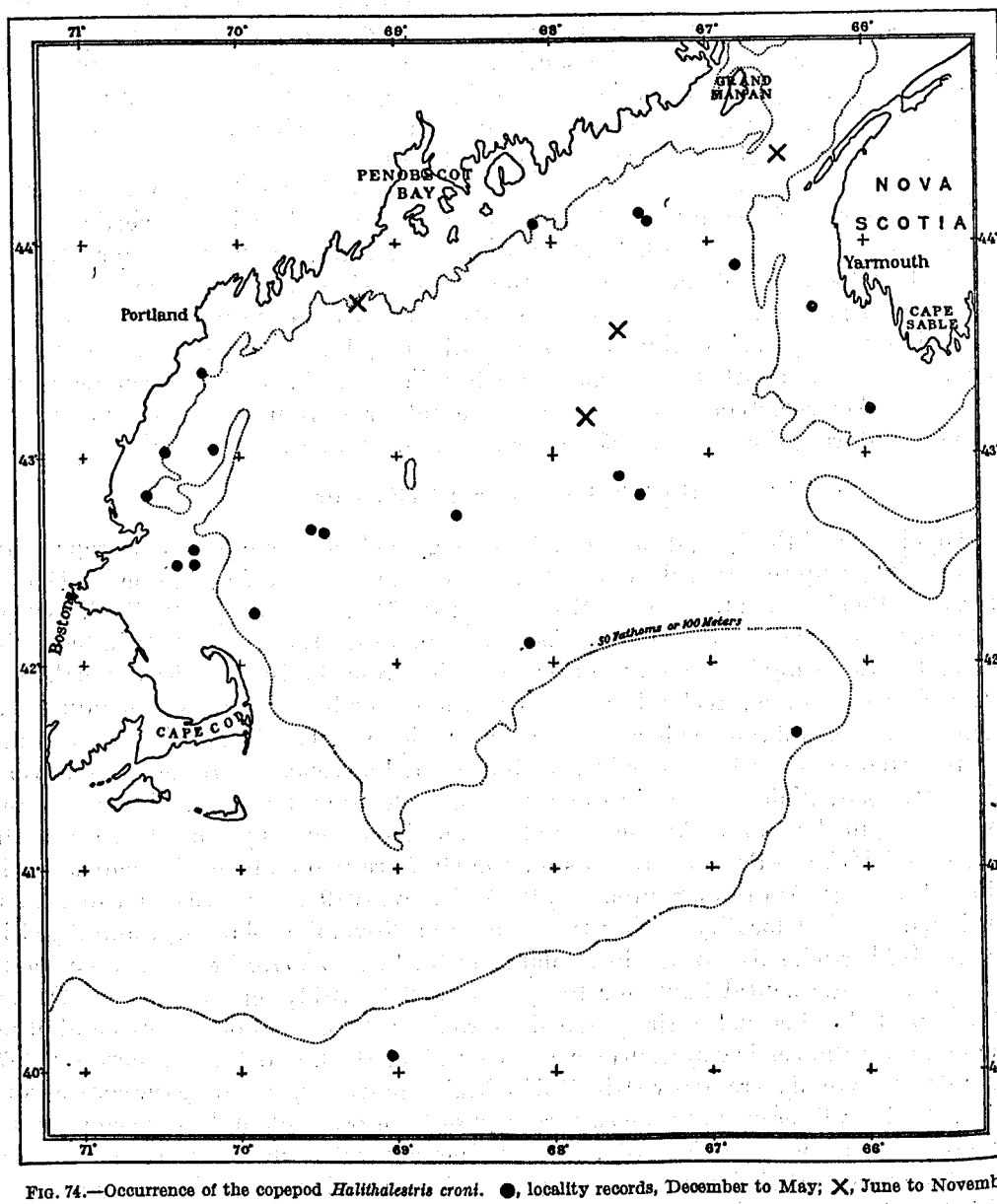


FIG. 74.—Occurrence of the copepod *Halithalestris croni*. ●, locality records, December to May; X, June to November

October that all the hauls missed it; but this conclusion may need modification when a greater number of surface hauls for the autumn have been examined. We have taken it in greatest abundance locally in August.

No seasonal localization of the species in one region or another is demonstrated within the gulf. In other seas *H. croni* has usually been taken at or near the surface, and the *Grampus* specimens of 1894, just mentioned, were likewise from hauls at or near the surface. Similarly, this copepod occurred in about 25 per cent of the surface hauls during the spring of 1920, but only in about 12 per cent of the verticals. Evidently it lives chiefly close to the top of water, but the fact that seven verticals took it at April and May stations when the surface net missed it, although the latter filtered much the larger volume of water, is evidence that its vertical range extends down at least for some few meters and possibly to a considerable depth. No information is available as to its presence or absence on the surface in the gulf during the remainder of the year.

*H. croni* has never been more than a very minor factor in the copepod fauna of the gulf, as revealed by the tow net. At the stations where it has been recognized it has averaged only about 1 per cent of the copepods; at the most 5 per cent. The numbers per square meter at the stations of record for the species have varied from a mere trace to a maximum of about 2,300 (station 10304, August 6, 1915). Although *H. croni* was taken at more stations during the spring months than in summer, the numbers per haul were less (average less than 150 per square meter for March, April, and May; maximum about 277) than in August, when there were 1,700 and 2,300 per square meter at the two stations (stations 10304 and 10309; table, p. 298); but it is not safe to draw conclusions as to the numerical fluctuations of the species from so few hauls.

Dr. C. B. Wilson, in a letter, speaks of the egg sacs of the females; therefore it is to be presumed that this copepod is endemic in the gulf, but no observations have yet been made on its season of reproduction there.

### Harpacticus littoralis G. O. Sars

This is a littoral species, known from the south and west coasts of Norway, where it is usually found in very shallow water, especially at the heads of flat, sandy creeks, and about Great Britain.[35] *H. littoralis* has not been reported previously from the American coast under its own name, but it is possible that it was included among the *H. chelifer* recorded by Sharpe (1911) from Woods Hole and from the vicinity of New York.

At St. Andrews Doctor McMurrich lists *H. littoralis* occasionally between December 12 and March 28, rather more frequently but always in small numbers during April and May (about 45 per cent of the stations), and not at all during the other months.

Judging from its littoral nature on the other side of the Atlantic there is no reason to suppose that it ever becomes planktonic outside the outer islands in the Gulf of Maine; but probably tow nets would take it in most of the harbors north of Cape Cod at some stage of the tide.

[35] See Sars (1903–1911) for the history of this species, previously confused with *H. chelifer* Müller.

### Harpacticus uniremis Krøyer

This harpacticoid becomes planktonic only occasionally or accidentally but normally lives on the bottom—according to Sars (1903–1911) on muddy bottom in 20 to 100 fathoms. The localities of capture which he quotes from various earlier authorities include the Scottish coast, Norwegian coast, Spitzbergen, Bear Island, polar sea north of Grinnell Land, and Bering Sea. Williams (1907) has also recorded it from Narragansett Bay and from the brackish Charlestown Pond in Rhode Island, Fish (1925) at Woods Hole, and the Canadian Arctic expedition collected it in surface tows at two localities off southern Alaska (Willey, 1920).

Doctor McMurrich, in his plankton lists, records this species occasionally at St. Andrews in December (one haul); in five hauls between March 28 and May 19; twice in June; not at all during the later summer or autumn; and Willey (1923) reports it from the stomachs of winter flounders (Pseudopleuronectes) caught there. In this region of violent tidal circulation it is perhaps swept up from the bottom by the active stirring of the water. It has not been taken in the open Gulf and is hardly to be expected there in the plankton.

### Heterorhabdus spinifrons (Claus)

Dr. C. B. Wilson contributes the following note on this species, which "is easily recognized by the asymmetry of the caudal rami and by the excessive length of one of the apical setæ attached to the left ramus. In the plankton taken continuously across the Atlantic by Herdman this species was found sparingly between mid-ocean and the Canadian shore, and hence is found considerably north of the Gulf of Maine. During the *Challenger* expedition it was taken at several widely separated stations in the North Atlantic, and at one place in the South Atlantic from a depth of 2,650 fathoms (Brady, 1883). Thompson and Scott (1903) have reported it in the Mediterranean, in the Indian Ocean, and near Ceylon. Esterly (1905) obtained only a single female of this species from the plankton at San Diego on the Pacific coast, and incidentally one or two specimens of three other species of the genus. In the Gulf of Maine it was obtained in only two vertical hauls—one in the open ocean southeast of Georges Bank and the other outside of Boston Harbor. The first haul was made on March 12, 1920, and this species had a percentage of four in the catch. The second haul was made on May 4, 1920, and *spinifrons* formed only 1 per cent of the catch. In none of the reports here enumerated was it found in any numbers, and the four per cent mentioned [indicating an absolute abundance of about 3,100 per square meter] is about its maximum anywhere."

In the Gulf of Maine it may be classed as an accidental visitor from warmer and more oceanic waters offshore.

### Idya furcata (Baird)

Sharpe (1911, p. 417) describes this as "perhaps the commonest and most widely distributed of all the Harpactoida." Probably it will eventually prove cosmopolitan in suitable situations, being recorded from widely separated localities in the Arctic Ocean, including the Alaskan shore of Bering Strait and the Arctic

coast of Canada (Willey, 1920), and from north European coasts generally inward to the mouth of the Baltic. Brady (1878–1880) calls it ubiquitous around Great Britain, and Sars (1903–1911) names it the commonest of Norwegian harpactoids. It occurs in the Mediterranean and Red Seas and about New Zealand and the Chatham Islands in the Pacific.[36] Like most of its group it chiefly inhabits the littoral zone, among seaweed, often in tide pools, and only occasionally, perhaps accidentally, it becomes pelagic out at sea.

In northeastern American waters it has previously been reported from Narragansett Bay, Rhode Island (Williams, 1907), and from Woods Hole, where Sharpe (1911) collected it in summer, both among floating algæ and eel grass (Zostera) in water about 10 fathoms deep and in the so-called "eel pond," an inclosed tidal pool.

At St. Andrews, Idya, like other Harpactoida, is perhaps swept up into the upper waters by the violent tides. Doctor McMurrich lists it three times between January 26 and March 28; in nearly 50 per cent of the hauls from March 28 to May 19; and in 25 per cent of the hauls from May 20 to July 6; but not at all during the later summer, autumn, or early winter. It has not been detected in the plankton of the open gulf and is hardly to be expected there except perhaps as a stray from the littoral zone with the masses of eel grass (Zostera) and rock weed (Fucus) so often seen drifting on the surface.

In estuarine situations, where this little copepod is plentiful, it may be an important article of diet for fishes, Willey (1920, p. 35) having found it in abundance in the stomach of the winter flounder (Pseudopleuronectes) at St. Andrews.

### Labidocera æstiva Wheeler

This species was described by Wheeler (1901) from Woods Hole, where he found it very common in the tow during June and September, and where Parker (1902, p. 103) speaks of it as "one of the commonest species." Williams (1906 and 1907) did not find it in Narragansett Bay nor Fowler (1912) off New Jersey, but Dr. C. B. Wilson writes me that it is "in considerable numbers along the Atlantic coast south of New England," and in August, 1916, it was taken at three stations off the mouth of Chesapeake Bay (Bigelow, 1922, p. 146). Fish (1925) had it at Woods Hole from June through November. Up to the present time it is known only from the American side of the North Atlantic.

The only previous records of it from east or north of Cape Cod are T. Scott's (1905) mention of it in the Gulf of St. Lawrence and Willey's (1919) two citations of it in Northumberland Strait and between Prince Edward Island and Cape Breton Island in the Gulf of St. Lawrence, but the towings of 1920 and 1921 extend its range into the Gulf of Maine.

There are only three records for it in the Gulf of Maine—that is, western basin, March 24, 1920 (station 20087); off Penobscot Bay, April 10, 1920 (station 20097); and again on January 1, 1921 (station 10496)—always in minimal amounts. Thus it is evidently very rare in the gulf, and probably only a straggler there from its center of abundance in the Woods Hole region. This species, having no constant place in the local plankton, is chiefly interesting here as the subject of Parker's (1902)

[36] Sars (1903–1911) and Sharpe (1911) summarize its distribution as known.

experiments on the vertical migrations of copepods, which lead to the conclusion that while it is at all times negatively geotropic—that is, tends to swim upward against gravity—the phototropism of the females, whether positive or negative, depends upon the intensity of the light, weak attracting and strong repelling them, whereas the males show a weak negative phototropism under all conditions. Thus, he concludes, the females may be expected to rise with the setting sun, as the light weakens, and to descend again after sunrise, when they become positively phototropic enough to counteract their negative geotropism. The males, he believed, follow the females because chemically attracted to them. What little is known of the vertical movements of Labidocera at liberty in the sea conforms to this schedule, for Parker found them at the surface from sunset to sunrise.

This species is an important article of diet for copepod-eating fishes farther south, writes Dr. C. B. Wilson, but probably it is never sufficiently plentiful for this in the Gulf of Maine.

### Lucicutia grandis Giesbrecht [37]

This species was founded on a single male specimen obtained off the west coast of South America just north of the Equator. The two Gulf of Maine specimens are interesting because there has been no subsequent report of it except one female from the North Atlantic doubtfully referred to it by Wolfenden (1904). The Gulf of Maine collections contain two males from a vertical haul from 1,000–0 meters off the southeast slope of Georges Bank, March 12, 1920 (station 20069), indentified by Dr. C. B. Wilson (table, p. 299).

### Metis ignea Philippi

This small, brilliant, blood-red harpacticoid, originally described from the Mediterranean, has since been redescribed as "*Ilyopsyllus coriaceus*" from the Irish coast by Brady (1883) and by Brady and Robertson (1873); Sars (1903–1911) also found it at several localities on the coast of Norway. *M. ignea* has not been reported definitely from American waters, but Williams's (1907) "*Ilyopsyllus natans*" from Narragansett Bay is a very closely allied form, if not identical, as Sars (1903–1911, p. 346) suggests. So, also, is the "*I. sarsi*" described by Sharpe (1911) from Woods Hole. Brady and Robertson described *M. ignea* as living among black peaty mud and roots of seaweed near high-tide mark; Sars also found it in moderate depths on a muddy bottom amid decaying algæ, and Sharpe (1911) took his *sarsi* among floating algæ at Woods Hole. Another species of the genus *M. holothuriæ* [38] was taken from a holothurian. On the other hand, Williams (1907) described his *natans* as swimming at the surface in Narragansett Bay, so that the genus is both bottom dwelling and planktonic.

The Gulf of Maine records of *M. ignea*, nine in number, are for the months of December, March, April, May, June, and October, proving it present the year round with no definite seasonal maximum, and always in numbers so small that no haul yielded more than a few specimens. At the most it was 1 per cent of the copepods, meaning about 20 to 28 specimens per square meter, and usually only one or two were detected per haul.

[37] Originally described by Giesbrecht (1895) as *Leuckartia grandis*, but this generic name being preoccupied he later (Giesbrecht and Schmeil, 1898) replaced it by Lucicutia.

[38] Described by Edwards (1891) as *Abacola holothuriæ*.

All but two of the records are inshore from the general 100-meter contour—that is, off Boston Harbor (stations 20089, 10488, and 10505, April 5 and December 29, 1920, and March 5, 1921); outer part of Massachusetts Bay (station 10323, October 1, 1915); near Chatham, Cape Cod (station 10336, October 26, 1915); near Mount Desert Island (station 10286, June 14, 1915), and on German Bank (station 10271, May 6, 1915)—but one of the stations of record lies in the central part of the basin (station 20114, April 17, 1920) and another outside the 100-meter contour off Cape Cod (station 20116, April 17, 1920). The locations of the several locality records are not such as to suggest that the specimens in question had been swept up from the bottom by some current, for most of them are in regions where vertical currents are comparatively weak; and it is significant that *M. ignea* was not taken at any of the stations where the surface tows contained sand brought up by active stirring of the whole column of water. It may therefore be concluded that in the Gulf of Maine this copepod is regularly planktonic in small numbers; but judging from its habitat in other seas it is also to be expected on the bottom in shoal water, and probably in greater abundance.

The data of capture point to the upper 100 meters as the habitat of this species where it is planktonic, probably because this covers the normal depth zone of the stock living on the bottom, some of which take to a pelagic life. It will be noted, however, that none of the surface hauls made during the spring of 1920 took it, this negative evidence suggesting that it is more apt to be at some little depth than close to the top of the water. No observations have been made on the breeding of this species.

### Mecynocera clausi J. C. Thompson

Dr. C. B. Wilson contributes the following note on the general geographic range of this species:

> The original specimens were obtained near the Canary Islands and at Malta, to which localities Giesbrecht (1892) has added Naples and the tropical Pacific from the surface to a depth of 1,000 meters. Thompson and Scott (1903) reported the species from the Red Sea and throughout the Indian Ocean, Wolfenden (1905) among the Maldive Islands, and A. Scott (1909) in the Malay Archipelago. Wheeler (1901) obtained a single specimen from the Gulf Stream 70 miles south of Marthas Vineyard, and Esterly (1905) found the species at San Diego on the Pacific Coast. Esterly's specimens were taken on December 30, while Wheeler's were captured July 25. It is thus very widely distributed but does not seem to occur anywhere in any but small numbers. This, coupled with its small size, makes it of practically no economic importance.

Except for Wheeler's specimen just mentioned, this species had not been taken anywhere along the Atlantic coast of North America, hence its presence at three stations in the Gulf of Maine in September, 1915—one near Cape Elizabeth on the 20th (station 10319) and two in Massachusetts Bay on the 29th (stations 10320 and 10321)—is interesting as extending its known range.

### Metridia longa (Lubbock)

This brilliantly phosphorescent copepod is a true Arctic species, though its distribution in the Gulf of Maine suggests that Farran's (1910, p. 70) characterization of it as "probably the most typically arctic copepod of whose distribution there is any accurate knowledge" needs some modification. Except for one record from the

Indian Ocean (van Breemen, 1908), it is known only from the North Atlantic and polar oceans. It is commonly distributed over the parts of the polar basin crossed by the *Fram* on her famous drift (Sars, 1900); in the Kara Sea; between Norway, Spitzbergen, Greenland, and Iceland; and southward regularly to the Greenland–Faroe and Faroe–Shetland channels. It is widespread in the Norwegian sea, numerous in the deeps of the Norwegian fjords, and occurs southward to the Skager-Rak, where it is usually present in fair numbers. There are isolated records of it in the central part of the North Sea, and it has been taken to latitude 55° 23′ N., longitude 11° 6′ W., west of Ireland (Wolfenden, 1904), this being the most southerly record of it off Europe.

On the American side it is recorded from Baffin Bay and from the Arctic coasts of Alaska and western Canada (Willey, 1920), hence is no doubt circumpolar. On the east coast of North America the Canadian fisheries expedition found it widespread in the Gulf of St. Lawrence, over the continental shelf along Nova Scotia, and outside the neighboring continental slope, but, curiously enough, not at all in the Green Bank–St. Pierre Bank region off Newfoundland. It also occurs with some regularity in the Gulf of Maine and over the shelf south of Marthas Vineyard, which so far as known is its most southerly outpost along the eastern seaboard of America.

*Distribution in the Gulf of Maine.*—*M. longa* was not recognized at any of our stations in the gulf during the summer of 1912 or the following winter, nor can it have been other than very rare during that period, if actually present at all, for Dr. C. O. Esterly examined many samples of the copepods. In July and August, 1913, however, he detected it in small numbers at four stations east and north of Cape Cod (20 per cent of the stations). In the summer of 1914, as in 1912, not one was detected in the gulf, or for that matter along the outer coast of Nova Scotia, although special watch was kept for it; and if not actually altogether absent from the gulf then, it must at least have been extremely rare, for it is so easily distinguishable in general body form from its relative *M. lucens* that it could not have been overlooked had it occurred in such numbers as we have subsequently found in the gulf. The year of local abundance for it was 1915, when it was detected in vertical hauls at about 65 per cent of the stations right through the season from May to October. It again dropped wholly out of sight in the gulf in the summer and early autumn of 1916, when it was not found in the preliminary examination of any of the hauls (Bigelow, 1922, p. 147), although this was a very cold season, which is evidence that the low temperatures of that summer were reminiscent simply of extreme winter chilling and of tardy vernal warming resulting from local climatic conditions, and not due to any unusual flood of cold northern water. A few *M. longa* must, however, have existed in the gulf during the autumn of 1916, for Willey (1921) reports it as occasional at St. Andrews on November 2 and December 8 of that year, with a scattering of it in the tow on February 23, 1917.

Owing to the interruption of all oceanographic research in the open gulf by the war, no information is available as to the local status of *M. longa* during the remainder of 1917, 1918, or 1919, but it occurred in 81 per cent of the vertical hauls during the spring (March to May) of 1920 and at 90 per cent of the stations during December of that year and in January and March of 1921 (tables, pp. 299, 304). Thus it

is evident that *M. longa* fluctuates widely in the gulf from year to year, being extremely rare, if not altogether absent, in some years but widespread in others. The years 1912 and 1914 and the summer of 1916 were periods of scarcity, while 1915, the winter of 1916–17, and 1920 were times of plenty. The relationship of temperature to these annual differences is discussed below (p. 252).

*Seasonal distribution.*—During the years 1915, 1920, and 1921, which may be taken as representative of the periods when *M. longa* is at a maximum in the gulf, it was taken at the following percentages of the stations:

| Months | Percentage of stations | Months | Percentage of stations |
|---|---|---|---|
| January | 100 | June | 60 |
| February | 17 | August | 75 |
| March | 74 | September | 60 |
| April | 87 | October | 86 |
| May | 72 | December | 87 |

This suggests that on the whole *M. longa* is apt to be found most widespread in the gulf during the late autumn, winter, and early spring, and least so during the summer and early autumn. The low percentage of stations at which it was recognized in February, 1920 (only station 20046), would upset this rule were it a regular annual phenomenon; but it is more likely that that month marked the beginning of a period of abundance which endured throughout 1920, and that still fewer stations, if any, would have yielded it during the preceding January or December. In fact, a February station was most prolific of this species at St. Andrews during the winter of 1916–17, as noted above (Willey, 1921).

Seasonal fluctuations in the actual abundance of *M. longa*, as reflected in the numbers of specimens per square meter, did not parallel the seasonal rise and fall in the percentage of stations at which it occurred, it being much more plentiful in the vertical hauls in August and October than from March to June or in September of the years 1915 and 1920, as shown in the following table:

| Date | Average number per square meter at stations where it occurred | Average number per square meter, all stations included | Date | Average number per square meter at stations where it occurred | Average number per square meter, all stations included |
|---|---|---|---|---|---|
| March, 1920 | 990 | 692 | August, 1915 | 14,850 | 13,637 |
| April, 1920 | 1,650 | 1,429 | September, 1915 | 2,453 | 1,533 |
| May (1915 and 1920 combined) | 2,504 | 1,808 | October, 1915 | 8,601 | 7,280 |
| June, 1915 | 3,193 | 1,552 | | | |

It is unfortunate that only four vertical hauls were made during August, 1915, when the species averaged so much more plentiful than we have ever found it before or since in the gulf. It may have been only a chance that the net hit local swarms, and more vertical hauls might have proved barren of *M. longa*, thus reducing the month's average. However, the fact that this northern species should have been so plentiful (from 10,300 to 23,400 per square meter) at three late summer stations

when the temperature was near the maximum for the year, and at localities as widely separated as the eastern basin (station 10304), the mouth of Massachusetts Bay (station 10306), and the western basin (station 10307), is an interesting and an unexpected find, for we have seldom found more than two or three thousand per square meter even during its years of abundance.

The numbers per square meter can not be stated for December, 1920, and January, 1921, when *M. longa* was nearly universal in the northern parts of the gulf, for want of vertical hauls; but although the percentages of *M. longa* among copepods as a whole averaged larger then than in any other month except August (table, p. 304), the total catches of copepods were so scanty that the number of specimens concerned was small. Even during its periods of maximum abundance *M. longa* has never been more than a minor element in the total copepod population of the gulf, the average percentages in the vertical hauls for 1915 and 1920 combined being as follows at the stations at which it occurred:

| Months | Average percentage | Months | Average percentage |
|---|---|---|---|
| February | 10 | June | 9 |
| March | 10 | August | 17 |
| April | 9 | September | 4 |
| May | 3 | October | 9 |

If the stations at which it was not taken be counted in, the February percentage is thereby reduced to 2 per cent, August to 12 per cent, and percentages for all the other months by 1 to 3 per cent. The table suggests that in its years of abundance in the gulf *M. longa* is relatively least important in the plankton at seasons when the Calani are most plentiful, irrespective of fluctuations in its own numerical strength and in the generality of its distribution over the gulf.

*Vertical distribution.*—In the polar basin north of Europe and Asia *M. longa* seems indifferently distributed from the surface downward to 300 meters (Sars, 1900), and Nordenskiöld (1882) has given an interesting account of its occurrence in great abundance along the tide line in water-soaked snow in Spitzbergen.

Passing southward in the eastern Atlantic, European observers have described this species as tending to keep deeper and deeper. Thus, it occurs chiefly between 50 and 200 meters in the seas between Spitzbergen and Greenland, though to some extent at the surface (Damas and Koefoed, 1907); in the Norwegian seas (Damas and Koefoed, 1907) and fjords (Sars, 1903) it has been taken in greatest number below 200 meters, rarely at the surface; chiefly below 300 meters between the Faroes and Iceland (Damas and Koefoed, 1907); and its most southerly record—west of Ireland—was from 540 to 720 meters (Wolfenden, 1904).

It likewise occurs more regularly in the deeper levels than at the surface off the American coast, figuring in only 30 per cent of the surface hauls in the Gulf of Maine for the spring of 1920, contrasted with its presence in 46 per cent of the verticals during that same period; but it is worth noting that at two stations it was taken in the surface but not in the vertical hauls (stations 20081 and 20092),

on the second occasion with 100 specimens in a total of only 400 copepods of all kinds. Willey (1919) also records it much more often from vertical than from surface hauls in the Gulf of St. Lawrence and off Nova Scotia.

I can offer no data on its presence or absence at the surface in the Gulf of Maine during the summer months; but Willey's (1919) tables, which show that a larger proportion of the records of it obtained by the Canadian Arctic expedition were from the surface in May and June than in July and August, suggest that it tends to sink down into cooler strata as the seasonal warming of the top of the water progresses.

The vertical distribution of this species in other seas makes it probable that it ranges right down to the deepest levels in the Gulf of Maine, but the data are not sufficient to show whether it tends to gather at any particular level or is more evenly and indifferently distributed vertically.

When the locality records for *M. longa* are plotted (fig. 75) it is evident that in the years when it is most plentiful in the gulf it becomes generally distributed over the entire area of the latter, indifferently in the peripheral zone, in the central basin, and over the offshore banks as far west as Marthas Vineyard. It should be noted that the absence of summer and autumn records on Georges and Brown's Banks, and in the southeastern part of the gulf generally, is actually not a contradiction, because there were no, or at least very few, *M. longa* in the gulf during 1914, the year when we made our chief midsummer cruise in this region. The apparent predominance of records in the western side of the gulf is equally deceptive, due simply to the fact that we have worked more there than elsewhere.

*Immigration and breeding.*—The periodic appearances and disappearances of *M. longa* in the Gulf of Maine, coupled with its Arctic nature in general, identify it as primarily an immigrant to the gulf from the north, depending on frequent accessions from more prolific centers to maintain the local stock. But the fact that, unlike most of the immigrant species, it is not localized in the eastern side and around the peripheral belt of the gulf is evidence either that the visiting specimens come in such abundance and live so long that they spread universally over the entire extent of the latter before they perish, or that they succeed in breeding within the gulf to an extent sufficient for the dispersal of the resulting generations to hide the routes of entrance of their parents. In this connection it is instructive to find the distribution of *M. longa* paralleling the spring status of *Calanus hyperboreus*, a species similarly of northern affinities but for which a certain amount of local reproduction within the gulf seems sufficiently demonstrated.

The locations of the stations (fig. 76) where more *M. longa* have been taken than the average numbers per square meter for their respective months (in which respect *M. longa* closely parallels *Calanus hyperboreus*) are further evidence of this. In spring and early summer (the season when the influx of northern water is at its height, and when consequently the greatest invasions of *M. longa* are to be expected) two distinct lines of immigration are suggested by the rich catches—the one inward into the eastern side of the gulf via the northern and eastern channels, and the other westward along the continental edge of Georges Bank. The rich spring catches made in the western side of the gulf in 1920 might have been the result either of local

propagation or of invasion (probably of the latter, judging from the scarcity of the species in the preceding February, as shown in the table on p. 299); but the rich gatherings of *M. longa* made there during August, September, and October, 1915,

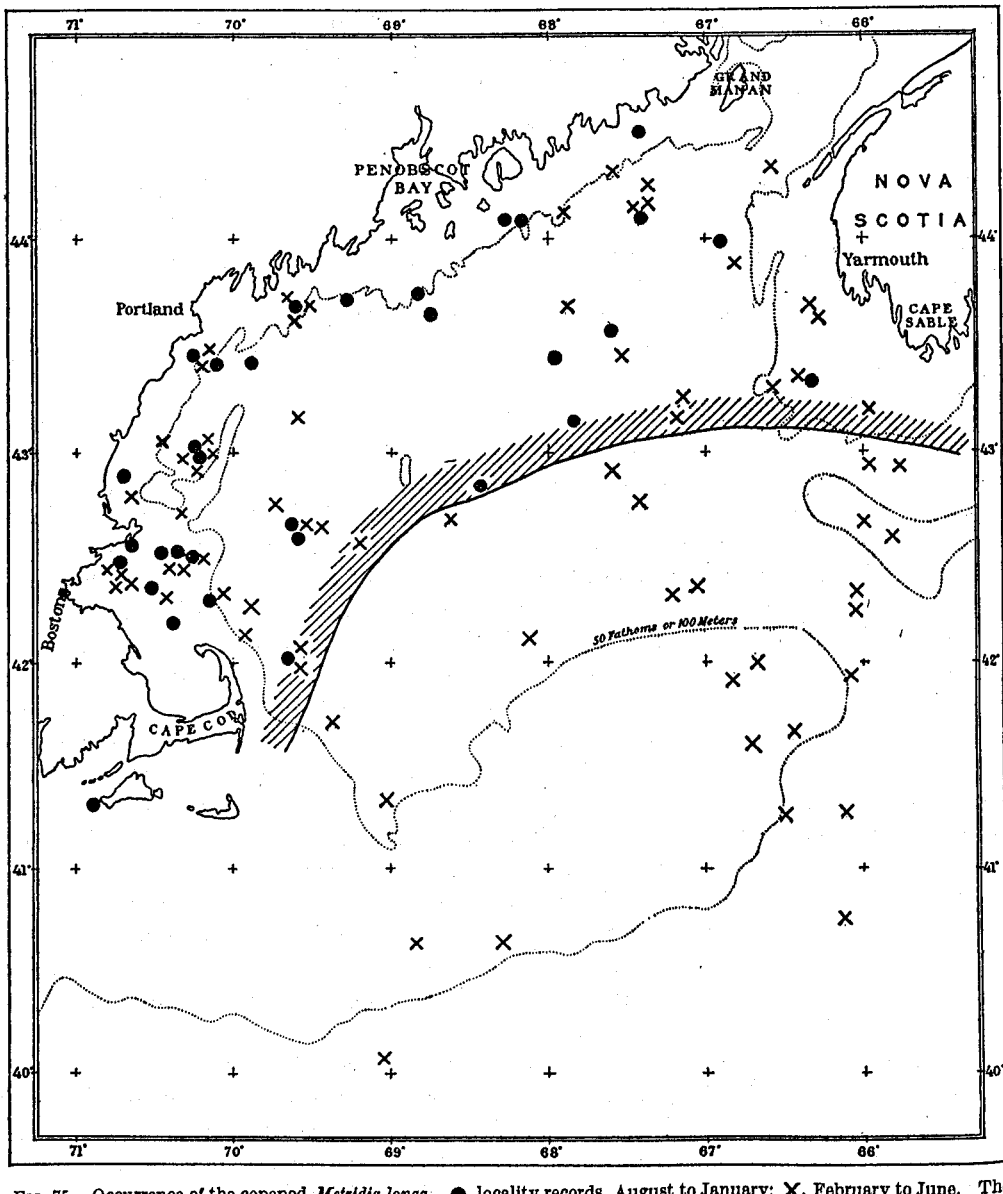


FIG. 75.—Occurrence of the copepod *Metridia longa*. ●, locality records, August to January; X, February to June. The hatched curve incloses the area where it has been found in summer and autumn

are the clearest evidence, short of the actual discovery of breeding adults and of young stages, that active reproduction had been taking place locally, because there was nothing in the plankton in general, in the salinity, or in the temperatures of that

year to suggest that any unusual influx of northern water or immigration of Arctic animals had entered the gulf during that summer. The large catch of *M. longa* on October 21, 1915, near Marthas Vineyard (station 10331, about 9,000 per square

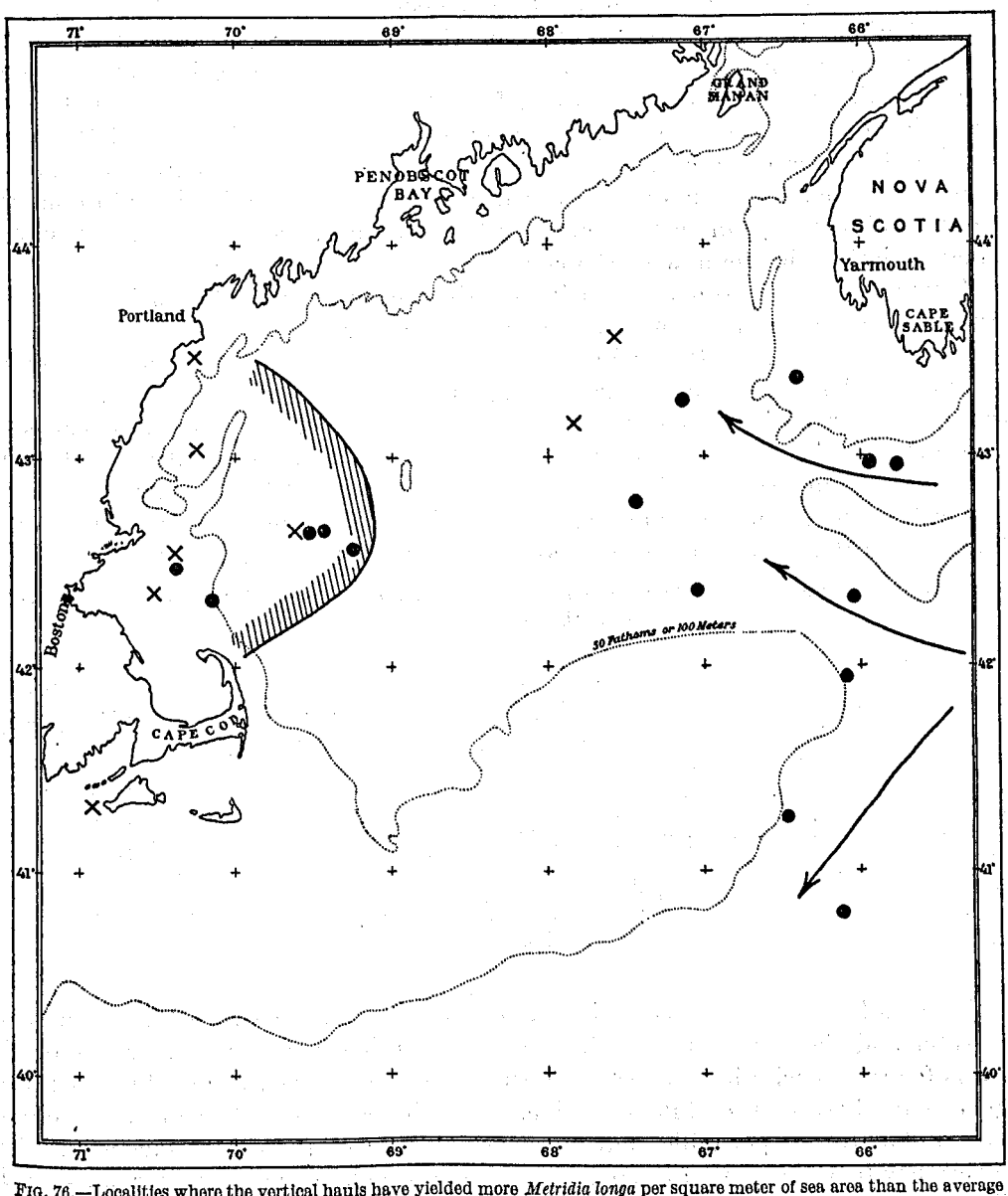


FIG. 76.—Localities where the vertical hauls have yielded more *Metridia longa* per square meter of sea area than the average for the respective month. ●, March to June; X, August to October. The arrows indicate the chief migration routes; the hatched curve incloses the area where reproduction probably takes place within the Gulf

meter), at a location much farther west and south than the species had ever been taken before, is especially instructive in this connection, for in this case there is no possibility that any direct influx had taken place from Nova Scotian waters for

several months previous. Probably the specimens in question had drifted thither around Cape Cod from the center of abundance in the southwestern part of the gulf.

Granting that *M. longa* is able to breed in the gulf to some extent, its periodic disappearances are sufficient evidence that it does so only sporadically and temporarily. Perhaps it is only able to carry on through one or two generations in the high temperatures in which it must exist there, and failing accessions of new stock dies out until there is a fresh invasion from the north. Evidently such fluctuations in local reproduction and migrations mirror the physical features of the water in which this little crustacean lives, but it is not yet possible to state the precise relationship which its temporary appearances in the Gulf of Maine bear to temperature and salinity there or in the waters to the east and north, or to the seasonal or annual variations in the flow of the currents.

There is every reason to class it a cold-water species in the gulf, and it has actually been taken there in water a fraction cooler than zero (at St. Andrews, February, 1917; Willey, 1921); but having been found widespread in the summer and autumn of 1915 in temperatures as high as 8 to 10°, it can survive and perhaps even breed over a wider range than has generally been supposed in European seas, where 6.75° is the highest temperature of record for it (Farran, 1910), and where most of the captures have been from water of 2.25 to 3.25°. *M. longa* was in comparative abundance and apparently in good condition off Marthas Vineyard at 14.5° (station 10331), but it is hardly conceivable that it could have lived long there.

*Minimum temperatures at any depth at stations where Metridia longa is recorded for August, September, or October, 1915*

| Station | Date | Minimum temperature in degrees C. | Station | Date | Minimum temperature in degrees C |
|---|---|---|---|---|---|
| 10304 | Aug. 6 | 4.78 | 10325 | Oct. 4 | 5.28 |
| 10306 | Aug. 31 | 5.78 | 10326 | do | 5.39 |
| 10307 | do | 5.1 | 10327 | Oct. 9 | 9.4 |
| 10309 | Sept. 1 | 5.72 | 10328 | do | 9.4 |
| 10311 | Sept. 2 | 9.4 | 10329 | do | 8.95 |
| 10315 | Sept. 7 | 10 | 10331 | Oct. 21 | 14.5 |
| 10318 | Sept. 16 | 8.61 | 10333 | Oct. 22 | 11.89 |
| 10319 | Sept. 20 | 8.5 | 10337 | Oct. 26 | 10.39 |
| 10321 | Sept. 29 | 11.22 | 10338 | Oct. 27 | 9.4 |
| 10323 | Oct. 1 | 6 | 10339 | do | 7.28 |
| 10324 | do | 6.78 | | | |

More information is needed before the relationship between the salinity of the water and the occurrence of *M. longa* in the gulf can be traced. Most of the records for this species in the northeastern Atlantic have been from salinities rather higher than those of the Gulf of Maine, where it has been taken most commonly in water of 32 to 33.5 per mille; but Nordenskiöld's account (p. 248) suggests that in the very low temperatures of the polar sea it may be able to exist in water but slightly saline, and we took it in salinities of 31 to 32 per mille on several occasions during the spring of 1920 and once in 29.94 per mille (station 20096, surface haul). Probably *M. longa* is never plentiful enough to be of much importance in the natural economy of the Gulf of Maine, but no doubt it serves to some extent as fish food, having been

found in the stomach of the Arctic cod (*Boreogadus saida*) in the Greenland Sea (Damas and Koefoed, 1907, p. 566).

### Metridia lucens Bœck

This species has a more southern range than *M. longa*, being widely distributed over the temperate and boreal parts of the North Atlantic but hardly entering the Arctic zone. On the European side it occurs regularly west of France, at the mouth of the English Channel, south and west of Ireland, between the Faroes and Iceland, in the northern part of the North Sea to the Skager-Rak, and northward along the west coast of Norway to the Lofoten Islands. There are a few records of it north of the Murman coast and in the Greenland Sea[39]. To the southward it occurs in the Mediterranean, and it has also been recorded from the Gulf of Suez (van Breemen, 1908). Presumably *M. lucens* ranges right across the North Atlantic, though Herdman did not find it on his passages between England and the Gulf of St. Lawrence (Herdman, Thompson, and Scott, 1898), for the Canadian fisheries expedition had it generally in and off the mouth of the Laurentian channel, along Nova Scotia, and occasionally in the Gulf of St. Lawrence (Willey, 1919, p. 202, fig. 27).

*M. lucens* is a common species in the Gulf of Maine. Wheeler (1901) reports it from Woods Hole (as "*M. hibernica* Brady and Robertson") and Fish (1925) found it there in winter. During the summers of 1913, 1914, and 1916 the *Grampus* towed it at about a dozen stations on the outer part of the shelf and outside the continental edge southward from off Cape Cod to abreast of Chesapeake Bay (Bigelow, 1915, p. 295; 1917, p. 290; 1922, p. 147), as well as at two localities near land—off Long Island (station 10083, August 1, 1913) and off Delaware Bay (station 10375, August 4, 1916). West of Cape Cod it seems to keep offshore, for Williams (1906 and 1907) does not list it from Narragansett Bay nor does Fowler (1912) from New Jersey. The latitude of Chesapeake Bay, in the one direction, and the deep water between the Scotian and Newfoundland Banks and the Gulf of St. Lawrence, in the other, are, respectively, the southern and northern limits to its known range along eastern North America.

*M. lucens* is also known from the Pacific, being described by Esterly (1905) as one of the most abundant copepods in the plankton at San Diego, Calif., both in summer and winter.

As van Breemen (1908) has pointed out, this is one of the few copepods which is luminescent, and as it is chiefly responsible for the phosphorescence on the Irish coast in spring (Farran, 1903, p. 12), no doubt it is partly responsible for the brilliant phosphorescence so often seen in the Gulf of Maine.

*Distribution in the Gulf of Maine.*—Next to *Calanus finmarchicus* and *Pseudocalanus elongatus*, *M. lucens* has appeared most frequently in the towings in the gulf, but with considerable fluctuation in the regularity of its distribution and in the numerical strength of the local stock from year to year. In the summer of 1912 it was recognized at 26 per cent of the offshore stations and at 30 per cent during the ensuing winter; but this was the poorest period for it in our experience, for Doctor Esterly

[39] For a summary of what is known of its distribution see Sars (1903) and Farran (1910).

found it at 76 per cent of all the stations east and north of Nantucket in the summer of 1913 and at 60 per cent of the July-August stations of 1914. The year 1915 yielded *M. lucens* in the vertical hauls at 58 per cent of the stations right through the season, irrespective of locality in the gulf (table, p. 297), and 1920 and 1921 were the best years, with *M. lucens* occurring at 84 to 85 per cent of the stations, both for the spring months and for December and January. In addition to the captures of this species on the recent cruises of the *Grampus*, *Albatross*, and *Halcyon*, Wheeler (1901, p. 176, as "*M. hibernica*") describes it as very common in Plymouth Harbor, Mass., in August, 1899, while Dr. A. G. Huntsman (Willey, 1919) and Dr. J. P. McMurrich [40] have taken it frequently in the neighborhood of St. Andrews.

Plotting the stations at which *M. lucens* has and has not been taken (fig. 77) shows that it occurs over the whole extent of the Gulf of Maine, on the offshore banks as well as inshore, across the whole breadth of the shelf off Marthas Vineyard, and along the continental slope; and although we failed to find it in the harbors of Gloucester, Rockport, Kittery, or Portland during July and August, 1912, its presence in Plymouth Harbor and at St. Andrews proves that it inhabits estuarine and inclosed waters as well as the open sea. The rather confused picture presented by the chart of distribution is simplified if the records be classed as summer-autumn and winter-spring, for all the years combined, and if the gulf be divided as follows:

1. Coastal zone out to 150 meters, Cape Cod to Grand Manan. Summer-autumn, present at 53 per cent of the stations; winter-spring, present at 70 per cent of the stations. (In the Massachusetts Bay region it was present at 77 per cent of the summer-autumn stations.)

2. Off Lurcher Shoal. Occurred at all the stations, both summer-autumn and winter-spring.

3. Coastal banks west of Nova Scotia, out to German Bank. Occurred at all the stations, both summer-autumn and winter-spring.

4. The basin in general, west of longitude 68° 30′. Summer-autumn, at 56 per cent of the stations; winter-spring, at 73 per cent.

5. Basin in general, east of longitude 68° 31′ W, including the Fundy Deep. Summer-autumn, 75 per cent of the stations; winter-spring, 75 per cent.

6. Northern channel. Occurred at all the three stations for which the copepods have been listed, spring and summer.

7. Browns Bank. Occurred at one of two stations in summer, and at the two spring stations for which the copepods have been listed.

8. Eastern channel. Occurred at all the stations, four in number, for which copepods have been listed, summer as well as spring.

9. Eastern half of Georges Bank, east of longitude 68° W. Present at one and absent at one summer station; present at all five spring stations.

10. Georges Bank west of longitude 68° W, and continental shelf off Marthas Vineyard and Nantucket. Present at three of eight summer-autumn stations for which the copepods have been listed and at one station in July, 1916; present at all three winter-spring stations.

[40] In his unpublished lists of the plankton for St. Andrews.

11. Outside the continental edge abreast of the gulf, off Cape Sable, and off Marthas Vineyard. Present at two out of seven summer-autumn stations and three out of four winter-spring stations.

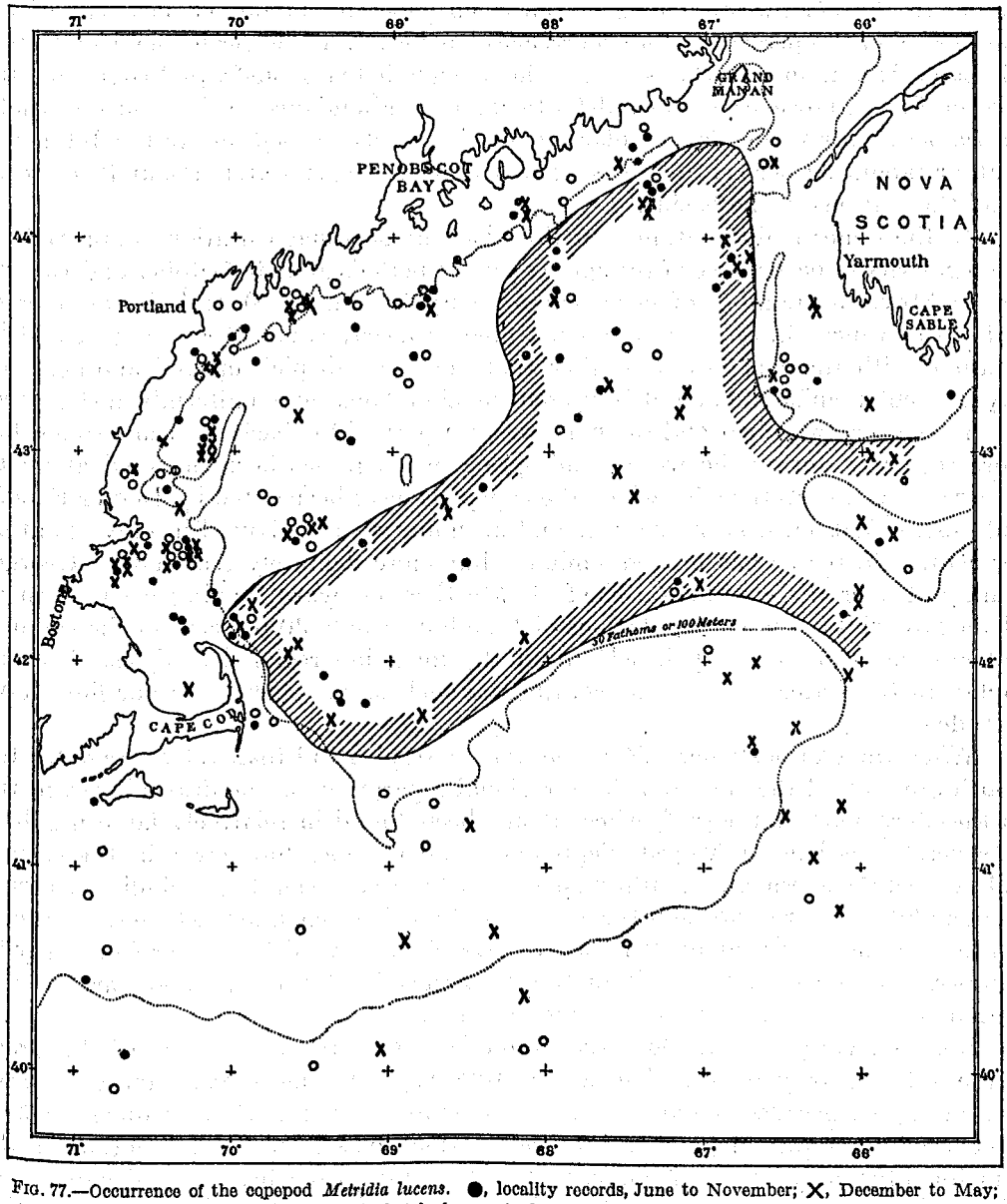


FIG. 77.—Occurrence of the copepod *Metridia lucens*. ●, locality records, June to November; X, December to May; O, stations where it was not found. The hatched curve incloses the area where it has been taken at 75 per cent of the stations, irrespective of the year or season

Irrespective of the time of year *M. lucens* has appeared more regularly in the towings made in the two deep entrances to the gulf (eastern and northern channels) and along the eastern slope of the basin, where every station in every year has yielded

it, than anywhere else in the gulf. Its occurrence has been nearly as universal over the whole eastern half of the basin and in the southern part right across to Cape Cod (recorded at 75 to 80 per cent of all the stations), but it has been decidedly less regular in the northwestern part of the basin generally (about 63 per cent of the stations), and the percentage of occurrences has been much lower in the deep trough off Cape Ann than anywhere else. The trough between Jeffreys Ledge and the Isles of Shoals, however, seems a definite center of abundance for it. On the whole, *M. lucens* occurs rather less regularly over the coastwise belt out to the 100-meter contour (about 59 per cent of the stations) than in deeper water (about 72 per cent of all the stations in the basin).

In the richer region outlined on this chart no seasonal variation is apparent in the regularity of occurrence of the species for the periods June to October and December to May, the number of occurrences being the same (28) and the number of stations at which *M. lucens* was not detected as nearly equal (6 and 3) as could be expected with the constant possibility that one net will pick up and another miss any particular animal unless it is present in abundance and uniformly distributed.

In the coastwise belt and the northwestern part of the basin it occurs somewhat more regularly during the winter and spring, when it has been detected at about 66 per cent of the stations for which the copepods have been listed by Doctor Esterly and Doctor Wilson, than in summer and autumn, when it figured in only about 45 per cent. *M. lucens* has proved similarly but more definitely seasonal on Georges Bank and over the continental shelf off Marthas Vineyard, having been taken at all the late winter and spring stations of 1920 but at only 30 per cent of the summer and autumn stations; as pointed out in the foregoing regional analysis, this also applies to the waters outside the continental shelf as far offshore as our lines have extended.

When the stations where *M. lucens* was more plentiful than the average for the month are plotted (fig. 78), a definite regional separation can be drawn between the northeastern part of the gulf, where it has been found in relatively large numbers on several occasions in August, September, and October but never in the spring, and the southeastern and southern parts of the area generally, including Georges Bank and its offshore slope and the eastern and northern channels, where rich catches of Metridia have been made in February, March, and April but never from May to October. In the coastwise belt in the western side of the gulf there are "rich" stations both for spring and for summer–autumn.

Seasonal variations in the actual numerical strength of the stock of *M. lucens* in the gulf can only be stated in a tentative way until more extensive data have been gathered, because the annual fluctuations in its abundance introduce a source of error of unknown magnitude into calculations based on a combination of the data for different years; and unfortunately the only year when vertical hauls were taken at frequent intervals from spring until autumn (1915) was one in which this copepod occurred less regularly than it sometimes does. Furthermore, *M. lucens*, like most other copepods, has proved decidedly "streaky" in its distribution. This phenomenon was illustrated off Gloucester on May 4, 1920, when, with the *Albatross* lying at anchor, a vertical haul at 3 p. m. (station 20120) yielded this species at the

rate of 16,500 per square meter (an unusually rich catch for it in the gulf), but a second vertical haul with the same net, hauled up at the same rate of speed and from a

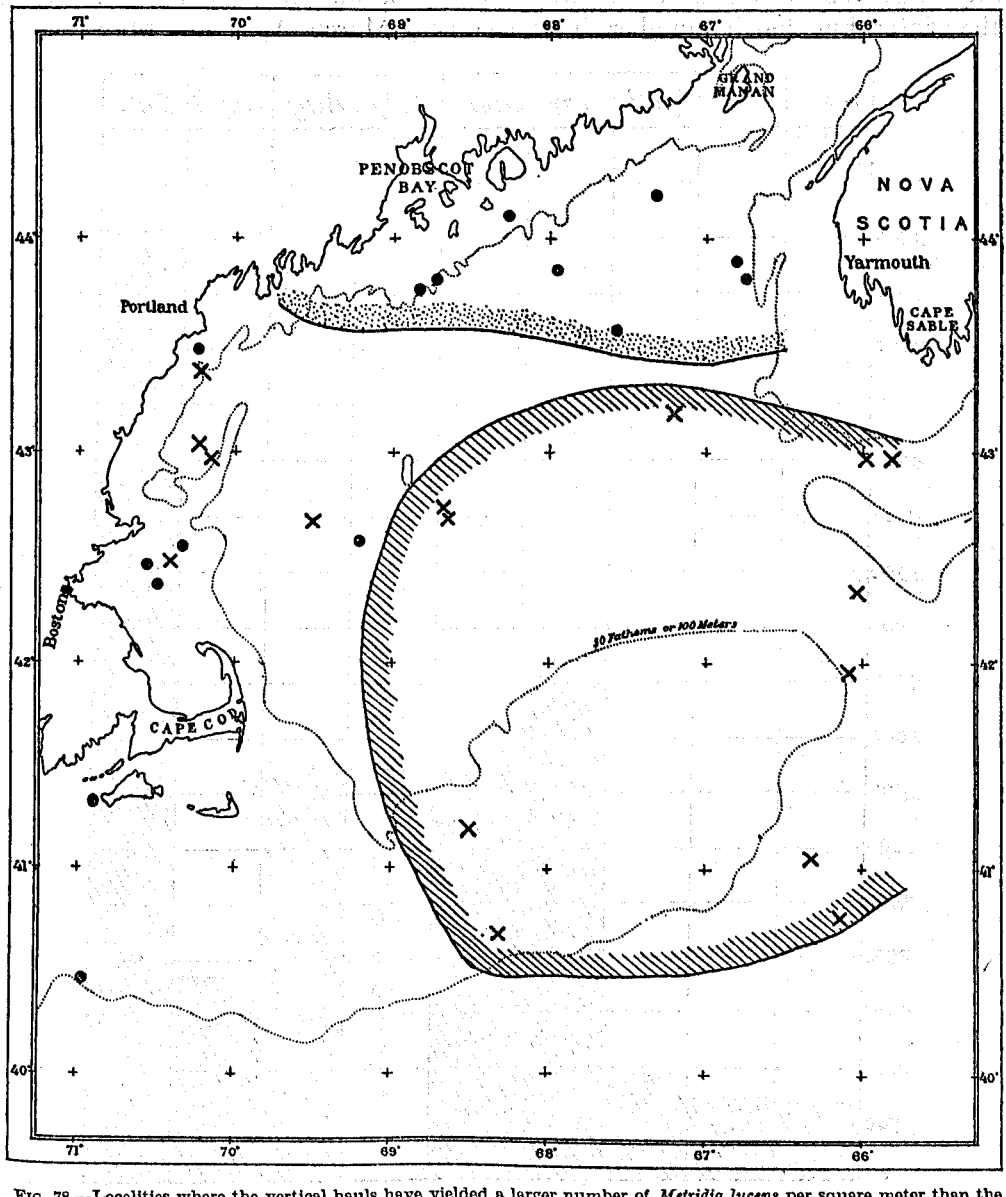


FIG. 78.—Localities where the vertical hauls have yielded a larger number of *Metridia lucens* per square meter than the average for the respective month. ●, June to October; ✕, February to May. The hatched curve incloses the area where it has been found notably abundant only in late winter and spring; the stippled curve where it has been found abundant only in summer and autumn

slightly greater depth (55 meters) at 10 p. m., gave a frequency of only 252 per square meter. Evidently the shoal encountered by the first haul had drifted past with the tide during the 7-hour interval before the second haul was made. Never-

theless, the average numbers per square meter, calculated by months, for the seasons of 1913, 1915, and 1920 combined (fig. 79), are consistent enough to suggest, though hardly to prove, that on the whole *M. lucens* is at a low ebb numerically at the end of the winter, but that its numbers increase during March, April, and May.

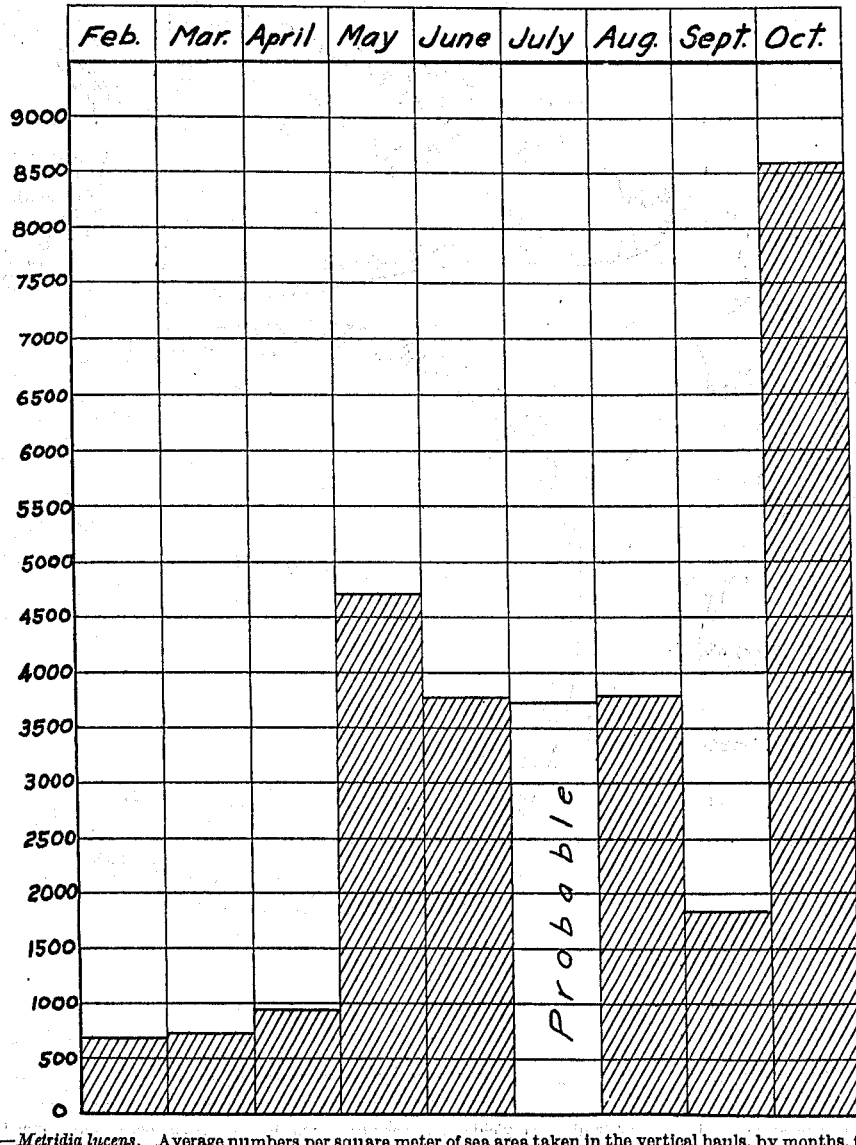


FIG. 79.—*Metridia lucens*. Average numbers per square meter of sea area taken in the vertical hauls, by months, for all the years and stations combined

Off Gloucester the number rose from nothing on March 1, 1920 (station 20050), to 150 per square meter on April 9 (station 20098) and to 16,500 in one haul on May 4, but only 252 in another, as just noted. Off the Isles of Shoals the increase was from none on March 5 (station 20061) to 1,500 per square meter on April 9 (station 20093).

In the western basin the number per square meter rose from none on February 23 (station 20049) to 5,550 on March 24 (station 20087), and then declined again to only 200 per square meter on April 18 (station 20015). It is probable, however, that this decline was local, one haul hitting and the other missing a shoal, for a few miles to the eastward. The interval from March 2 (station 20052) to April 17 (station 20114) saw the number of *M. lucens* increase from 1,250 per square meter to 3,000. Increases were likewise registered in the southeastern part of the basin, in the eastern and northern channels, and over the eastern part of Georges Bank from March to April. In the year 1915 the average number of *M. lucens* at 4 stations in the inner part of the gulf was about 8,000 in May, but one very rich catch, at the rate of about 26,000 per square meter off the Isles of Shoals (station 10278), was chiefly responsible for this large figure.

In 1920 the vernal augmentation of *M. lucens* was apparent earliest in the season over a belt extending west-east across the gulf from the Massachusetts Bay-Cape Elizabeth region to the southeastern part of the basin; but no general change of this sort can have taken place in the northeastern part of the gulf generally until a month or more later, because all the early spring catches were decidedly scanty there (at the most 550 per square meter), and in most instances the March figure was somewhat larger than the April count. Neither did the numbers of *M. lucens* taken in the southwestern part of the basin and over the western end of Georges Bank in that year show any change sufficient to be classed as seasonal, some of the later catches being the larger, some the smaller. Off the southeastern slope of Georges Bank there was an apparent falling off in the numbers of *M. lucens* from March 12 (stations 20067 to 20069) to April 16 (station 20109), but a high frequency (2,360 per square meter) on the east slope of the bank on the 16th (station 20108) makes it likely that the apparent seasonal drop actually reflected nothing more significant than a streakiness in the distribution of the species. However this may be, our failure to find *M. lucens* at the stations outside the slope of Georges Bank in July, 1914 (stations 10218, 10220), argues against the idea that this region is the site of a vernal augmentation such as takes place in the inner part of the gulf.

An average of about 3,300 per square meter at 14 stations in the inner part of the gulf for August, 1913, ranging from 600 to 9,000 at the individual stations (Bigelow, 1915, p. 286), does not indicate any notable alteration in the numerical strength of the stock of this species during the summer. One August station for 1915 (10304, eastern side of basin) was unusually productive of *M. lucens*, the vertical haul taking it at the rate of about 23,000 per square meter, but probably the net chanced to pass through a local shoal of these little crustaceans on this occasion.

In 1915, which may or may not have been a typical year, some multiplication of *M. lucens* seems to have taken place from August to October, for though the differences between the numbers taken are not large they are consistent. Thus none at all were taken in a vertical tow off Gloucester or in the basin off Cape Ann on August 31 (stations 10306 and 10307), but the stations in the coastal zone between Cape Cod and Cape Elizabeth (stations 10319, 10320, and 10321) gave an average of about 2,400 per square meter on September 20 to 29. On October 1 to 4 three stations along the same zone (stations 10323, 10324, and 10325) gave an average of

nearly 6,000, and *M. lucens* averaged about 8,000 per square meter at two stations at the mouth of Massachusetts Bay on October 27 (stations 10338 and 10339).

The count off Penobscott Bay rose similarly from 590 per square meter on September 16 (station 10318) to 12,250 per square meter on October 9 (station 10329), and from none at all off Machias, Me., on September 11 (station 10316) to 7,687 per square meter on October 9 (station 10327). In no case did we find the numbers of *M. lucens* decrease from September to October at any given locality. Though the evidence just detailed is not precise, with each example being explicable as the result of chance, when all are taken together they point to a more or less definite autumnal maximum for *M. lucens* within the Gulf of Maine.

The scarcity of *M. lucens* in the Woods Hole region in summer, deducible from the fact that the only specimen which Wheeler (1901) saw there was taken in December, contrasted with large catches of 11,700 and 16,300 per square meter made close in to Marthas Vineyard and offshore on this line on October 21, 1915 (stations 10331 and 10333), suggests a similar autumnal augmentation for the species as far west and south as it regularly inhabits the shoal waters over the inner part of the continental shelf.

Unfortunately no vertical hauls were made, and consequently the numbers per square meter can not be stated for the later autumn or until February in any year; but it is probable that the numbers existing over the Gulf of Maine as a whole suffer a sharp drop in November because the catches of copepods in the horizontal hauls during the midwinter of 1920–21 were uniformly very scanty, *M. lucens* averaging only about 8 per cent of them.

*Vertical distribution.*—In other seas *M. lucens* has been found from the surface down to 2,000 meters. In the North Atlantic it is, on the whole, most abundant between 50 and 100 meters, with a decided tendency to swim up to the surface at night and to sink again by day (Farran, 1910); but in the San Diego region on the Pacific coast of the United States, where Esterly (1912, p. 301) describes it as "overwhelmingly more abundant and frequent on the surface between 10 p. m. and 2 a. m." and "practically absent from the surface between 8 a. m. and 8 p. m.," its daytime plurimum is much deeper—200 to 300 fathoms.

In the gulf of Maine it is decidedly more numerous at some little depth than at the surface, and the frequency of its presence at the top of the water is apparently a factor of the time of year, to some extent, as well as of the time of day. Thus, during the spring of 1920 it was recognized in 24 surface hauls (table, p. 303), widespread over the gulf, and in 62 verticals. It has been listed only five times at the surface in July and August—twice in 1912 (Bigelow, 1914, table, p. 115), three times in 1914 (Bigelow, 1917, table, p. 290), and not at all in 1913, although this was a summer when it was nearly universal east and north of Cape Cod. No data are available for 1915. As regards the time of day, sixteen of the spring records for it at the surface were from between 6 p. m. and 8 a. m., and eight between 8 a. m. and 6 p. m. All but one of the summer records were between sunset and sunrise, the single exception (station 10245, August 12, 1914) being for 10.30 a. m., but at a locality near Lurcher Shoal where considerable vertical stirring of the water by tidal currents is to be looked for. Thus, in the Gulf of Maine *M. lucens* is more apt to come to the surface

in spring than in summer, and its excursions upward to the top of the water are not so closely confined to the hours of darkness in spring as they are during July and August.

The vertical hauls shoaler than 100 meters yield further evidence of a diurnal migration of *M. lucens*, for the catches have averaged decidedly larger between 6 p. m. and 8 a. m. (average 4,246 per square meter for 26 stations) than between 8 a. m. and 6 p. m. (average 896 per square meter for 21 stations); and if further separated into two groups by months—February to May and September to October—the same holds good, as follows:

| | 6 p. m. to 8 a. m. | 8 a. m. to 6 p. m. |
|---|---|---|
| Average number per square meter, February to May | 1,601 | 287 |
| Average number per square meter, September to October | 7,854 | 4,553 |

To compensate for this, smaller averages might be expected by night and larger by day in the deeper hauls as the Metridia swim up and sink back. Interpretation of these and comparison of the deeper hauls with the shoaler is complicated by the fact that we have one unusually rich catch of almost 23,000 per square meter in a vertical haul from 200 to 0 meters (station 10304, August 6, 1915) by night, but it is obvious that if the specimens in question were concentrated near the surface, as is perfectly possible, a shoal haul would have caught nearly or quite as many. This applies to any individual haul, but when deep hauls consistently average more productive than shoal, with a greater difference than can be accounted for by the longer column of water fished through, it is safe to say that the animals are concentrated in the lower levels.

The greater the number of hauls, the greater the dependence which can be placed on the average results. In the present case the number of hauls is not large enough to warrant definite conclusions. If the one very rich deep haul just mentioned be omitted, we have 1,190 as the average number per square meter in vertical hauls from deeper than 200 meters from 8 a. m. to 6 p. m. and 1,200 from 6 p. m. to 8 a. m. This does not suggest any diurnal migration as deep as 200 meters.

It is obvious that the contour of the bottom of the gulf largely determines the depth range of this copepod or of any other animal, for such of the stock as inhabit the coastal zone are necessarily confined to a very shoal stratum. No copepod can sink as deep in the Gulf of Maine, where the greatest depth is only about 330 meters, as it can off San Diego. Apart from this limitation by topography, however, the level of plurimum abundance of this species is about the same in the gulf as in the eastern North Atlantic—namely 50 to 150 meters. Thus all but one [41] of the vertical hauls which have yielded 5,000 or more per square meter have been from depths of 200 meters or less, more than half of them shoaler than 100 meters, irrespective of the time of day or part of the gulf in which the stations were located. The depths of the five richest catches of all (those yielding *M. lucens* at the rate of more than 15,000 per square meter) have likewise varied from shallow to deep.

[41] The exception is station 20087, Mar. 24, 1920, from 250 meters.

| Station | Date | Number of Metridia lucens per square meter | Depth in meters | Station | Date | Number of Metridia lucens per square meter | Depth in meters |
|---|---|---|---|---|---|---|---|
| 10278 | May 14, 1915 | 26,250 | 150–0 | 10333 | Oct. 22, 1915 | 16,300 | 80–0 |
| 10304 | Aug. 6, 1915 | 23,450 | 200–0 | 20120 | May 4, 1920 | 16,500 | 48–0 |
| 10328 | Oct. 9, 1915 | 17,100 | 60–0 | | | | |

These average numbers of this copepod per square meter, calculated from the vertical hauls, do not suggest that the strata of water below 150 to 200 meters added appreciably to the catches, although not enough deep hauls were made for a positive assertion.

| Depth of vertical hauls | Average number per square meter |
|---|---|
| Between 30 and 100 meters | 2,750 |
| Between 101 and 199 meters | 3,136 |
| Deeper than 200 meters | 2,562 |

*Local breeding and immigration.*—No direct observations have been made on whether or to what extent *M. lucens* spawns in the Gulf of Maine. Consequently, its geographic and seasonal distribution is the only basis on which to judge whether the local stock is chiefly the result of local reproduction or depends upon immigration from richer centers of propagation for its maintenance. The regularity of occurrence and comparative abundance of the species within the gulf is a strong argument that it is regularly native there. Its regularly increasing numbers during the spring and the pronounced augmentation in its numerical strength in September and October likewise point to vernal and autumnal waves of propagation. However, no definite areas of abundance which might be looked upon as local centers of reproduction have yet been demonstrated for this species in the gulf, notwithstanding the large numbers of locality records and counts of actual abundance which the *Grampus*, *Albatross*, and *Halcyon* cruises have afforded. The fact that it has been found most regularly in the eastern and southern parts of the gulf points to a certain amount of immigration via the two channels and across Browns Bank from the continental shelf off Nova Scotia, where the Canadian fisheries expedition found it widespread (Willey, 1919).

Until its status is better understood in the gulf the latter may be looked on as a regular and important breeding center for it, but with the local stock augmented by immigration.

*Relationship to physical conditions.*—In other seas *M. lucens* has been found over a wide range of temperatures from 4.83 to 20.5°, usually upwards of 5.5°; and in salinities ranging from 28.1 to 35.4 per mille, most commonly in 33.3 to 35.3 per mille (Farran, 1910; Esterly, 1912). The Gulf of Maine records bring the lower limit of temperature down to 0.33 to 0.78° (station 20062, March 5, 1920); and its presence on the surface in the coastal waters of the gulf in late winter and early

spring (e. g., stations 20056, 20058, 20060, 20061, 20077, 20081, and 20083, March, 1920) makes it unlikely that any temperature that may be experienced in the open gulf is fatally cold for this species, though it may not be able to survive the subzero temperatures of ice-laden seas. On the other hand, one of the records of it on the surface of the western basin (station 10256, August 23, 1914) was from nearly as high a temperature (19.56°) as it has ever been found in, although it could have reached decidedly cooler water by sinking a few meters. Most of the records of this copepod in the gulf have been from temperatures between 4 and 15°, but, like Esterly (1912), I have found it impossible to correlate its regional and seasonal variations in abundance with changing temperature. Nor is it likely that its distribution within the gulf is governed by local differences in salinity, the whole of that body of water being well within the limits within which *M. lucens* occurs commonly elsewhere.

*Economic importance.*—While no definite observations seem to have been made on the extent to which *M. lucens* is eaten by plankton-feeding fishes, it is generally assumed to be an important article in the diet of the mackerel in Irish waters. No doubt mackerel, all the herring tribe, and the other copepod eaters consume it to some extent in the Gulf of Maine, but it averages such a small numerical percentage of the catch of copepods compared with the dominating swarms of *Calanus finmarchicus*, which its adults about equal in size, that it can vie with the latter in economic importance only when local shoals gather.

*Average percentage of Metridia lucens, by months, in the total catches of copepods*

| Hauls | Percentage | Hauls | Percentage |
|---|---|---|---|
| March, 1920, verticals | 8 | September, 1915 | 4 |
| April, 1920, verticals | 7 | October, 1915 | 12 |
| May, 1915 and 1920, verticals | 5 | December, 1920, horizontals | 6 |
| June, 1915, verticals | 9 | January, 1921, horizontals | 12 |
| August, 1913 and 1915 | 5 | | |

On three occasions in October, 1915 (stations 10327, 10328, and 10329), *M. lucens*, forming 25 to 30 per cent of a moderately abundant copepod community (table, p. 298) and about equaling Calanus, would have offered an attractive pasture for the schooling fishes. This was also the case off Gloucester on May 4, 1920 (*M. lucens* constituted 30 per cent at station 20120). In every other instance, however, when we have found it forming 25 per cent or more of the copepods the total catch of all kinds has been extremely scanty.

### Monstrilla serricornis Sars

G. O. Sars described this species in 1921 from two male specimens taken off the west coast of Norway. Occasional specimens from four surface hauls in the Gulf of Maine in March and April, 1920 (table, p. 303), are the second record of its occurrence; but these four, including Browns Bank, the northeastern part of Georges Bank, the neighborhood of Lurcher Shoal, and Mount Desert Island, indicate that it is to be expected anywhere in the gulf. It is the only representative of its family yet reported there.

### Oithona similis Claus

This species has variously been described as "world-wide" (Farran, 1910) and as Arctic, with southern extension (Willey, 1920). The first would seem to fit it best, for it has been taken from Barents Sea, Spitzbergen, and from the Arctic coasts of Alaska and Canada (Willey, 1920) in the north, right down the whole extent of the North and South Atlantic to latitude 35° S., and beyond that to latitude 60 to 65° S. in the Antartic south of Kerguelen Island. It is likewise widespread in the Red Sea and in the Indian Ocean and about Ceylon; it is also reported from the Pacific and New Zealand, occurs in the Mediterranean, has been taken at the Canaries, is plentiful about the British Isles, enters the Baltic, and is abundant along the whole coast of Norway, in the Norwegian sea, and in Barents Sea.[42] It occurred in practically every one of Herdman's gatherings right across the North Atlantic and through the Gulf of St. Lawrence from Liverpool to Quebec (Herdman, Thompson, and Scott, 1898). T. Scott (1905) also lists it from the Gulf of St. Lawrence, but the only other published records for it on the eastern coast of North America are for Woods Hole (Wheeler, 1901; Fish, 1925) and Rhode Island (Williams, 1907).

This species appears in Doctor McMurrich's plankton lists for St. Andrews during December and January in about two-thirds of the hauls; less frequently during February and March (about 50 per cent of the hauls). During the late spring, summer, and early autumn until mid-October, it was found in about 11 per cent of the hauls. This indicates a winter plurimum for the species, but at no season was it as abundant as the larger calanoids, being almost always recorded in the lowest of the four classes of abundance (1 to 4) used by Doctor McMurrich.

*Oithona similis* was not found in any of the earlier towings in the open gulf, but being so frequent at St. Andrews and so widely distributed over the high seas elsewhere, probably this slender little copepod has usually slipped through the comparatively large-meshed nets used for the vertical hauls and for the horizontals for which the copepods have been listed. This seems the more likely because the Canadian fisheries expedition did not take it at all in many hauls in the Gulf of St. Lawrence, where Herdman found it in almost every gathering. This is corroborated by Doctor Wilson's report of it at several stations in 1920 and 1921, as noted below in his supplementary note on the copepods (p. 306).

Perhaps no marine planktonic copepod exists over a wider range of temperature and of salinity than does this little cyclopid. Equally at home in the tropic Indian Ocean, in polar seas close to the freezing point, in the brackish Baltic (it has been found there in salinity as low as 7 per mille), and in the very salty surface water of the Gulf of Suez and Red Sea (salinity upwards of 38 per mille), it is not likely that either of these factors determines its seasonal periodicity or regional distribution in the Gulf of Maine.

### Paracalanus parvus (Claus)

This species is probably cosmopolitan in temperate and tropical seas, the localities from which it has already been reported being almost "world wide" (Farran, 1910, p. 61) except for the Arctic and Antarctic. These include the northeastern Atlantic

[42] For further details see Giesbrecht (1892); Sars (1918); Farran (1910); Thompson and Scott (1903); Wolfenden (1911); Willey (1920); van Breeman (1908).

up to Denmark Strait and to the north of Iceland (With, 1915); the Faroes; the west and south coasts of Norway; the English Channel; southern part of the North

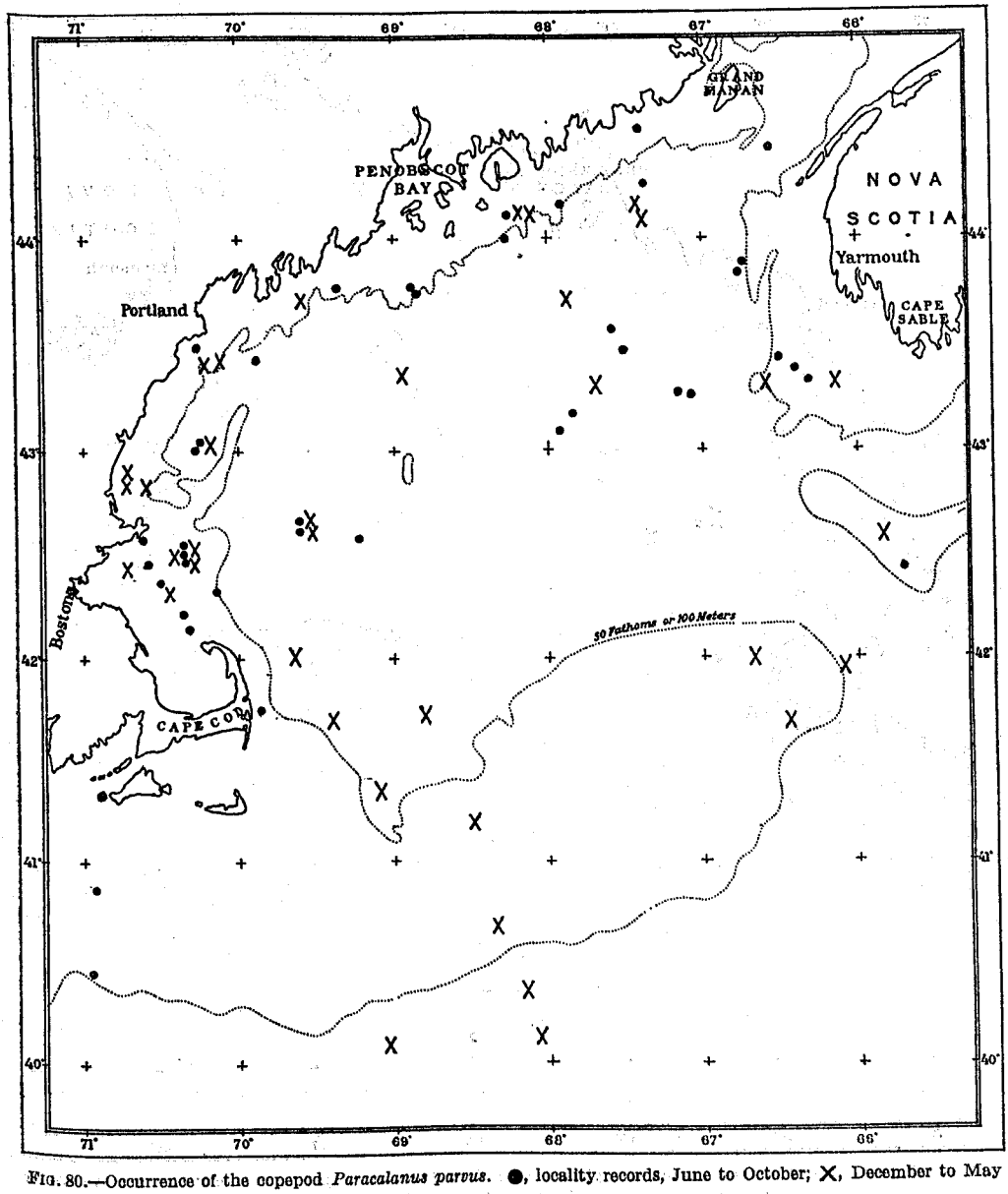


FIG. 80.—Occurrence of the copepod *Paracalanus parvus*. ●, locality records, June to October; X, December to May

Sea, Skager-Rak, and west Baltic; the Mediterranean and Black Seas; the Gulf of Guinea (T. Scott, 1894[43]); the south Atlantic off the Cape of Good Hope; the Red and Arabian Seas and the Indian Ocean (A. Scott, 1902 and 1909; Cleve, 1901); the Malay

[43] Wolfenden (1911) questions whether these specimens of Scott's were correctly identified.

Archipelago; New Zealand (Brady, 1901); and from various other localities in the Pacific between latitudes 61° N. and 55° S.[44]

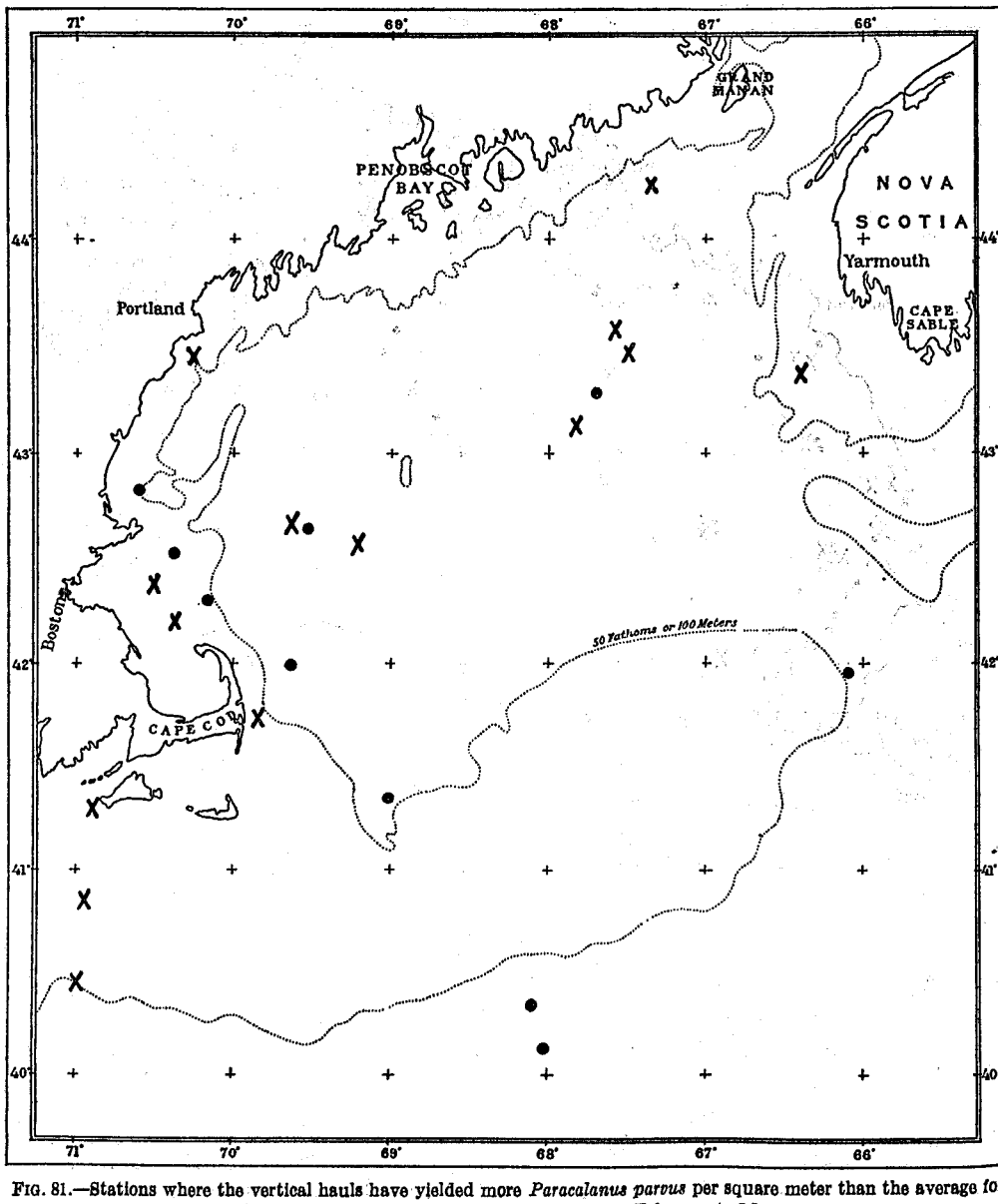


FIG. 81.—Stations where the vertical hauls have yielded more *Paracalanus parvus* per square meter than the average for the respective month. X, June to October; ●, February to May

There are only three previous records for it on the east coast of North America—that is, Gulf Stream off Woods Hole (Wheeler, 1901), Woods Hole (Fish, 1925), and

[44] For a more complete account of the distribution of this species as at present understood see Thompson and Scott (1903), Farran (1910), and With (1915).

Gloucester Harbor (Esterly, in Bigelow, 1914, p. 116). Farran (1910) has classed it as a tropical and temperate form, which is corroborated by Willey's (1919) failure to find it in the collections of the Canadian fisheries expedition off Nova Scotia and Newfoundland or in the Gulf of St. Lawrence, where it has never been reported, and by its absence from the plankton collections made by Herdman off the Straits of Belle Isle (Herdman, Thompson, and Scott, 1898); but it ranges eastward along Nova Scotia for some distance past Cape Sable, for the *Grampus* took it at three stations across the continental shelf off Shelburne, Nova Scotia, on June 23, 1915 (stations 10291, 10293, and 10294), and the *Albatross* found it again near Roseway Bank (station 20074) and outside the continental edge on this line (station 20077) on March 19, 1920.

*Paracalanus parvus* may have been overlooked in the earlier towings in the Gulf of Maine because it is so tiny (it is the smallest of calanoids), but the collections of 1915, 1920, and 1921 prove it present in the gulf in every month in the year except July and November, when no hauls were made—that is, a year-round resident. In spite of its brief history in our towings its records extend widespread over the gulf, indifferently outside the continental edge, over the offshore banks, in both sides of the deep basin, and all around the coastal belt (fig. 80). There are also records over the continental shelf off Marthas Vineyard (stations 10331 to 10333; table, p. 298).

In spite of the seasonal fluctuations outlined below, the regional distribution is as general in the cold half of the year as in the warm half, and Paracalanus occurs in all parts of the gulf and about as regularly in one region as another. The plotted records might suggest a concentration in the inner parts of the gulf, but in reality this merely reflects the greater number of hauls which have been made there, and more especially the fact that no towing was done in the southern or eastern parts of the basin or on Georges Bank during the summer of 1915. In short, this copepod is to be expected anywhere in the region at any time of year. I have not been able to subdivide the gulf into regions "rich" or "poor" for this species, whether for the year as a whole or for the individual months, the stations where catches were larger than the monthly average being widely distributed (fig. 81) (having reference to the regional distribution of the hauls in different years and seasons) both for the winter-spring and for summer-autumn; but we have taken it in much larger numbers off Marthas Vineyard (station 10332 and 10333) than anywhere east or north of Nantucket, suggesting that the waters over the continental shelf south of southern New England are a center of abundance for it.

*Seasonal fluctuations.*—*P. parvus* has been taken at the following percentages of the stations for 1915, 1920, and 1921 (tables, p. 298):

| Date | Percentage of stations | Date | Percentage of stations |
|---|---|---|---|
| March, 1920 and 1921 | 29 | September, 1915 | 75 |
| April, 1920 | 23 | October, 1915 | 93 |
| May, 1915 and 1920 | 80 | December, 1920 | 50 |
| June, 1915 | 100 | January, 1921 | 40 |
| August, 1915 | 100 | | |

Cautioning the reader that the difference may be partly explicable as evidence of "rich" and "poor" years for the species, the percentages indicate that it is practically universal in the inner half of the gulf throughout the summer and early autumn but less plentiful during winter and spring. The average number per square meter likewise shows it to be most abundant in the inner part of the gulf during the warm months.

The average numbers of *P. parvus* per square meter in vertical hauls, counting only the stations where it occurred, are as follows:

| Date | Average number | Date | Average number |
|---|---|---|---|
| March, 1920 | 455 | August, 1915 | 14,042 |
| April, 1920 | 600 | September, 1915 | 4,065 |
| May, 1915 and 1920 | 3,656 | October, 1915 | 9,045 |
| June, 1915 | 1,015 | | |

If the table were made to include the stations where it was absent, or at least so rare that the vertical net failed to take it, the discrepancy between March and April and the other months would be still greater. The hauls for February, 1920 (stations 20044 to 20048), are omitted from this table because the high average resulting from them (about 2,000 per square meter) is due to catches of 5,000 and 3,000 per square meter at the two stations outside the continental edge (stations 20044 and 20045), which would undoubtedly be several times too high for the inner waters of the gulf at this season.

In the western side of the basin Paracalanus increased in number in 1915 from about 1,000 per square meter on May 5 (station 10267) and 1,300 on June 26 (station 10299) to 16,100 on August 31 (station 10307).

In the eastern side of the basin where there were only about 1,100 Paracalanus on June 19 (station 10288) the vertical haul took 23,450 per square meter on August 6 (station 10304). On September 29 there were 850 per square meter at a station in Massachusetts Bay (10320), and the number had risen to about 14,000 by October 27 (mean of stations 10338 and 10339). A change of the opposite order at a neighboring location near Gloucester, where the number per square meter declined from more than 25,000 on May 4 (station 10266) to about 2,500 on August 31 (station 10306) and about 3,000 on October 1 (station 10324), shows how the formation and dispersal of local shoals may more than offset the general seasonal augmentation of the species at any particular locality.

Off the Isles of Shoals a slight decrease took place from 5,250 per square meter on May 14 (station 10278) to 3,170 on October 4 (station 10325); on German Bank the figure remained about stationary from May 7 (1,500 per square meter at station 10271) to June 19 (1,500 at station 10290) and September 2 (1,600 at station 10311).

Notwithstanding these irregularities, not one of the October stations yielded less than 2,000 *P. parvus* per square meter, and the maxima within the gulf were much greater in October (30,750 off Cape Cod, station 10336, and 24,450 in Massachusetts Bay, station 10338) than in September (6,650 per square meter, station 10319). Thus it seems that there are actually more *P. parvus* in the gulf in mid-autumn than

a month earlier in the season; probably more than in summer, though perhaps no more than in May. This parallels its seasonal periodicity off northern Europe, for it is usually most plentiful in the English Channel in autumn (Farran, 1910), with its plurimum falling in late summer and early autumn in the northeastern Atlantic up to Iceland (With, 1915).

Another fact clearly brought out is that this species, like most other copepods, may be decidedly streaky in its distribution at times. For instance, when we made one of our richest catches of it (24,450 per square meter at station 10338) on October 27, 1915, there were hardly one-sixth as many a few miles inshore (station 10339; about 4,040 per square meter). As a less striking example, there were respectively 3,600 and 3,400 at two stations (10321 and 10324) at the mouth of Massachusetts Bay on September 29, but only 850 per square meter at a third station (10320). This makes it impossible to draw any but the most general conclusions from the numbers of specimens taken until a much larger body of information has been accumulated.

I have purposely refrained from discussing seasonal periodicty for *P. parvus* on the offshore banks for want of sufficient data. Until something is known of its status there during the summer and autumn all that can be said is that it was slightly more plentiful on Browns Bank on June 29, 1915 (470 per square meter, station 10296) than on March 13, 1920 (60 per square meter, station 20072), but both catches were so scanty and the difference between them so small that it is not significant. On the eastern part of Georges Bank it was not taken at all at two stations on March 11, 1920 (stations 20065 and 20066), but was comparatively plentiful on April 16 and 17 (3,400 per square meter at station 10310; 1,640 at station 10311). Off the southwestern slope of the bank, on the contrary, it was much more numerous on February 22 (5,000 and 3,000 per square meter, respectively, at stations 20044 and 20045) than on May 17 (only 400 per square meter at station 20129), contradictory observations from which no conclusions can be drawn.

*Vertical distribution.*—With (1915) has described the species as usually near the surface in the northeastern Atlantic, and the majority of records of it in other seas have been from shoal towings. In the Gulf of Maine, however, it showed no tendency to congregate in the uppermost strata during the spring of 1920, for it was detected in a smaller percentage (10 per cent) of the surface hauls than of the vertical hauls, and only in small numbers at these few (table, p. 303). Little can be said of its vertical distribution in other months of the year because the copepods have not yet been listed from any of the surface hauls for 1915 or subsequently, and a record from a vertical haul merely locates the specimen somewhere between the top and the bottom of the water. It is probable, however, that most of the specimens collected by the *Halcyon* in 1920–1921 (table, p. 304) came from the general level at which the nets were working horizontally—that is, from depths varying from 20 to 240 meters.

The average depth of all the vertical hauls which had more than the average number of *P. parvus* is 127 meters, and the four richest catches of all—that is, those with more than 20,000 *P. parvus* per square meter (stations 10332, 10333, 10336, and 10338)—were, respectively, from 50–0, 80–0, 50–0, and 80–0 meters, locating the zone of chief abundance for the species as shoaler than 100 to 125 meters.

*Relationship to temperature and salinity.*—The geographic distribution of *P. parvus* in the ocean in general points to moderately high temperatures as most favorable for it, justifying Farran's (1910) characterization of it as a tropical and temperate species. The many records of it in the Red Sea, around Ceylon, and in the Malay Archipelago, often from hauls no deeper than the intake pipe of a steamer's pump (A. Scott, 1902), make it probable that no temperature ever prevailing in the open sea is fatally high or even unfavorably so for it. Toward the other extreme, the presence of *P. parvus* at so many localities in the Gulf of Maine in February and March (table, p. 299) proves it able to survive cooling down to 3 to 5°. In fact, the actual localities and depths of capture locate it in water fractionally cooler than 2° at three different stations;[46] but most of these February-March records are from localities where the temperature was above 3° at some level between the surface and the bottom (stations 20044, 20045, 20046, 20048, 20054, and 20081). Specimens drifting into colder regions or levels of the gulf in early spring may perish, as any animal finding its optimum environment in high temperature probably would.

Thus, the zone close to the coast may well be a death trap for this copepod during the coldest season, but the stock living in the basin can avoid winter chilling by sinking to the deeper levels, where it would not experience a temperature lower than 4 to 5° in most years. Therefore, it would not be surprising if more extensive study proves its zone of maximum abundance in the gulf to lie at a greater depth during the coldest season than during summer and autumn. Tending to corroborate this prediction is the fact that the richest catches for March and April (stations 20054 and 20115) were in vertical hauls from 250 and 295 meters, respectively, where the temperature below 150 meters was 5° or higher; and that the vertical nets fished through zones of water warmer than 10° (below 100 meters) at the localities of the "rich" catches off the southwest slope of Georges Bank for February (stations 20044 and 20045).

Previous records locate *P. parvus* in salinities higher than 40 per mille in the Arabian Gulf and as low as 19.33 per mille in the Kattegat. In addition it appears indifferently oceanic or neritic, occurring from the open sea, on the one hand, to tide pools, on the other (*fide* Dr. C. B. Wilson). Therefore, it is not likely that the variations in salinity which obtain in the Gulf of Maine are an important factor in influencing its distribution there. Perhaps no member of the crustacean plankton of the open sea can accommodate itself to greater fluctuations in the salinity of the water than this little copepod.

*Endemicity and immigration.*—The spawning of *P. parvus* has not actually been recorded in the Gulf of Maine, but the fact that the species occurs there throughout the year and is about equally widespread from month to month, though with a definite periodic cycle in its abundance and in the regularity of its distribution, is strong evidence that *P. parvus* does reproduce successfully in the gulf, and that enough of the stock survives the winter to multiply to the frequencies recorded for summer and autumn. The monthly averages for the percentages of stations at which the species has been taken and for the numbers of specimens per square meter both point to May as the commencement of the breeding season in the gulf;

[46] Station 20056, whole column cooler than 1.19°; station 20058, whole column 1.39 to 1.43°; station 20081, surface 1.95°.

but it is not clear how continuously reproduction proceeds throughout the summer and autumn or whether the definite wave of propagation from September to October, which the catches for those months suggest, actually takes place.

*Economic importance.*—Numerically, *P. parvus* usually forms only a small fraction of the catches of copepods in the Gulf of Maine, the maximum percentage recorded for any station east and north of Nantucket being only 30 per cent in one instance (station 10303). The averages for the area thus limited have been about 11 per cent for March, 3 to 5 per cent for April to June, 15 per cent for August, and 6 to 8 per cent for September and October. Therefore, owing to its small size, it can never be of much importance as fish food within the gulf; but the shoals which we have encountered in the shallows off Marthas Vineyard (station 10332) may serve as a large item in the diet of the smaller and young fishes there. This may also apply at times outside the continental edge off Georges Bank, where *P. parvus* constituted 30 to 50 per cent of the copepods at two stations on February 22, 1920 (stations 20044 and 20045).

### Parathalestris jacksoni (Scott)

The localities where this species has been taken (assembled by Sars, 1903–1911) are mostly Arctic and exclusively coastwise, including the polar islands north of Grinnell Land, Franz Josef Land, and the north coasts of Norway and Finland. He found it occasionally on the west and south coasts of Norway, the latter being the most southerly station for it previously reported.

Doctor McMurrich lists *Parathalestris jacksoni* occasionally between December 28 and January 20 at St. Andrews, New Brunswick; more frequently (about 44 per cent of the hauls) from January 20 until mid-May, but not at all during the summer or autumn. The greatest frequency—late winter and spring—falls during the coldest season, which corresponds to its Arctic nature.

Probably *P. jacksoni* will be found all around the coast line of the Gulf of Maine in similar situations and in the littoral zone generally to Cape Cod, but not farther south except as a stray.

It was never sufficiently numerous at St. Andrews to suggest that it has any great importance in the economy of the estuarine waters of the gulf, much less in the offshore parts of the latter, where it has not yet been found.

### Phyllopus bidentatus Brady

This species, first described (Brady, 1883) from a single specimen from the south Atlantic off the mouth of the Rio de la Plata in a haul from 2,650 fathoms, has since been recorded by Giesbrecht (1892) from the eastern equatorial Pacific, from the Gulf of Guinea at a depth of 5 fathoms at night and 360 by day by T. Scott (1894); at San Diego, Calif., by Esterly (1905); in the Malay Archipelago by A. Scott (1909); and off the west coast of Ireland by Thompson (1903), Wolfenden (1904), and Farran (1905); but in subsequent publications (Farran, 1908; Wolfenden, 1911) the last two authors have referred their Irish specimens to two new species since described by Farran (1908) from that same region under the names *belgæ* and *impar*.

So far as I can learn, the genus Phyllopus has not previously been reported anywhere along the eastern seaboard of North America, hence two female specimens recognized by Dr. C. B. Wilson in a vertical haul from 80 meters off Penobscot Bay, April 10, 1920 (station 20097), are of interest.

## Genus Pleuromamma

Four species of this genus have been taken occasionally in the Gulf of Maine—*P. abdominalis* (Lubbock), *P. gracilis* (Claus), *P. robusta* (Dahl), and *P. xiphias* (Giesbrecht). These are all true oceanic forms, widespread on the high seas in tropical and temperate oceans, and as they are only strays in the Gulf of Maine a brief outline of their geographic distribution will suffice.

*P. abdominalis* has been taken at many localities in the eastern side of the Atlantic from the Cape of Good Hope (Wolfenden, 1911) to the west of Ireland (Farran, 1908), in the North Atlantic between England and longitude 46°, and in the Gulf of St. Lawrence (Herdman, Thompson, and Scott, 1898). There are many records for it in the Mediterranean; it has been taken repeatedly in the Red Sea and right across the northern part of the Indian Ocean (Thompson and Scott, 1903; Wolfenden, 1905); commonly in the Malay Archipelago (Cleve., 1901; A. Scott, 1909); and at stations widely distributed over the Pacific, both south and north of the Equator, including San Diego, Calif., where Esterly (1905) describes it as common.

*P. gracilis* has been found over much the same geographic range in the eastern Atlantic (Ireland to the Cape of Good Hope), in the Mediterranean, Red Sea, Indian Ocean, and Pacific, but has not been recorded so often.

*P. xiphias* is so far known from the Atlantic between the latitudes of Ireland and the Cape of Good Hope, the Indian Ocean, Malay Archipelago, and Pacific, where it has been reported at San Diego (Esterly, 1905) and in the tropical belt between 3° S. and 20° N., 99° W. and 160° E. (Giesbrecht, 1892).

Up to the present time *P. robusta* is known only from the Atlantic between the tropical belt on the south (Dahl, 1893) and the latitudes of the Faroe Channel and the coast of Norway on the north (Sars, 1903), from the Mediterranean, and from the Red Sea. It is, it seems, the most northerly of the four species of the genus here mentioned and the only one which has occurred often enough at the stations of the International Committee for the Exploration of the Sea in the northeastern Atlantic province to be treated by T. Scott (1911) in his résumé.[46]

Previous records for the four species of Pleuromamma off the Atlantic seaboard of North America, outside the Gulf of Maine, are as follows:

*P. abdominalis*, near Sambro Bank and outside the continental edge off Nova Scotia, June and July, 1915 (Willey, 1919, three stations); also Gulf of St. Lawrence, as just mentioned.

*P. gracilis*, two stations on a line across the continental shelf off Marthas Vineyard, August, 1914, and one off the continental edge southeast of Georges Bank, July 22 of that same year (stations 10220, 10258, 10260, and 10261; also one record east of the Grand Banks (Murray and Hjort, 1912, p. 654).

[46] The more important locality records for the genus have been collected by Giesbrecht (1892), Thompson and Scott (1903), A. Scott (1909), Wolfenden (1911), Farran (1908), T. Scott (1911), Sars (1903), and van Breemen (1908).

*P. robusta*, two stations outside the continental edge between the latitudes of Delaware Bay and New York, July, 1913 (stations 10064 and 10071); one station outside the edge off Shelburne, Nova Scotia, July 28, 1914 (station 10233); one Canadian fisheries expedition station outside the continental edge and three over the outer part of the shelf off Nova Scotia, July, 1915 (Willey, 1919); and one *Michael Sars* station east of the Grand Banks (Murray and Hjort, 1912, p. 654).

*P. xiphias*, one station outside the continental edge off Delaware Bay, July 20, 1913 (station 10071). The Canadian fisheries expedition of 1915 had it at one June station in deep water off the mouth of the Laurentian channel, one July station near Sambro Bank and one outside the continental edge off Cape Sable (Willey, 1919); it was also listed by Sars from the same *Michael Sars* station east of the Grand Banks which yielded *gracilis* and *robusta* (Murray and Hjort, 1912, p. 654).

It is probable that when the ranges of these four Pleuromammas are better understood it will be found that all of them are universal away from land over the temperate and tropic latitudes of all oceans. Off the eastern coast of America, the continental edge and the outer part of the continental shelf would seem their normal inshore boundary, along which all of them may be expected in the warm, highly saline waters of the inner edge of the so-called "Gulf Stream" as far north as the Grand Banks; but the presence of *abdominalis* in the Gulf of St. Lawrence and the Gulf of Maine records to be mentioned next show that on occasion they may drift into distinctly neritic situations.

One other species of the genus, *P. boreale*, is to be expected in the Gulf of Maine, having been found by the Canadian Fisheries Expedition of 1915 at five stations off Nova Scotia (Willey, 1919) side by side with the others; but as yet it has not been detected in the Gulf of Maine towings.

The several Pleuromammas, like other planktonic animals which are purely immigrants, and uncommon ones, in the Gulf, have most often been found in the eastern side—that is, nearest their path of entrance (fig. 82)—and in the southwest part, which they may fairly be assumed to have reached via the anticlockwise eddy which dominates the circulation of the gulf.

If the data so far obtained are fairly representative, *abdominalis* (only one record) is the least common of the four species in the Gulf of Maine, whereas it is the only Pleuromamma yet reported from the Gulf of St. Lawrence and the most common at San Diego (Esterly, 1905). Pleuromamma has been represented by scattering specimens in the Gulf of Maine tows, its numbers per square meter working out as follows for the spring stations of 1920:

| Species and station | Number per square meter | Species and station | Number per square meter |
|---|---|---|---|
| *P. gracilis*: | | *P. xiphias*: | |
| 20056 | 10 | 20048 | 10 |
| 20103 | 26 | 20072 | 50 |
| 20114 | 200 | 20102 | 9 |
| *P. robusta*: | | 20117 | 175 |
| 20089 | 50 | | |
| 20098 | 12 | | |

The summer records inside the gulf and over the shelf off Marthas Vineyard have likewise been for odd specimens, but on August 26, 1914 (station 10261), *P.*

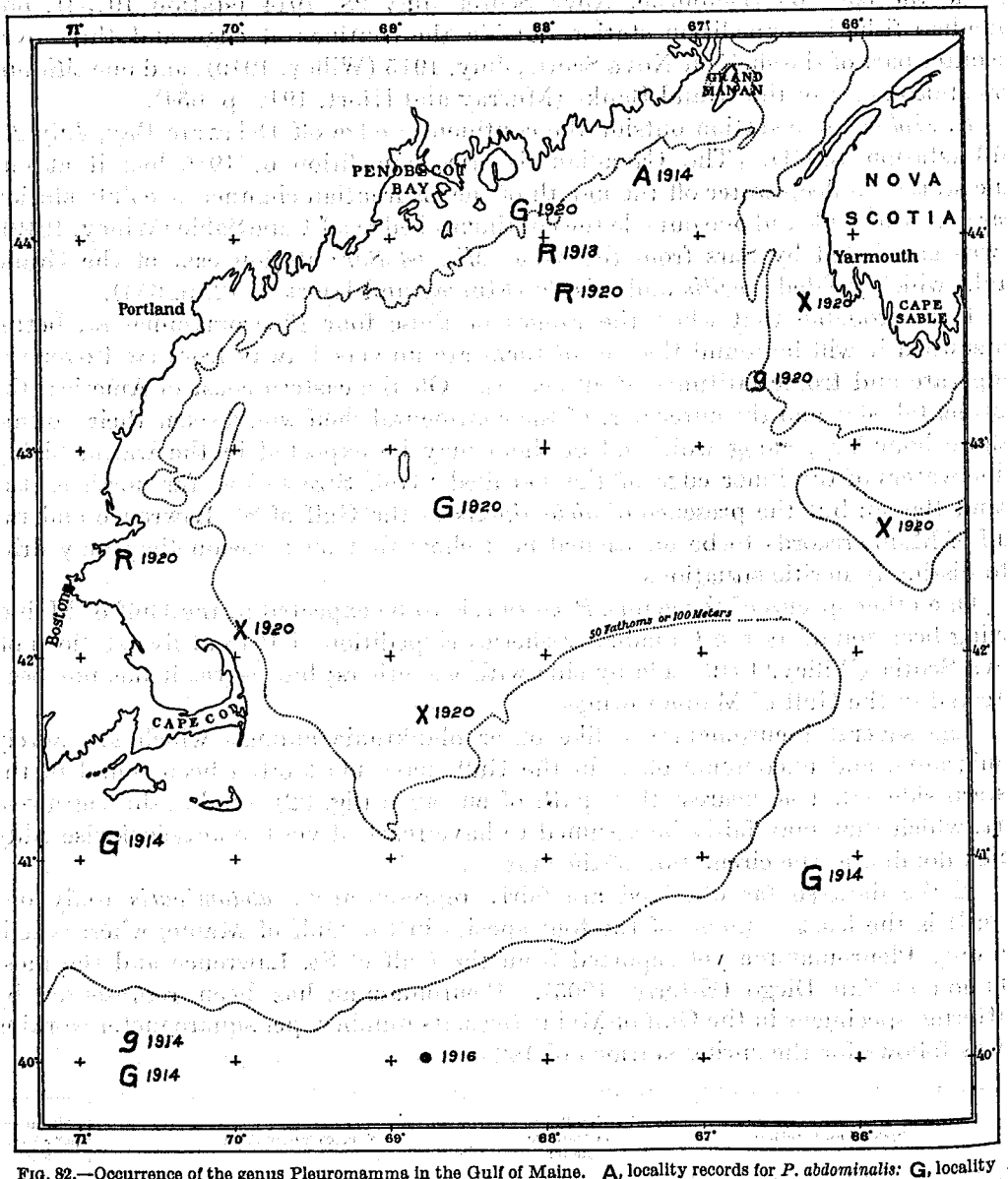


FIG. 82.—Occurrence of the genus Pleuromamma in the Gulf of Maine. A, locality records for *P. abdominalis:* G, locality records for *P. gracilis:* R, locality records for *P. robusta:* X, locality records for *P. xiphias:* ●, locality records for Pleuromamma species (?). The dates are the years of record

*gracilis* was the dominant copepod outside the continental edge off Marthas Vineyard, as *P. robusta* was at the same relative position off New York on July 11, 1913 (station 10064: Bigelow, 1915, p. 287).

It is interesting that 80 per cent of the 10 records of occurrence within the offshore banks of a genus whose source is undoubtedly the oceanic basin outside the continental edge should be for March and April, when the temperature is lowest, and only two for the summer-autumn season (*P. robusta*, station 10100, August 13, 1913; *P. abdominalis*, station 10246, August 12, 1914), whereas our summer stations alone have yielded this genus outside the banks.[47] However, with the possibility that a rare species may be overlooked among the masses of Calanus and other of the more plentiful copepods taken in the horizontal hauls, the few records do not show at what season the genus as a whole (or any one of its several species) is most likely to enter the Gulf of Maine.

It is not likely that Pleuromamma succeeds in breeding in the gulf; but the geographic distribution of the records indicates that individual specimens may be long-lived there. No relation is apparent between the occurrences of Pleuromamma in the gulf and high temperature, for its presence has been established there in readings as low as 0.49 to 1.95° (station 20056), and the two midsummer records *may* have been from water as cold as 4.22° and 7.58°, though, equally, the few specimens involved may have been picked up by the open net near the surface in a much higher temperature.

Pleuromamma has not been taken on the surface in the Gulf of Maine, but none of the hauls producing it have been from deeper than 175 meters and all but three of them were as shoal as 100 meters, or shoaler, pointing to the strata above the latter level as the region which it usually inhabits in the gulf. At San Diego Esterly (1912) found both *P. abdominalis* and *P. gracilis* coming nearly or quite to the surface during the night and sinking to considerable depths by day, chiefly to deeper than 150 meters. Similar diurnal migrations, though not so deep, are to be expected of the few specimens unfortunate enough to stray into the Gulf of Maine.

### Pseudocalanus elongatus Bœck[48]

This is a northern species and one of the most widespread and abundant copepods in the North Atlantic region and in the Arctic, where it is circumpolar. The records of its distribution have recently been summarized by Farran (1910) and by With (1915). On the European side its southern boundary seems to be the Black Sea (Sars, 1903, p. 154), the Mediterranean, and the Gulf of Suez (Thompson and Scott, 1903), which it would seem to have reached via the Suez Canal, not being known from farther down the Red Sea or from the Indian Ocean. It is widespread, probably universal, northward from Gibraltar to the North Sea, along the entire length of the coast of Norway, and far up into the Baltic. It is recorded near the New Siberian Islands, repeatedly and at many localities in the White Sea, about Spitzbergen, off Jan Mayen, in the Norwegian and Greenland seas, about the Faroes, Iceland, northward to Disko along West Greenland, from East Greenland, and right across the North Atlantic from England to the Gulf of St. Lawrence.

[47] None at stations 20044, 20045, 20068, 20069, 20077, 20109, February-April, 1920.

[48] According to With (1915) the *P. minutus* of Krøyer was based on immatures of this species, which should therefore bear the name *minutus;* but until the change is generally accepted by students of the group (Willey's (1920, 1921) recent communications still use *elongatus*) it is as well to follow the more general usage in a paper not concerned with systematics.

In American waters it has been taken as far south on the Pacific coast as Puget Sound (Giesbrecht and Schmeil, 1898), but apparently it does not reach San Diego, not having been found there by Esterly. Willey (1920) records it from south of the Alaska Peninsula, from Bering Sea, and from several localities along the Arctic coasts of Alaska and Canada. On the Atlantic side it occurs in the Labrador current off the Straits of Belle Isle (Herdman, Thompson, and Scott, 1898). The Canadian fisheries expedition found it one of the most plentiful of copepods in the Gulf of St. Lawrence and had it at most of the stations between the Newfoundland and Scotian Banks, as well as along Nova Scotia, though not in such abundance (Willey, 1919). Wright (1907) also describes it as abundant off Canso, Nova Scotia, in July and August; and as I have remarked in several previous communications, Pseudocalanus is one of the most characteristic members of the copepod community of the Gulf of Maine. West and south of this it is much less abundant and more seasonal. In warm summers it probably finds its farthest bound about New York, judging from the fact that it has not been reported at Woods Hole during the warm half of the year, though Fish (1925) found it there in winter, and from our failure to find it at any of the nine southern stations in 1913 (Bigelow, 1915). In the cool August of 1916 it was recognized at three stations on the continental shelf off New York (stations 10363, 10364, and 10365) and may have occurred at others, for only a preliminary examination has been made. In September, 1914, it was taken just outside the continental edge off Marthas Vineyard (station 10260), and in October, 1915, it occurred at all three stations across the continental shelf on this line (stations 10331 to 10333; table, p. 298). It enters Narragansett Bay in January and February (Williams, 1907), and Dr. C. B. Wilson (in a letter) writes that he has "examined specimens taken in winter as far south as the thirty-seventh parallel of latitude, opposite the mouth of Chesapeake Bay," this being the most southerly record of it along the seaboard of eastern North America.

*Gulf of Maine.*—Pseudocalanus is nearly as universal as *Calanus finmarchicus* in the gulf, indifferently in the coastal zone, in the deep parts of the open basin, and on the off-shore banks. Evidently it is a constant member of the plankton of Gulf of Maine harbors, the *Grampus* having had it in Gloucester, Rockport, and Kittery (Bigelow, 1914, p. 116). Doctor McMurrich took it at St. Andrews, where he lists it for 71 per cent of the 160 tows covering all seasons of the year. Since 1913 it has been recognized in the following proportion of the stations for which the copepods have been listed:[49]

| Date | Percentage of stations with Pseudocalanus | Date | Percentage of stations with Pseudocalanus |
|---|---|---|---|
| February, 1920 | 83 | September, 1915 | 90 |
| March, 1920 and 1921 | 94 | October, 1915 | 91 |
| April, 1920 | 90 | December, 1920 | 88 |
| May, 1915 and 1920 | 77 | January, 1921 | 80 |
| June, 1915 | 77 | | |
| August, 1913, 1914, 1915, and 1922 | 69 | General average | 83 |

[49] The summer of 1912 and winter of 1912–13 are not included in this calculation because there is reason to believe that Pseudocalanus is underestimated in the published lists because of the nets employed (Bigelow, 1914, p. 115; 1914a, p. 409).

We have found it at 77 per cent of the stations on Georges Bank and the shelf off Marthas Vineyard, 72 per cent of the stations in the basin as inclosed by the 100-meter contour, 86 per cent in the coastal zone inside 100 meters from Cape Cod to Grand Manan, 77 per cent in the coastal zone along western Nova Scotia, 86 per cent in the eastern and northern channels, but at only half the stations on Browns Bank and 65 per cent of the stations outside the continental edge.

Thus, on the whole, *Pseudocalanus elongatus* is somewhat more nearly universal close along shore than out at sea in the gulf (fig. 83); but the regional difference is so small inside the continental edge that it may be of no general significance and merely the result of one haul chancing to pick up and another to miss scattered specimens at times and places where the species is scarce. Probably the apparent infrequency of this copepod on Browns Bank is to be explained in this way.

Although *P. elongatus* is so nearly universal, the numbers actually present at any given time have usually averaged larger in the basin, in the entrant channels (northern and eastern), and along the offshore slope than anywhere in the coastal belt of the gulf inside the 100-meter contour. The locations of the stations where the number of specimens per square meter has been larger than the average for the respective month and year afford a graphic illustration of this localization of the rich catches in the deeper parts of the gulf, for 22 out of 36 have been outside and only 14 inside the 100-meter contour (fig. 84). Otherwise expressed, only 20 per cent of the shoal catches have been above average, as contrasted with 40 per cent of the deep hauls.

The "rich" catches in the basin have been distributed indifferently from the west side to the east; but this correlation between the abundance of Pseudocalanus and the topography of the bottom does not apply in the southern part of the area, for rich hauls have been made over the outer part of Georges Bank and on the continental shelf off Marthas Vineyard, while all records of the species so far obtained from farther west and south than this along the coast have been well inside the 100-meter contour.

*Vertical distribution.*—In the northerly part of its range *P. elongatus* has been found commonly at the surface in other seas as well as at various deeper levels, and its presence is established down to about 900 meters by the use of the closing net (Wolfenden, 1904), but its chief zone of abundance lies above 200 meters. The Canadian fisheries expedition took it as regularly at the surface in the Gulf of St. Lawrence as in deep tows down to 150 meters, and apparently about as abundantly.

The great majority of records for this species in the Gulf of Maine have been based on hauls from depths greater than 50 meters, not so much because of a concentration in deeper water as because the deeper hauls, horizontal or vertical, have been the basis for most of the lists of copepods. During the *Albatross* cruise of 1920 Pseudocalanus was found regularly at the surface as well as at deeper levels from the last week in February until the last week in March (about 90 per cent of the stations), irrespective of locality, but less frequently (only about 42 per cent of the stations) through April and May (table, p. 303). It is probable that this change resulted from a general tendency on its part to desert the uppermost stratum as the season advances. It was detected at only three of the six stations where the surface net yielded enough

copepods to be worth listing in the summer of 1914, but its constant presence in surface tows at St. Andrews the year round (p. 276), with the *Grampus* captures of it at the

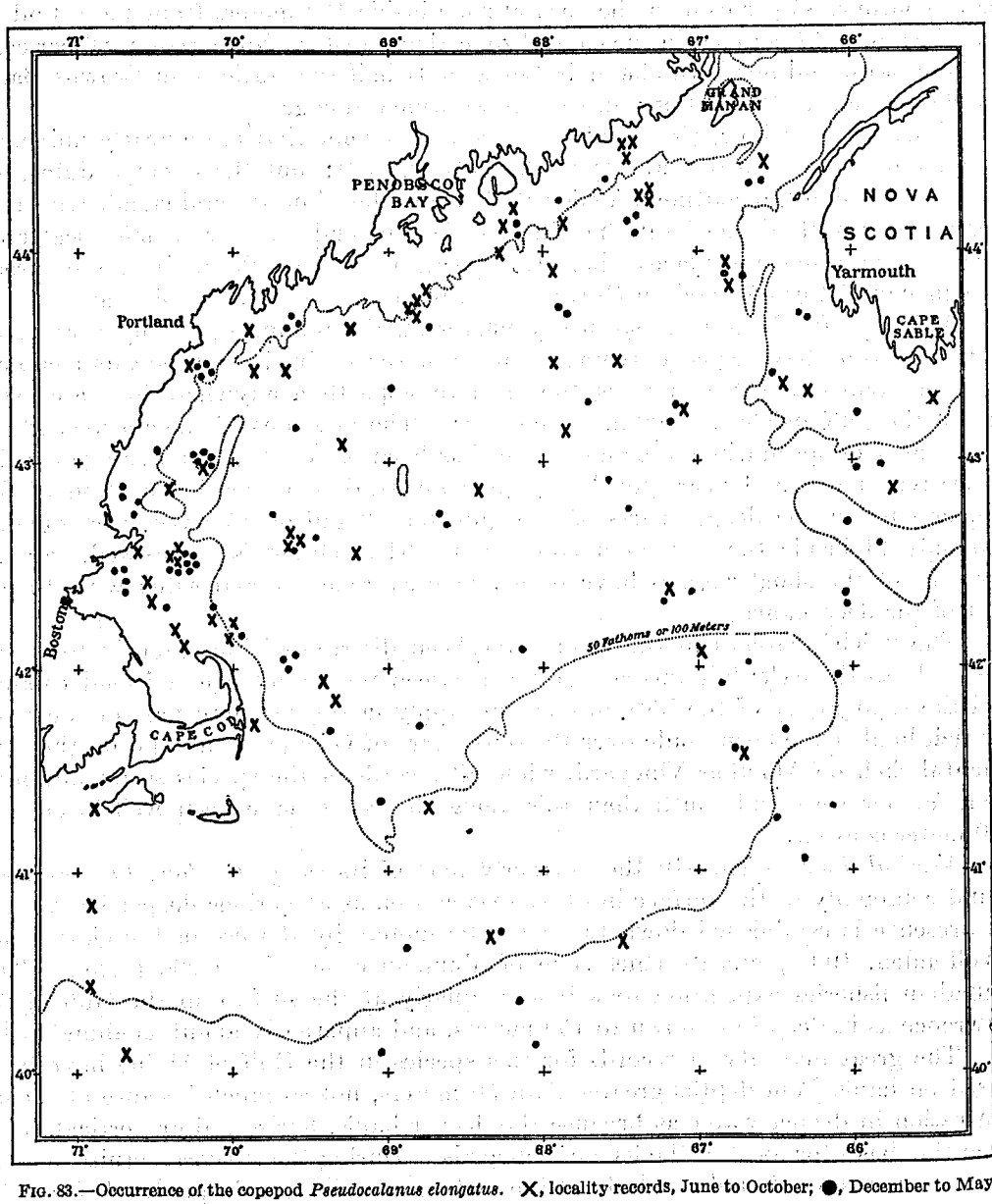


FIG. 83.—Occurrence of the copepod *Pseudocalanus elongatus*. X, locality records, June to October; ●, December to May

surface in other harbors in midsummer, proves that it is always to be expected a few meters down and is brought up by the mixing effect of moderately strong tidal currents.

I have been unable to find evidence of a stratification of this species at any definite depth in the gulf. The concentration of the richer catches of Pseudocalanus

in the deeper parts of the gulf, together with the fact that the average depth of the 36 hauls yielding more than the average number of specimens per square meter for the respective month and year has been 164–0 meters, but only 113–0 meters for the

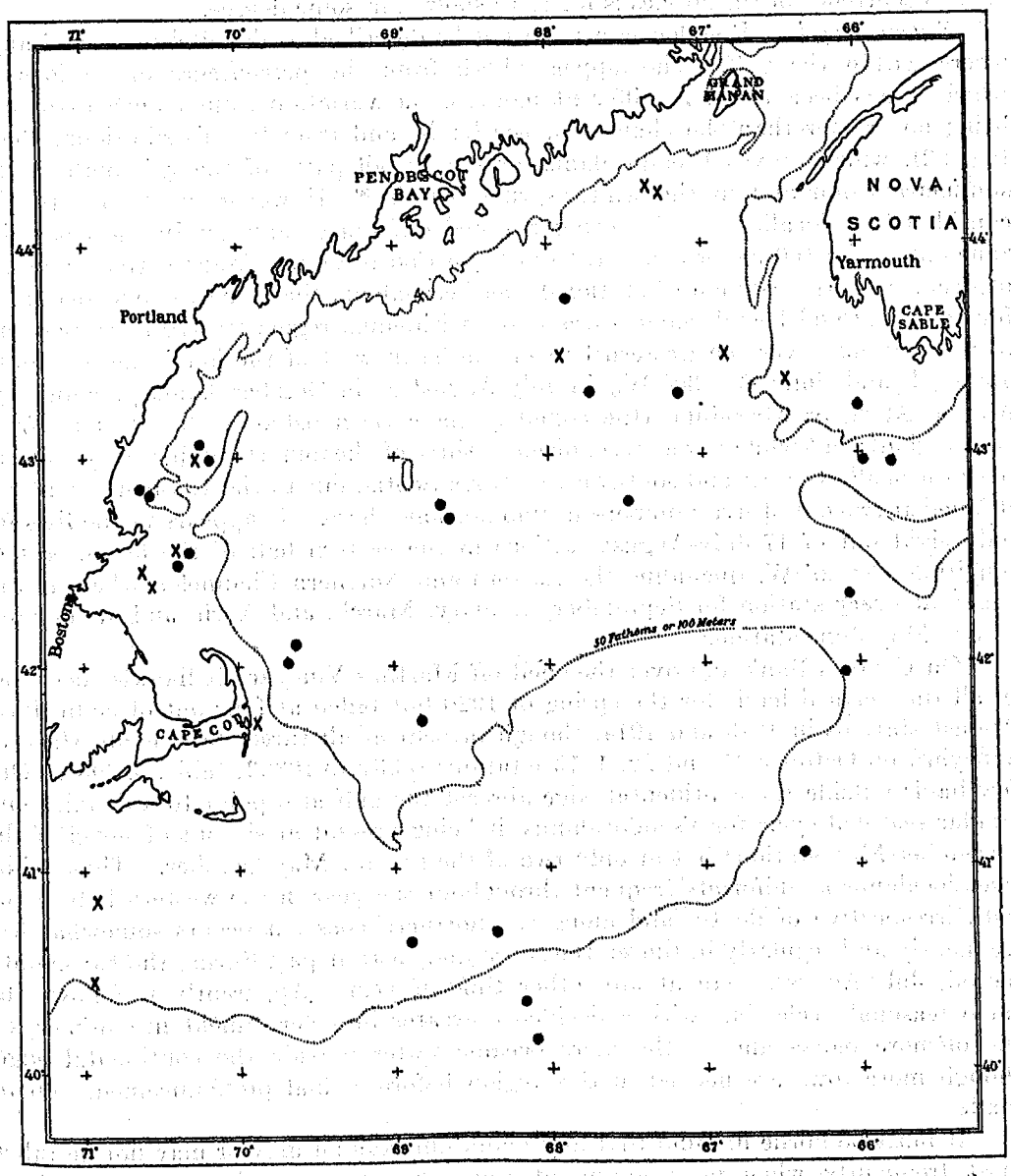


FIG. 84.—Localities where the vertical hauls have yielded more *Pseudocalanus elongatus* per square meter of sea area than the average for the respective month. X, June to October; ●, February to May

80-odd hauls yielding less than the average number of specimens, does not suggest any impoverishment of Pseudocalanus in the deep strata of the gulf, such as is demonstrated for *Calanus finmarchicus* (pp. 203, 205). On the other hand, there is nothing

in the data here offered to indicate any tendency on the part of *P. elongatus* to keep to the deepest levels, nor can I offer any evidence of diurnal vertical migration on its part, though this is so common a phenomenon among copepods that more detailed study of the occurrence of the species is likely to show it in some degree.

*Seasonal cycle.*—Pseudocalanus can not be described as definitely seasonal anywhere within the gulf. This appears both from the percentages of stations at which it has been taken in different months, the variation from month to month being no greater than the chances of the hauls, and from the distributional chart (fig. 83), which proves Pseudocalanus present in all parts of the gulf both in the summer-autumn and in the winter-spring seasons.[50] However, if the records be considered by locality, the following regional differences appear: In the coastwise zone out to the 100-meter contour, from Cape Cod to Grand Manan, the frequency of occurrence (percentage of stations) has been about the same for one season as for another,[51] and Pseudocalanus was taken with equal regularity (70 to 80 per cent of the stations) over the western half of the basin west of the longitude of Mount Desert Island (long. 68° 30′ W.) in July-August as in October-January, February-March, April, or May-June (the copepods have been listed at 39 stations from that region); but while it was recognized at three of the four December-May stations over the shallows west and southwest of Nova Scotia, out to the 100-meter contour, it failed at two out of five summer-autumn stations there. It appears in the lists for only eight out of 17 July-August stations in the eastern half of the basin, east of longitude 68° 30′ W. (including the Eastern and Northern Channels), where it was taken at every station for September, January, March, and April, and at four out of five May-June stations.

On Georges Bank and over the shelf off Marthas Vineyard it likewise occurred in all the vertical hauls for the spring of 1920 but failed at four out of eight July-August stations in 1913 and 1914, though present at all three stations off Marthas Vineyard on October 21 and 22, 1915 (stations 10331 to 10333; table, p. 298). Our few hauls outside the continental edge abreast the gulf also point to a definite and similar seasonal cycle for Pseudocalanus, it being present at six out of seven of the December-May stations but at only two of the five for May-October. Thus, while Pseudocalanus is uniformly frequent throughout the year in the western half of the gulf, irrespective of depth, and along the northern coast, it occurs somewhat less frequently and regularly in the southeastern and eastern part during the two-month period, July-August, than at any other time of year. Apparently it follows the same seasonal cycle, but with a decidedly greater impoverishment in summer, on the offshore banks and in the more oceanic water outside the continental edge, though more tows are needed in this region before a final pronouncement can be made.

It must be borne in mind that any planktonic animal may or may not be taken most frequently when most abundant (may even be most frequent when least numerous), the relationship between the two measures of occurrence depending on the uniformity of distribution. In the case of *P. elongatus* the data afforded by

[50] In contrast, compare the seasonal fluctuations in the regional distribution of such an immigrant species as *Sagitta serratodentata* (p. 320).

[51] Eighty-five per cent for December-May, 90 per cent for June-October; total number of hauls, 51.

the vertical hauls for 1915 and 1920 (tables, pp. 297, 299) point to a greater absolute abundance over the area as a whole in late summer and autumn than in early spring, constantly increasing from March until October, with average numbers per square meter, by months, for the years 1915 and 1920, as follows: February–March, 685; April, 501; May–June, 2,238; August–September, 5,723; and October, 8,456.

If the year 1913 be included in the calculation (Bigelow, 1915, table, p. 286), the August average would mount to 19,834, making this the seasonal maximum; but the possibility of an annual as well as a seasonal fluctuation must always be kept in mind.

The seasonal cycle for 1915 and 1920 in the coastal zone between Cape Cod and Grand Manan paralleled the figures just given for the gulf as a whole, with the average numbers of *P. elongatus* augmenting from about 300 per square meter in March–April, to 2,124 for May–June (or 1,699, if the stations where it failed as well as those where it occurred are counted), 2,819 or 3,947 for August–September, and 7,622 or 8,710 for October, depending on which basis of calculation be employed. The vertical hauls in the deeper parts of the gulf show a similar seasonal augmentation from early spring to September, whether for the basin as a whole or for its eastern half separately, as follows:

*Average numbers per square meter, by months, counting only the stations of occurrence*

| Locality | February–March | April | May–June | August–September | October (only 1 station) |
|---|---|---|---|---|---|
| Basin as a whole | 1,068 | 656 | 2,914 | 8,963 | 9,110 |
| Basin east of longitude 68° 30′ W | 1,083 | 811 | 3,149 | 6,752 | ---------- |

Unfortunately, nothing can be said as to seasonal fluctuations in the abundance of *P. elongatus* as distinguished from its frequency on Georges Bank or outside the continental edge, no vertical hauls being available thence for summer.

*Breeding habits.*—In the northeastern Atlantic sexually adult specimens of both sexes have been reported repeatedly at various dates between April and September (for a summary see With, 1915), and since Willey (1919) describes females with eggs and attached spermatophores from the Gulf of St. Lawrence for August, the breeding season for Pseudocalanus might be expected to fall in late spring and through the summer in the Gulf of Maine. Dr. C. B. Wilson writes, in a letter:

> In this connection it is of interest to report that although the present collection includes specimens of this species taken in every month of the year except November, not a single specimen was observed with eggs.

However, as he points out, Sars's (1903, p. 21) discovery that the ovisac is so very fragile that it becomes detached at the slightest touch "readily explains Willey's (1919) statement that the ovisacs of all the females were ruptured, and the fact that no females with eggs were found in the present collection."

Next to the actual discovery of egg-bearing females, the constant presence of this species in the gulf, its universal distribution and considerable abundance there, and the unmistakable seasonal cycle in its abundance are the strongest evidence that it is

regularly endemic there and that the maintenance of the local stock is primarily by local reproduction. The seasonal fluctuations in the numerical strength of the stock point to breeding as taking place most actively from June until September and to the entire gulf as its site.

*Relation to temperature and salinity.*—*P. elongatus* has been taken over a wide range of temperature. Judging from its abundance in polar seas, it thrives in temperatures close to the freezing point; but, on the other hand, notwithstanding its northerly distribution (p. 275), it has been found living in the warm Mediterranean and in upwards of 20° in the Gulf of Suez. However, the species reaches its maximum abundance and frequency in seas and at levels where the water is cooler than about 15°.

In the Gulf of Maine its presence has been definitely established in water as warm as 20° (surface, station 10254, August 22, 1914) and 19.56° (surface, station 10256, August 23, 1914); but its usual scarcity at the surface during the warmest months (pp. 24, 277) and the great preponderance of records (vertical and subsurface horizontal hauls) from temperatures below 12 to 15° would seem to set this as the upper limit for its optimum environment, even though much warmer water is not fatal either to its existence or even to its reproduction—witness its Mediterranean range. If the rising temperature of spring is actually the factor which tends to drive Pseudocalanus down into the deeper and cooler water in summer, this does not take place until the uppermost stratum of water has warmed from its winter minimum to warmer than 7 to 8°, for Pseudocalanus occurred rather more frequently on the surface in May, 1920, when the surface temperature averaged about 7.9° at the *Albatross* stations, than in April at an average temperature of about 3.5°.

Any species living indifferently in the inner Baltic, on the one hand, and in the open Atlantic and Mediterranean, on the other, necessarily exists over a much wider range of salinity than obtains in the Gulf of Maine. Therefore, it is not likely that the details of distribution of Pseudocalanus in the gulf are governed by the local and temporal variations in salinity obtaining there, nor does any parallel between the two appear from what is known so far.

*Economic importance.*—In the English Channel, Lebour (1919, 1919a, and 1920) found that Pseudocalanus was, on the whole, the copepod chiefly preyed upon by all kinds of larval fishes and young fish fry; and since it may be expected to play the same rôle in the Gulf of Maine (though there are no local observations bearing on this point), probably it ranks next to *Calanus finmarchicus* in its importance in the natural economy of the gulf. Granting Pseudocalanus second rank in this respect, it must still fall far behind Calanus, not only because its individuals are much smaller but because it is seldom as numerous anywhere in the gulf. Thus, Pseudocalanus outnumbered Calanus in only eight out of 139 vertical hauls between the longitudes of Marthas Vineyard and Cape Sable during the years 1913, 1915, and 1920, and equaled it in three others. As a rule there have been from five to ten times as many Calanus as Pseudocalanus at any given station. Taking the vertical hauls together for all years, for all localities west of Cape Sable, and for all seasons, Pseudocalanus has averaged about 11 per cent of the copepods. Assuming the Pseudocalanus to

have been uniformly distributed vertically, the numbers present per cubic meter of water work out as follows for our richest catches of the species:

| Station | Date | Number | Station | Date | Number |
|---|---|---|---|---|---|
| 10092 | Aug. 11, 1913 | 119 | 10332 | Oct. 21, 1915 | 958 |
| 10095 | Aug. 12, 1913 | 666 | 10333 | Oct. 22, 1915 | 382 |
| 10096 | do | 330 | 10336 | Oct. 26, 1915 | 287 |
| 10097 | Aug. 13, 1913 | 306 | 10388 | Oct. 27, 1915 | 306 |

**Rhincalanus cornutus Dana**

This species has its center of distribution in the Tropic belts of the three great oceans. It has been described from the Sulu Archipelago, from the Philippines (Brady, 1883), and from the western Pacific between latitudes 7° S. and 15° N. (Giesbrecht, 1892). It is common in the Malay Archipelago (Cleve, 1901; A. Scott, 1909). Thompson and Scott (1903) had it at ten stations in the Indian Ocean; A. Scott (1902) reports it from the Red Sea; but up to the present I have found no record of it in the Mediterranean. The German South Polar expedition found it widespread in the South Atlantic (Wolfenden, 1911). To the northward it is reported from the equatorial belt off Africa; from the Gulf of Guinea, where T. Scott (1894) found it one of the most common and widely distributed species; and in the eastern side of the Atlantic at a few stations up to latitude 52° (Thompson, 1903). The only previous report of it on the American side is from one station outside the continental edge off Cape Sable by the Canadian fisheries expedition, July, 1915 (Willey, 1919). So far as eastern North American waters are concerned, the true home of this species lies well outside the continental edge, in almost Tropic temperatures and high salinities.

In the Gulf of Maine this species is an accidental stray, appearing in the lists for nine hauls, including both horizontals and verticals (fig. 72; tables, p. 298–305), the captures within the gulf being in the northeastern part of the basin, off Penobscot Bay, off Cape Elizabeth, off the Merrimac River, and in Massachusetts Bay, a localization along the northern and western shores which parallels the distribution of other immigrants. There are also two station records for it on the continental shelf off Marthas Vineyard.

Two of the records for *R. cornutus* in the inner part of the gulf are for March, two for September, and three for December. Evidently it may enter at any time of year, and is about as apt to do so at one season as another. The records off Marthas Vineyard were for October 21 and 22, 1915 (table, p. 298).

There is no reason to suppose that this copepod is able to breed successfully within the gulf or to establish a permanent foothold there, the records from within the gulf all being for scattering specimens, up to a frequency of about 455 per square meter off Massachusetts Bay, September 29, 1915 (station 10321), at most 2 per cent of the copepods. Off Marthas Vineyard, however, the vertical haul yielded about 2,000 per square meter at one station (10333).

**Rhincalanus nasutus Giesbrecht**

This is a typically oceanic species, warm temperate in its relationship to temperature, and wide ranging in all three great oceans. It has been recorded widely in the eastern Pacific (Giesbrecht, 1892; Esterly, 1905), in the Malay Archipelago (Andrew Scott, 1909 [52]), at several localities in the northern part of the Indian Ocean (Thompson and Scott, 1903; Wolfenden, 1905), and at the mouth of the Red Sea (A. Scott, 1902). In the Atlantic it is known from latitude 35° 10′ S., in the south (Wolfenden, 1911), to Denmark Strait, the sea south of Iceland, the neighborhood of the Faroes, the Norwegian sea, and the northern part of the North Sea in the north. Farran (1910) and With (1915), who have summarized what is known of its distribution, have both pointed out that in the northeastern part of its area of occurrence its range is coterminous with the ebbings and flowings of the highly saline and comparatively warm waters of the Atlantic current. This applies equally off the Atlantic seaboard of North America, where it has been taken outside the continental edge off Chesapeake Bay, off Delaware Bay, and off New York in the summer of 1913 (stations 10064, 10071, and 10076); off Georges Bank, July, 1914 (stations 10218 and 10220); off Cape Sable; off Sable Island; and off the mouth of the Laurentian Channel between the Nova Scotian and Newfoundland Banks, June–July, 1915 (Willey, 1919, 7 stations); also east of the Grand Banks by the *Michael Sars* (Murray and Hjort, 1912, p. 654).

Within the Gulf of Maine *R. nasutus* has much the same status as its close relative *R. cornutus* (p. 283), there being 10 records, all but one of them in the peripheral belt, around which they are scattered from Browns Bank and off Yarmouth, Nova Scotia, to off the tip of Cape Cod, a distribution quite typical for any planktonic animal reaching the gulf as an immigrant from the Atlantic basin and unable to survive long or to reproduce itself there.

The geographic locations of the stations where *R. nasutus* was taken (fig. 72) are also interesting in pointing to the upper 100 meters or so as the stratum in which it enters, for if it drifted into the gulf in the underlying waters it might be expected to follow the branches of the basin, as do the bathypelagic chætognaths *Eukrohnia hamata* (p. 328) and *Sagitta maxima* (p. 324), instead of circling along and inside the 100-meter contour.

Farran (1910) and With (1915) have described the vertical range of this species as uniform from the surface down to 1,800 meters. Most of the captures listed by Willey (1919) in Canadian waters were in open vertical hauls from depths of 200 to 375 meters; once on the surface. The *Michael Sars* record just mentioned was in a closing net at 950 to 525 meters. The captures within the Gulf of Maine have all been in open nets—horizontal (station 10225) or vertical—from depths of from 48–0 down to 240–0 meters; none from the surface.

The Gulf of Maine records for *R. nasutus* are for the months of March (three), April (two), May (four), and one for July; [53] but with so few records it is questionable whether this seasonal periodocity actually means that *R. nasutus* is more apt to enter

[52] He uses the name *Rhincalanus gigas* Brady for it.

[53] In addition to the stations listed in the tables, (p. 297), *R. nasutus* was taken at station 10225 on July 23, 1914, and at stations 10272 and 10273 on May 10, 1915.

the gulf in spring and early summer than at other seasons, or whether it has been an accidental feature of the towings.

It should be noted that the presence of *R. nasutus* in the Gulf of Maine at any particular temperature or salinity does not necessarily bear any relation to the range of these factors in which it finds its most favorable environment, but simply means that once swept into the eastern side of the gulf by the entrant eddy it has been able to survive long enough to drift to the place where found. The present records prove such survival possible for a time in water as cold as 2 to 3° (stations 20072 and 20095) and in salinities no higher than 29.16 to 31.36 per mille (station 20120), though its usual range in the open North Atlantic is nearly if not wholly limited to salinities higher than 34.9 per mille, and for the most part to regions where the water is warmer than 10° at some level. Geographic distribution suggests that *R. nasutus* finds temperatures and salinities appreciably lower than these figures an effective preventative to successful reproduction.

The records for *R. nasutus* within the gulf have invariably been for small numbers of specimens, in three cases for single individuals noted in the catch of copepods (designated "T" (trace) in the accompanying tables), and only once for as many as 550 per square meter (station 20120). It has invariably been a minor element (5 to 10 per cent) in the copepod community, even along the continental slope, where it occurs more constantly, with a maximum abundance of about 1,000 to 4,000 per square meter (stations 20045 and 20069).

### Scolecithricella minor (Brady)

This species has its chief center in the North Atlantic and neighboring Arctic seas. In the northerly part of its range it has been found along the Norwegian coast as far as Lofoten; at many localities, but usually in small numbers, between Spitzbergen and Greenland northward to latitude 80° 17′ N.; and generally distributed about the Faroes and Iceland, in Denmark Strait, off southern Greenland, and northward to latitude 64° 54′ in Davis Strait (see With, 1915, for a summary of the records for this species so far published).

The *Michael Sars* did not find it off the western slope of the Grand Banks, but the Canadian fisheries expedition had it at six stations outside the continental edge at the mouth of the Laurentian Channel between Banquereau and Green Bank, off Sable Island, and off Cape Sable; also twice in the Gulf of St. Lawrence (Willey, 1919), and there are a few records for it in the Gulf of Maine, to be noted below. It has not been reported south of Cape Cod in the western Atlantic. In the eastern Atlantic it is common west of Ireland (Farran, 1905 and 1908), and while not known in the Mediterranean or anywhere in the north-central Atlantic, it was found by T. Scott (1894) in two samples from the Gulf of Guinea, one of them taken so close in to the mouth of the Congo River that the water was visibly brownish. *S. minor* has not been reported either from the South Atlantic, the Pacific, or from the tropical part of the Indian Ocean, but the original specimens of the species were from the subantarctic zone of the latter, west of the Crozet Islands, in latitude 46° 46′ S., longitude 45° 31′ E., in a surface haul.

*Gulf of Maine.*—This species has not been reported previously from the gulf, nor for that matter from off the American seaboard south of Nova Scotia, but it appeared in one vertical haul off Yarmouth, Nova Scotia, and one off Shelburne, Nova Scotia, in 1915 (stations 10272 and 10313), off Boothbay Harbor on March 4 and again on April 10, 1920 (stations 20058 and 20096), and in one horizontal haul near the mouth of the Merrimac River on the 20th of the following December (station 10492), in each case for odd specimens only (tables, pp. 297 and 299).

This copepod is typically warm oceanic, though tolerance for low temperature is evidenced by its more northerly distribution in the Arctic–Atlantic area. In the Gulf of Maine it occurs only as one of the rarest of strays from outside the continental edge. The localization of the records of capture (fig. 72), in which it agrees with Rhincalanus, points to the upper 100 meters as the stratum in which it most often enters the gulf, where, like other immigrants, it circles first north, then west, then south around the periphery, drifting in the great anticlockwise eddy. If it were swept in with the deeper lying water along the bottom of the eastern channel it would be more apt to be found along the two branches of the basin; and since it has been taken over a wide range of depth elsewhere, from the surface downward, in low latitudes as well as high, and most often from 20 to 400 meters (With, 1915), odd captures of it may be expected in the deepest strata of the gulf. So far it has not been detected in any surface haul in the Gulf of Maine.

The present records, with those of the Canadian fisheries expedition off Nova Scotia and in the Gulf of St. Lawrence (Willey, 1919), cover so many different months that this copepod may be expected in the Gulf of Maine at any season, a fact instructive for its bearing on the question of the periodicity of oceanic circulation in the region.

The biology of this species must be understood better before the relationship of its distribution to temperature and salinity can be stated. The records of capture locate it over a wide range of each—that is, in temperatures as low as −1.6° to −1.8° along East Greenland to upward of 24° in the Gulf of Guinea, while in the Greenland Sea the *Belgica* (Damas and Koefoed, 1907) found it nearly universal in salinities ranging from about 32 per mille on the Greenland side to nearly 35 per mille about Spitzbergen.

So far as temperatures and salinities *per se* are concerned, the Gulf of Maine is thus wide open to it, and its presence there in any particular temperature and salinity is simply the result of the particular drift which the specimens in question have taken and of its ability to survive wide fluctuations, something which is true of most copepods.

Scolecithricella is never sufficiently numerous in the Gulf of Maine to figure in the natural economy of the local plankton, but its immigrant nature being beyond dispute, with the Atlantic Basin as the source, it is among the most instructive of natural floats when it appears there, as showing the course followed by the indraft.

**Temora longicornis Müller**

This copepod is neritic in the sense that its areas of abundance are confined to the continental shelves of the continents or large islands and to their close vicinity. The vast majority of the records obtained for it have been from one or other side of the North Atlantic,[54] none from either the South Atlantic or from any part of the Pacific. It enters the Mediterranean to some extent (Thompson and Scott, 1903) and has been recorded from the Indian Ocean (van Breemen, 1908). Off the coasts of Europe its range as now known is confined between the latitudes of about 35° and 74° N., and it reaches its maximum development in the English and Irish Channels, in the North Sea region generally, whence it extends far up into the Baltic, and along the whole southern and western coasts of Norway. Except for a few records between northern Europe and Spitzbergen (Farran, 1910), its range seems hardly to encroach on the Arctic Seas. It has not been found in the Greenland Sea, but Sars (1903) reports it from Iceland.

On the American side the most southernly station for it is off Chesapeake Bay (Bigelow, 1922, p. 146). It is an important member of the coastwise plankton from New York eastward, including the Gulf of Maine, the continental shelf all along Nova Scotia, along the southerly aspect of the Newfoundland Banks, and in the Gulf of St. Lawrence, where the Canadian fisheries expedition collected it at about 70 per cent of the tow-net stations in 1915, locally in abundance (Willey, 1919). It has also been found in the Labrador current off the Straits of Belle Isle and thence eastward to latitude 55° 24′, longitude 41° 10′, south of Greenland (Herdman, Thompson, and Scott, 1898), which is the most northerly station known for it in the western side of the North Atlantic.

*Gulf of Maine.*—As the chart (fig. 85) shows, *T. longicornis* is widespread in the shoaler parts of the gulf, not only from land out to 10 to 12 miles outside the 100-meter contour, from Cape Cod to Cape Sable, but on Browns and Georges Banks as well, and across the whole breadth of the continental shelf off Marthas Vineyard and Nantucket. It is a creature both of the open sea and of harbors, common in winter right up to the dock at Woods Hole (Wheeler, 1901, p. 175), in Portland Harbor (Bigelow 1914), and at St. Andrews (from Doctor McMurrich's unpublished plankton lists), but recorded at only 10 to 12 per cent of the stations farther out in the deep basin of the gulf. Within this neritic area, as bounded above, and between longitudes 65° and 71° W., it has been recognized at about 41 per cent of all the tow-net stations for which the copepods have been determined, irrespective of year, season, or precise locality. Its independence of the distance from land, within the bounds of the continental shelf, may be further illustrated by the fact that Dr. W. C. Kendall, in his field notes (p. 12), mentions "small brown copepods," which from the context were almost certainly Temora, as plentiful in haul after haul on the northwestern part of Georges Bank and over the shelf out from Nantucket in August and September, 1896.

The neritic nature of Temora is further brought out by its quantitative distribution, for only three of the 20-odd stations where we have taken a greater number of specimens per square meter than the average for the respective month and year

[54] Sars (1903) and Farran (1910) have summarized its distribution; the reader is referred to them for more detailed information.

have been as far as 16 miles out from the 100-meter contour, and the only two swarms of this species which we have encountered (p. 290) have been well inside the 100-meter line. Among all the records of it in American waters west of the longitude of Sable

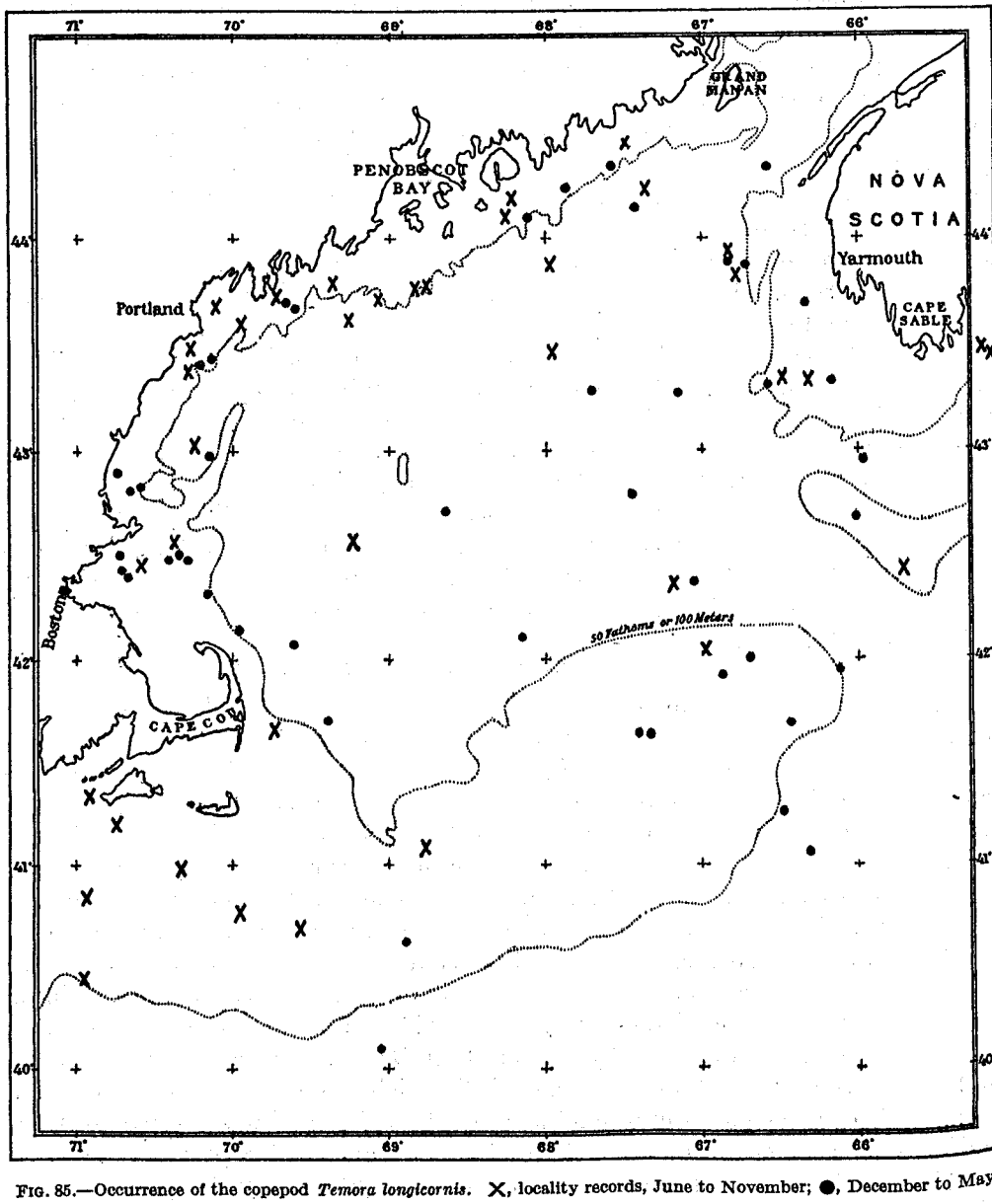


FIG. 85.—Occurrence of the copepod *Temora longicornis*. X, locality records, June to November; ●, December to May

Island, which have now been gathered by the cruises of the *Grampus*, *Albatross*, and *Halcyon* and by the Canadian fisheries expedition, not one has been from outside the continental edge as outlined by the general contour line for 400 meters; but it drifts out to the Laurentian channel between Nova Scotia and Newfoundland

and over the deep trough within the Gulf of St. Lawrence (Willey, 1919), and its range extends far out into the ocean off Labrador, as just noted (p. 287).

*Seasonal distribution.*—McMurrich (1917) has remarked that Temora occurred at intervals at St. Andrews during the autumn of 1914 and up until January 27, 1915 (on which date it was the dominant component of the plankton), but not at all from February to mid-May. His unpublished plankton lists for November, 1915, to October, 1916, carry the observations a step farther, showing Temora constantly present at St. Andrews, and in considerable numbers, from mid-September through January, but only at intervals, and represented by odd individuals, during the other months. Wheeler (1901) and Fish (1925) have likewise found it much more plentiful at Woods Hole in winter than in summer.[55]

*Temora longicornis* has been recorded in the open waters of the Gulf of Maine in every month in the year except November and February, when few tows have been studied for their copepods. In the coastwise belt the frequency of occurrence has been highest during the period September to January, and again from March to April, as indicated by the percentage of stations at which it occurred (about 50 per cent in each case), and lowest during the June–August quarter, when it was recorded at only 22 per cent of the stations in this region. However, this may reflect an annual and not a seasonal fluctuation, because Temora occurred in a much larger percentage of our hauls in July and August of 1913 (about 50 per cent in the gulf, on Georges Bank, and off Nantucket) than in those months in 1912. It was again scarce in the summer of 1914 (14 per cent of the stations on Georges Bank and in the gulf; not at any of the stations off Marthas Vineyard); but the year 1915, when Temora occurred at about 42 per cent of the stations right through the season from May to October, apparently saw the local stock increase once more. The percentage of occurrence has been about the same (33 to 38 per cent of the stations) for July–August as for February–May on the offshore banks and over the shelf off Nantucket and Marthas Vineyard.

In short, such analysis as I have been able to make does not prove a definite periodicity in the frequency of this species in the open gulf beyond suggesting the possibility that there is a minimum in midsummer.

The evidence of the vertical hauls (tables, pp. 297 and 299) is that Temora is seldom if ever dominant anywhere in the open gulf at any time, for at the maximum it has constituted only 20 per cent of the catch of copepods (station 20062);[56] and in only six of the many vertical hauls anywhere between the longitudes of Marthas Vineyard and Cape Sable has it constituted as much as 10 per cent of the copepods, the average for all being only about 3 to 4 per cent of Temora, even if the calculation be limited to those stations where this copepod was plentiful enough to be picked up by the vertical net. If the stations where it was missed be included, its average percentage drops below 2 per cent. The absolute numbers of individuals per square meter have been correspondingly insignificant, compared to those of *Calanus finmarchicus*, at the maximum being only about 18,000 within the gulf, 18,760 off Shelburne, Nova Scotia (station 10313, September 6, 1915), and about 33,000 near Marthas

[55] Williams (1907) reported it as abundant throughout the year in Narragansett Bay.
[56] 28 per cent off Shelburne, Nova Scotia, Sept. 6, 1915, Station 10313.

Vineyard on October 21, 1915 (station 10331). But perhaps less reliance can be placed on quantitative calculations based on vertical tows for this species than for any of the other copepods of frequent occurrence in the gulf, because, as Farran (1910, p. 72) has remarked (which our own experience corroborates), it "has the habit, more marked than in most copepoda, of forming swarms of great density but of limited extent." For this reason conclusions as to its abundance in any region may be entirely misleading unless a great number of hauls are made close together, both in time and in location.

On two occasions we have encountered such swarms (fig. 20) within the geographic limits covered by this report—first over Nantucket shoals on July 9, 1913 (station 10060), when Temora dominated the tow at 40 meters (Bigelow, 1915, p. 287),[57] and second on the surface off Gloucester on October 31, 1916 (station 10399), as recorded elsewhere (Bigelow, 1922, p. 135). Had a vertical net chanced to pass through either of these swarms, we would have obtained very much larger numbers per square meter than have ever resulted from the vertical hauls actually made. But were Temora as abundant in the Gulf of Maine (relative to other copepods) as Brady (1878–1880) describes it about the British Isles, along the Norwegian coast, at the mouth of the Baltic, or in the Gulf of St. Lawrence (where Willey (1919) found it locally constituting up to 62 and 70 per cent of the copepod catches of the surface nets), surely our many towings would more often have yielded it in comparative abundance instead of with monotonous scarcity.

Because the distribution of Temora is so often streaky and its frequency of occurrence varies so much in the gulf from year to year, numerical calculations based on vertical hauls scattered through different years, and often too far apart in miles, can not be depended upon to reflect its seasonal cycle correctly. But whereas the frequency of occurrence has been as high for March and April as for summer or autumn, the numbers of specimens actually taken per station have ranged smaller, averaging only about 200 per square meter for March and 300 for April at the stations where it was taken, with maxima of 1,075 (station 20068) and 1,300 (station 20105), respectively; and if the stations where the species failed were included in the calculation the averages would fall below 100 per square meter for both these months.

In summer Temora has usually been much more plentiful than this, if taken at all, the August catches for 1913 ranging from 600 to 18,000 per square meter (average 5,362), with 800 to 3,300 (average 1,484) for September, 1915.[58] In October, 1915, there were from 980 to 5,700 per square meter at the stations within the gulf (average 2,755), with 32,760 and 8,160 at two stations off Marthas Vineyard. No vertical hauls were made in November, December, or January, but the small percentages of Temora in the uniformly scanty catches of copepods in the horizontal hauls for December, 1920, and January, 1921 (table, p. 304), and our failure to take it at all off Gloucester during the winter of 1912–13 (Bigelow, 1914a, table, p. 409), point to this as a season of local scarcity.

Thus, there is some evidence, if not entirely conclusive, that while Temora is widespread in the open gulf in early spring it is usually very sparsely represented

[57] In the published account this and the preceding station are confused.

[58] Also 18,760 per square meter off Shelburne, Nova Scotia, station 10313.

anywhere at that season; but that as the existing stock, which has carried over the winter, dies out entirely in some localities between April and August, active multiplication takes place locally, which under exceptionally favorable circumstances may build up the shoals previously alluded to (p. 290) and which in any case raises the general average of abundance to several times its early spring level. It is not possible to set a definite date when this multiplication begins. In 1915 catches as large as 1,100 to 8,200 per square meter were made in the eastern side of the gulf by May 6 to 10 (stations 10270 and 10272; table, p. 297), but we found only 140 to 420 Temora per square meter at stations in the western side from the 4th to the 17th of the month in 1920. Probably the schedule varies over a period of several weeks from year to year, as do most periodic changes in northern seas, but it agrees essentially with the seasonal periodicity of the species in the Irish Sea, where it is most plentiful in summer,[59] and in the Baltic generally, where it is scarce in February, most common in August and November, and scarce or common in May, depending on the locality (Farran, 1910).

Comparison of the data just outlined for the open Gulf of Maine with Doctor McMurrich's plankton lists brings out the interesting difference that Temora commences to multiply three months or more earlier in the season out at sea than in the inclosed waters at St. Andrews, a difference which may be correlated with temperature.

*Vertical distribution.*—Obviously a species having its center of distribution within the 100-meter contour must be most plentiful above that level, and Temora has been found most numerous close to the surface. For example, the swarm off Nantucket of July 9, 1913 (station 10060), was so closely confined to the uppermost stratum that while the surface haul with a small net yielded thousands the haul from 40 meters with a large net caught only 25 specimens (Bigelow, 1915, p. 294). The Massachusetts Bay swarm of October 31, 1916, was likewise on the surface, with Calanus, not Temora, dominating the catch from 60 meters. Doctor McMurrich's St. Andrews records were all from within 7 meters of the surface, and many of them were immediately at the surface irrespective of season. Dr. W. C. Kendall also took it repeatedly in surface tows on Georges Bank in August and September, 1896. In the spring of 1920 the surface tows (table, p. 303) yielded it with about as great frequency and in about as great numbers as the vertical hauls, and as an extralimital instance of the same sort in neighboring American waters *Temora longicornis* dominated the surface tow between Block Island and Marthas Vineyard on November 10, 1916 (station 10405). It is plentiful in very shoal water at Woods Hole, and Willey (1919) found it regularly on the surface in the Gulf of St. Lawrence and about as often in surface as in vertical hauls on the Nova Scotian shelf. Herdman, Thompson, and Scott's (1898) records in the North Atlantic were all from within a couple of fathoms of the surface, and this copepod has repeatedly been taken in abundance at the surface in north European waters.

No direct evidence is available as to how deep Temora descends in the Gulf of Maine, but apparently the zone of greatest abundance for it hardly extends below about 50 meters. No attention has been paid to possible stratification of Temora

[59] This appears in the counts of copepods given by Herdman (1908 and 1919).

in the gulf within this depth zone, but at one of Doctor Kendall's stations off Nantucket shoals (September 2, 1896), when there was a difference of less than one degree of temperature between the surface (14.2°) and the 20-meter level (13.6°), the catch of "small brown copepods" in 5-minute tows at 10 meters, 20 meters, and 30 meters was roughly proportionate to the depth—that is, to the length of the column of water fished through—indicating that Temora was comparatively uniformly distributed down to that depth.

*Temperature and salinity.*—The distribution of *T. longicornis* in other seas proves it tolerant of a wide range in its physical surroundings from salinities as low as 6.54 per mille in the inner Baltic to upward of 35 per mille in the open Atlantic, in temperatures as low as about 2° and upwards of 20°. Its tendency to congregate near the surface makes it subject to a wide seasonal variation in temperature in many seas. Thus, at St. Andrews it survives temperatures as low as −1° to 0° in midwinter; at Woods Hole also. At the other extreme, one of our largest catches of Temora (station 10260, surface) was from water of 16°.

The highest temperature at which it has been definitely recorded in North American waters is 20.5° on the surface at a July station off New York (station 10066; Bigelow, 1915, p. 294), where sinking to a depth of only 30 meters would have lowered the temperature by 10°. But there is some reason to believe that it finds somewhere between 15° and 20° the upper limit of favorable temperature, for it was fairly well represented in the hauls from 25 and 10 meters, at another station off New York on August 1, 1916 (station 10362), levels at which the temperature was, respectively, about 12° and 16°, but was wanting at the surface in 21.1°. Within the Gulf of Maine any planktonic animal can always reach water cooler than 15° by sinking down less than 20 meters even at the warmest season and in the warmest region, but there is no direct evidence that Temora tends to sink below the warmest zone. The fact that Doctor Kendall, in his notes for August and September, 1896, records "small brown copepods" (in all probability *T. longicornis*) in several surface tows off the northwestern slope of Georges Bank and in the neighboring parts of the basin at temperatures of 17.5° to 20°, as well as repeatedly in 13° to 15° on the bank itself, makes it more likely that temperatures as high as 18° to 20° do not hinder its existence or growth.

It is not likely that differences in salinity within the limits prevailing in the Gulf of Maine affect the distribution of this copepod, but the high salinities of the oceanic basin, *per se*, or in conjunction with high temperature, may be the effective barrier which confines it to the banks water inside the inner edge of the Gulf Stream off the North American coast.

Why Temora (and this applies to many other neritic members of the plankton) should be so closely confined to comparatively shoal regions, irrespective of the physical state of the water within wide limits, when it has no connection with the bottom at any stage in its existence but is pelagic throughout its life, is a question to which no answer can yet be given.

*Breeding.*—No direct observations have been made on the breeding of Temora in the Gulf of Maine nor have its larval stages been detected there, but its distribution, regional and seasonal, is such as to leave no doubt that it is regularly endemic. Its

seasonal periodicity, both in the gulf and in the seas of northern Europe (p. 291), points to a wave of reproduction in the rising temperature of late spring or early summer, very little production taking place during the coldest months of the year; but with Temora occupying so broad a range in latitude and living under physical conditions so various, it is not likely that the precise temperature governs its periods of reproduction. Even in an area as confined as the Gulf of Maine there may be regional differences in this respect, for the comparatively large catches made at two stations in the eastern side of the gulf on May 6 to 10, 1915 (stations 10270 and 10272), at temperatures of 3° to 4°, point to reproduction in even colder water shortly previous, whereas Doctor McMurrich did not begin to find Temora a constant element in the tow at St. Andrews until the temperature of the water was near its annual maximum of 12° to 13° in September. It is questionable, however, whether it breeds successfully in temperatures higher than 15° to 16°.

*Economic importance.*—Wherever Temora abounds in northern seas it is one of the most important articles in the diet of herring (it is described by Willey (1921, p. 187) as "herring food *par excellence*"), of mackerel, and probably of other plankton-eating fishes. Lebour (1920) found it one of the copepods most commonly eaten by young fishes at Plymouth, England. Except for Willey's (1921) suggestion that fluctuations in the abundance of this and of other copepods may possibly be correlated with the weir catches of young herring ("sardines") in the Bay of Fundy, I know of nothing published on Temora as food for fishes in the Gulf of Maine. Certainly it can not rival *Calanus finmarchicus* in that respect in the open gulf, but on the occasions when it swarms any schooling fish in the vicinity would no doubt gorge on it, and large mackerel opened by Doctor W. C. Kendall off the northwest slope of Georges Bank on August 23, 1896, were full of these "small brown copepods" and of red feed (Calanus).

The frequency and comparative abundance of Temora at St. Andrews from September on suggests greater economic importance for it there than in other parts of the gulf.

### Temora turbinata (Dana)

This form is very closely allied to *T. longicornis* but is recognizable by a uniform and well-defined difference in the size and structure of the fifth legs of both male and female, a difference which Dr. C. B. Wilson writes he has been able to substantiate on a very large number of specimens from Chesapeake Bay. There are differences, also, in the relative length of the last two segments of the abdomen and in the structure of the two terminal setae of the furca, as described by Giesbrecht (1892).

*T. turbinata* is a more southern copepod than *T. longicornis,* previously published records for it including the tropical Pacific, Sulu Sea, China Sea, New Zealand, Malay Archipelago, and Gulf of Guinea. It has not been reported from the North Atlantic, but Dr. C. B. Wilson contributes the note that it "is present in great abundance in the plankton of Chesapeake Bay and vicinity," and he detected a scattering of *T. turbinata* at three Gulf of Maine stations in the spring of 1920—viz, off the continental slope of Georges Bank on February 22 and April 16 (stations 20045 and 20109) and in Massachusetts Bay near Boston Harbor on April 9 (station 20089). In the Gulf of Maine it is evidently a very rare stray from the south.

### Tortanus discaudatus (Thompson and Scott)

This species has so far been found only off the Pacific and Atlantic coasts of North America, either close to land or in partially inclosed waters. On the west coast it is reported from Puget Sound (Thompson and Scott, 1898) and from Bering Sea and Alaska (Willey, 1920). The Atlantic records are from the Gulf of St. Lawrence, whence it was first described (Thompson and Scott, 1898) and where it has since been found widespread and in abundance in the shoaler parts (T. Scott, 1905; Willey, 1919), and recently at Woods Hole (Fish, 1925). The Canadian fisheries expedition had it outside Cabot Strait and at two stations close to the outer coast of Nova Scotia (Willey, 1919). Wright (1907) records it from Canso, Nova Scotia, Willey (1921) has stated that it is plentiful at St. Andrews, and there are other Gulf of Maine records, as below. It has been found in considerable numbers at Woods Hole in July and occasionally in December and May (Wheeler, 1901; Sharpe, 1911; Sumner, Osburne, and Cole, 1913a), but it has not been found further south.

*Gulf of Maine.*—At St. Andrews this is one of the most frequent and abundant copepods. It appeared in about half the hauls from mid-May through June in Doctor McMurrich's plankton lists for 1915 and 1916, rising to its maximum during July, August, and September, for which quarter it is listed in almost every haul. In October and November it was much less constant (only about 50 per cent of the hauls), and when taken it was less abundant. In December Tortanus occurred in only about 25 per cent of the hauls, in January only once, and not at all in February, March, or April. During the late autumn and winter of 1916–17, Tortanus formed 46 per cent of the copepods in a gathering at St. Andrews on November 2, 9 per cent on December 8, 4 per cent on February 23, and was not detected at all on April 7, May 1, or May 17 (Willey, 1921). It is likewise plentiful in summer at Canso, Nova Scotia (Wright, 1907), and in the Gulf of St. Lawrence, Willey (1920, p. 22) describing it as composing "50 to 75 per cent of the summer copepod plankton off Souris, Prince Edward Island." On the whole, therefore, it may be classed as a summer species along the northeastern coast of America. A periodicity of this sort indicates one breeding period yearly, probably extending from early summer until early autumn, with little or no reproduction taking place in late autumn, winter, or early spring.

The abundance and frequency of Tortanus at St. Andrews, with its presence in Portland Harbor in July (Bigelow, 1914) and at Woods Hole, as just noted, suggest that it occurs in estuarine and inclosed waters all around the coast line of the gulf; but it is so closely confined to such situations that we have taken it only four times in the open gulf in all our towing—twice in Massachusetts Bay during the winter season of 1912–1913 (station 10048, November 20, and station 10053, February 12), once on German Bank (April 15, 1920, station 20103), and once in the northeastern corner of the basin off the mouth of the Bay of Fundy (January 5, 1921, station 10502). Not only is Tortanus extremely infrequent outside the outer headlands in the Gulf of Maine, but it is among the scarcest of copepods there, in numbers, the first three of the records just listed being based on one or two specimens each.

In the last instance there were 7 per cent of this species in a very scanty catch of copepods made with the open net towing horizontally at 150–0 meters.

It will be noted that the dates of these offshore captures do not correspond with the seasonal periodicity of the species at St. Andrews, but with a species as rare as this is out at sea it is largely a matter of luck whether any given haul chances to pick it up, and if the catch of other copepods be large, it is equally a matter of luck whether the particular sample of the tow examined chances to contain it.

*Tortanus discaudatus* is thus so strictly neritic in the gulf (decidedly more so than in the Gulf of St. Lawrence, where it is widespread over the shoal southern part) that it is hardly a factor at all in the offshore plankton, but probably it enters regularly into the diet of the small herring and other young fishes among the islands and in the harbors of the gulf, judging from its abundance at St. Andrews.

### Undeuchæta major Giesbrecht

This species is probably worldwide in temperate and tropic latitudes in the oceanic basins. It has been recorded off the west coast of Ireland in the north and from several stations below the Equator down to 40° S., 35° E., off South Africa in the south. It was originally described from the central Pacific and has since been taken off southern California (Giesbrecht, 1895) and at San Diego (Esterly, 1905) in that ocean. *U. major* has not yet been found in the Mediterranean but has been reported from the Indian Ocean (van Breemen, 1908) and among the Malay Archipelago (A. Scott, 1909).

Previous records for this species off the Atlantic coast of North America are one station outside the continental edge off New Jersey, in July, 1913 (Bigelow, 1915, p. 287, station 10071), and three Canadian fisheries stations in July, 1915—one outside the continental edge off La Have Bank, one at the same relative location somewhat farther east off Banquereau Bank, and the third in the oceanic basin off the mouth of the Laurentian channel between Sable Island Bank and the Newfoundland Banks (Willey, 1919). To these Dr. C. B. Wilson's table (p. 299) adds two vertical hauls in the Gulf of Maine—one of them on Browns Bank (March 13, 1920, station 20072) and the other on German Bank (April 15 of that year, station 20103). In each instance there were about 10 specimens in the catch, being at the rate of about 50 per square meter.

In the Gulf of Maine this copepod is one of the rarest of strays from the oceanic basin offshore, locally interesting when it occurs as an indicator of the prevailing indraught. Not having been taken farther in than German Bank, it may be assumed to be shorter-lived in the gulf than the species of Eucheirella, Pleuromamma, or Rhincalanus, which are similarly exotic and immigrant in the gulf.

### Undeuchæta minor Giesbrecht

The distribution of this species parallels that of *U. major* and it is equally oceanic. In the North Atlantic it has been reported as far north as the Faroe-Shetland channel (lat. 61° 20′ N.) and west of Ireland; as far south as latitude 35° (Wolfenden, 1911; With, 1915); it is known from the central Pacific and from off

southern California (Giesbrecht, 1892); also at San Diego, Calif. (Esterly, 1905), from the Indian Ocean (Thompson and Scott, 1903), and among the Malay Archipelago (A. Scott, 1909). Previous records for this species off the east coast of North America are one station off New York (July 11, 1913, station 10064) and four by the Canadian fisheries expedition—two of them off La Have Bank, one off Banquereau Bank, and one in the deep between the latter and the Newfoundland Banks (Willey, 1919). All these American records were from outside the continental edge.

*U. minor* was not detected in the Gulf of Maine until 1920, when Dr. C. B. Wilson found occasional specimens in the vertical hauls on Browns Bank on March 13 and on German Bank, April 15 (stations 20072 and 20103), these being the same two hauls that yielded *U. major* (p. 295).

Judging from the numbers of specimens taken, *minor* is, if anything, even scarcer than *major* in the gulf. In the Canadian hauls the reverse was true. So seldom entering the gulf, its chief local interest is as flotsam from the Atlantic offshore.

### Zaus abbreviatus G. O. Sars

This harpacticoid, described by Sars (1903–1911) as not rare off the west coast of Norway, appears in Doctor McMurrich's lists of plankton at St. Andrews, New Brunswick, in about 20 per cent of the gatherings between November 23 and January 26, occasionally in April and June, and not at all during the later summer or early autumn. Sars (1903–1911, p. 59) speaks of it as restricted to the red algæ, where it often occurs in considerable numbers. There is no reason to suppose that its presence in the plankton is anything but accidental, and it has not been found in any of the tow nettings in the open Gulf of Maine.

### Zaus spinatus Goodsir

This species is widespread on North Atlantic and Arctic coasts, Sars (1903–1911) enumerating the polar islands north of Grinnell Land, Nova Zembla, and Franz Josef Land in the Arctic, all along the Norwegian coast, the British Isles, Helgoland, and the coast of France. It has not been recorded previously from American waters. According to Brady (1878–1880) it lives among seaweeds from tide mark down to 10 to 12 fathoms. Under normal circumstances it is strictly littoral, living close to shore, but in regions of active vertical circulation it, like other littoral harpactoids, may be swept up to the surface. At St. Andrews, for example, Doctor McMurrich found it on one occasion (March 17, 1916), in a haul at 7 meters. It has not been detected in any of the tow nettings in the open Gulf of Maine nor in its other harbors.

*Percentages of the several species of copepods in vertical hauls, May to October, 1915, identified and tabulated by Dr. C. B. Wilson*

[In this and similar tables, T. = occasional specimen or trace; A. = abundant; C. = common; F. = few.]

| Station number | 10266 | 10267 | 10269 | 10270 | 10271 | 10272 | 10278 | 10279 |
|---|---|---|---|---|---|---|---|---|
| Month | May | | | | | | | |
| Day of month | 4 | 5 | 6 | 6 | 7 | 10 | 14 | 26 |
| Depth in meters | 125–0 | 260–0 | 115–0 | 175–0 | 70–0 | 90–0 | 150–0 | 65–0 |
| VERTICAL NET | | | | | | | | |
| Acartia clausi | 5 | 10 | 10 | 5 | 14 | 1 | 2 | 2 |
| Aetidius armatus | | | | | T. | | | |
| Anomalocera pattersoni | | | | | | | T. | |
| Calanus finmarchicus | 90 | 85 | 80 | 80 | 70 | 84 | 70 | 78 |
| Calanus hyperboreus | | 1 | 5 | 5 | 1 | 5 | 3 | 3 |
| Candacia armata | | | | T. | | | | |
| Centropages hamatus | | | | 1 | | | | |
| Centropages typicus | | | | 1 | | | | |
| Eucalanus elongatus | | | | T. | | | | |
| Euchæta norvegica | | 1 | | | | | | |
| Euchirella rostrata | | | | | | | T. | |
| Metis ignæa | | | | | T. | | | |
| Metridia longa | | | | 2 | | | 2 | 5 |
| Metridia lucens | | 1 | | 1 | | 3 | 15 | |
| Paracalanus parvus | 5 | 2 | 5 | 1 | 14 | 2 | 3 | 4 |
| Pseudocalanus elongatus | | | | 2 | 1 | 3 | 5 | 5 |
| Scolecithricella minor | | | | | | T. | | |
| Temora longicornis | | | | 2 | | 2 | | 3 |
| Development stages | A. | C. | C. | A. | F. | | F. | |
| Total number of copepods per square meter [1] | 511,000 | 50,000 | 48,000 | 411,500 | 11,000 | 55,000 | 175,000 | 189,000 |

| Station number | 10282 | 10283 | 10284 | 10286 | 10287 | 10288 | 10290 | 10291 | 10293 | 10294 | 10296 | 10299 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | June | | | | | | | | | | | |
| Day of month | 10 | 10 | 11 | 14 | 14 | 19 | 19 | 23 | 23 | 23 | 24 | 26 |
| Depth in meters | 180–0 | 180–0 | 80–0 | 80–0 | 70–0 | 200–0 | 60–0 | 70–0 | 75–0 | 170–0 | 60–0 | 200–0 |
| VERTICAL NET | | | | | | | | | | | | |
| Acartia clausi | 15 | 10 | 2 | 4 | 25 | 3 | 50 | 45 | 5 | 2 | 2 | 3 |
| Acartia longiremis | | | | | | | | | | | | 1 |
| Calanus finmarchicus | 75 | 50 | 70 | 80 | 60 | 80 | 25 | 20 | 50 | 58 | 78 | 40 |
| Calanus hyperboreus | 1 | 10 | 1 | 6 | 5 | 6 | 3 | 10 | 5 | 5 | 10 | 15 |
| Centropages bradyi | | | | | | T. | | | | | | |
| Dwightia gracilis | | | | | | | | T. | | | | |
| Eucalanus attenuatus | T. | | | | | | | | | | | |
| Euchæta media | | | T. | | | | | | | | | |
| Euchæta norvegica | 1 | | | | | 3 | | | | | 3 | |
| Halithalestris croni | 1 | | | | | | | | | | | |
| Metis ignæa | | | | T. | | | | | | | | |
| Metridia longa | | 10 | 15 | | | 3 | 15 | 10 | 15 | 25 | | 20 |
| Metridia lucens | | 5 | | | | | | | | 3 | | 15 |
| Paracalanus parvus | 3 | 10 | 6 | 4 | 5 | 2 | 7 | 5 | 10 | 5 | 5 | 3 |
| Pseudocalanus elongatus | 4 | 5 | 6 | 6 | 5 | 3 | | | 5 | | | 3 |
| Temora longicornis | | | | | | | | 10 | 10 | 2 | 2 | T. |
| Development stages | A. | F. | F. | S. | | | | | | | | |
| Total number of copepods per square meter [1] | 10,000 | 21,000 | 2,500 | 11,500 | 35,000 | 55,500 | 21,500 | 15,500 | 20,000 | 65,500 | 9,500 | 43,000 |

[1] From Bigelow, 1917, p. 319.

*Percentages of the several species of copepods in vertical hauls, May to October, 1915, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 10303 | 10304 | 10306 | 10307 | 10309 | 10310 | 10311 | 10313 | 10315 | 10316 | 10318 | 10319 | 10320 | 10321 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Months | August | | | | September | | | | | | | | | |
| Day of month | 4 | 6 | 31 | 31 | 1 | 2 | 2 | 6 | 7 | 11 | 16 | 20 | 29 | 29 |
| Depth in meters | 70–0 | 200–0 | 140–0 | 230–0 | 200–0 | 190–0 | 60–0 | 70–0 | 80–0 | 60–0 | 70–0 | 30–0 | 70–0 | 40–0 |
| VERTICAL NET | | | | | | | | | | | | | | |
| Acartia clausi | 30 | 1 | 1 | 10 | 6 | 10 | 40 | 6 | | 40 | 50 | 30 | 15 | 8 |
| Acartia longiremis | 6 | | | 5 | 2 | | 5 | 2 | | 40 | 4 | 5 | 5 | 4 |
| Aetidius armatus | | | | T. | | | | | | | | | | |
| Calanus finmarchicus | 30 | 65 | 60 | 30 | 80 | 80 | 30 | 30 | 45 | 10 | 30 | 20 | 45 | 15 |
| Calanus hyperboreus | | 1 | 3 | 1 | | | 5 | 2 | | | | | | |
| Candacia armata | | | | | | | | | | | | 5 | | |
| Centropages bradyi | | | | | | | | | | | | T. | | |
| Centropages hamatus | | | 1 | 1 | 1 | | | 2 | 1 | | 6 | 5 | | 15 |
| Centropages typicus | | | 1 | 1 | 1 | | | 5 | 2 | | | 5 | 10 | 40 |
| Eucalanus attenuatus | | | | | | | | | | | | | | T. |
| Eucalanus elongatus | | | | | | | | | | | | | T. | T. |
| Euchæta norvegica | | 2 | | 1 | 1 | | | | | | | | | |
| Eurytemora herdmani | | | | 1 | 1 | | | | | | | | | |
| Halithalestris croni | | 1 | | | 1 | | | | | | T. | | | |
| Mecynocera clausi | | | | | | | | | | | | T. | 1 | T. |
| Metridia longa | | 10 | 20 | 20 | 2 | | 3 | | 15 | | 6 | 5 | | 3 |
| Metridia lucens | | 10 | | | 1 | | 2 | | 5 | | 4 | 5 | 5 | 4 |
| Paracalanus parvus | 30 | 10 | 5 | 15 | 3 | 3 | 4 | 10 | 15 | | | 10 | 2 | 8 |
| Pseudocalanus elongatus | | | 10 | 15 | 3 | 7 | 4 | 15 | 15 | 10 | | 5 | 15 | 2 |
| Rhincalanus cornutus | | | | | | | | | | | | | T. | 1 |
| Scolecithricella minor | | | | | | | | T. | | | | | | |
| Temora longicornis | 4 | | | | | | 2 | 28 | 2 | | | 5 | 2 | |
| Development stages | | C. | C. | C. | A. | A. | A. | C. | C. | F. | | | | |
| Total number of copepods per square meter [1] | | 234,500 | 51,500 | 104,000 | 173,000 | 114,500 | 41,000 | 67,000 | 47,000 | 39,700 | 14,700 | 66,500 | 42,500 | 45,500 |

| Station number | 10323 | 10324 | 10325 | 10326 | 10327 | 10328 | 10329 | 10331 | 10332 | 10333 | 10336 | 10337 | 10338 | 10339 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | October | | | | | | | | | | | | | |
| Day of month | 1 | 1 | 4 | 4 | 9 | 9 | 9 | 21 | 21 | 22 | 26 | 26 | 27 | 27 |
| Depth in meters | 80–0 | 150–0 | 175–0 | 145–0 | 60–0 | 60–0 | 60–0 | 30–0 | 50–0 | 80–0 | 50–0 | 60–0 | 80–0 | 70–0 |
| VERTICAL NET | | | | | | | | | | | | | | |
| Acartia clausi | 10 | 15 | 6 | 15 | 30 | 10 | 15 | 5 | 15 | 6 | 15 | 10 | | |
| Acartia longiremis | 10 | 2 | 9 | 5 | | 2 | 8 | | 5 | 2 | | | | |
| Aetidius armatus | | | | | | | T. | | | | | | | |
| Anomalocera pattersoni | | | | | | | T. | | | | | | | |
| Calanus finmarchicus | 30 | 30 | 70 | 55 | 25 | 25 | 30 | 15 | 15 | 25 | 50 | 50 | 50 | 50 |
| Calanus gracilis | | | | | | | | 1 | T. | | | T. | | |
| Calanus hyperboreus | | | | | 4 | | | | | | | | | |
| Candacia armata | | | | | | | | | | | T. | | | |
| Centropages hamatus | 10 | | | | | | | 25 | 5 | 6 | 7 | 6 | 10 | 8 |
| Centropages typicus | 10 | | | | 2 | 3 | | 25 | 5 | 6 | 6 | 6 | 10 | 10 |
| Dwightia gracilis | | | | T. | T. | | | | | | | | | |
| Eucalanus attenuatus | T. | | | | | | | | | | | T. | | |
| Euchæta media | | | | | | | | | | | | | | |
| Eurytemora herdmani | | | T. | | | | | | | | T. | | | |
| Metis ignæa | T. | | | | | | | | | | | | | |
| Metridia longa | 10 | 30 | 6 | 7 | 7 | 10 | 8 | 4 | | 2 | | 4 | 5 | 8 |
| Metridia lucens | 10 | 15 | 4 | 4 | 25 | 30 | 25 | 5 | | 8 | | 4 | 5 | 8 |
| Paracalanus parvus | | 3 | 2 | 7 | 7 | 5 | 8 | 3 | 40 | 25 | 15 | 10 | 10 | 8 |
| Pseudocalanus elongatus | 10 | 5 | 6 | 7 | | 5 | 4 | 3 | 15 | 15 | 7 | 10 | 10 | 8 |
| Rhincalanus cornutus | | | | | | | | | T. | 1 | | | | |
| Temora longicornis | | | 1 | | | 10 | 2 | 14 | T. | 4 | | | | |
| Total number of copepods per square meter [1] | 77,000 | 112,500 | 158,500 | 86,000 | 30,700 | 57,000 | 49,000 | 234,000 | 319,500 | 204,000 | 205,000 | | 244,500 | 50,500 |

[1] From Bigelow, 1917, p. 319.

*Percentages of the several species of copepods in vertical hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*

| Station number | 20044 | 20045 | 20046 | 20047 | 20048 | 20049 | 20050 | 20052 | 20053 | 20054 | 20055 | 20056 | 20057 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | February | | | | | | March | | | | | | |
| Day of month | 22 | 22 | 22 | 23 | 23 | 23 | 1 | 2 | 3 | 3 | 3 | 3 | 4 |
| Depth in meters | 150-0 | 150-0 | 50-0 | 50-0 | 150-0 | 200 0 | 150-0 | 200-0 | 225-0 | 250-0 | 225-0 | 100-0 | 120-0 |
| VERTICAL NET | | | | | | | | | | | | | |
| Acartia clausi | | | | | | | | | 4 | | | | |
| Acartia longiremis | | | | | | | | | 1 | | | | |
| Calanus finmarchicus | 5 | 6 | 10 | 2 | 75 | 90 | 80 | 35 | 64 | 66 | 90 | 70 | 75 |
| Calanus hyperboreus | 5 | 14 | 5 | 2 | 3 | 3 | 2 | 5 | 5 | 1 | 2 | 2 | 5 |
| Candacia armata | | | | | | | | | 1 | | | | |
| Centropages typicus | | | | 18 | | 7 | | | | | | | |
| Eucalanus elongatus | 5 | 10 | | | | | | | | | | | |
| Euchæta norvegica | | 20 | | | | | | 10 | 2 | | 4 | | |
| Halithalestris croni | | | | | | | | | 1 | | | 2 | |
| Metridia longa | | | 10 | | | | | | 10 | | 1 | | |
| Metridia lucens | | | 30 | 60 | 2 | | | 25 | 3 | 1 | 1 | 6 | |
| Paracalanus parvus | 50 | 30 | 30 | 3 | 10 | | 4 | | | 15 | | 10 | 15 |
| Pleuromamma gracilis | | | | | | | | | | | | T | |
| Pleuromamma xiphias | | | | | T | | | | | | | | |
| Pseudocalanus elongatus | 30 | 10 | 15 | 15 | 10 | | 14 | 25 | 8 | 15 | 2 | 10 | 5 |
| Rhincalanus nasutus | 5 | 10 | | | | | | | | | | | |
| Temora longicornis | | | | | | | | | 1 | 2 | | | |
| Temora turbinata | | | T | | | | | | | | | | |
| Development stages | A | C | A | A | A | C | A | C | C | F | | | |
| Number of adult copepods per square meter of sea surface (approximate) | 10,000 | 10,000 | 3,750 | 1,250 | 8,750 | 37,500 | 10,750 | 5,000 | 15,000 | 12,500 | 15,000 | 150 | 500 |

| Station number | 20058 | 20059 | 20060 | 20061 | 20062 | 20063 | 20064 | 20065 | 20066 | 20067 | 20068 | 20069 | 20071 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | March—Continued | | | | | | | | | | | | |
| Day of month | 4 | 4 | 4 | 5 | 5 | 10 | 11 | 11 | 11 | 12 | 12 | 12 | 13 |
| Depth in meters | 45-0 | 60-0 | 90-0 | 175-0 | 50-0 | 190-0 | 340-0 | 80-0 | 70-0 | 90-0 | 150-0 | 1000-0 | 150-0 |
| VERTICAL NET | | | | | | | | | | | | | |
| Acartia clausi | | 30 | 5 | | 30 | 10 | 5 | 20 | 5 | 1 | | | |
| Acartia longiremis | | 5 | 8 | | 5 | 30 | 1 | 5 | 2 | 1 | | | |
| Calanus finmarchicus | 60 | 25 | 75 | 70 | 6 | 40 | 80 | 40 | 60 | 70 | 96 | 60 | 75 |
| Calanus hyperboreus | 1 | 1 | 1 | | | | 1 | 1 | 2 | | | 2 | |
| Dwightia gracilis | | | | | | 3 | | | | | | | |
| Eucalanus elongatus | | | | | | | | | | | | 5 | |
| Euchæta norvegica | | | | | | | 4 | 3 | | | 1 | 10 | |
| Heterorhabdus spinifrons | | | | | | | | | | | | 4 | |
| Lucicutia grandis | | | | | | | | | | | | | T |
| Metridia longa | 20 | | 2 | 10 | 1 | 1 | 4 | 25 | 25 | 20 | | 10 | 10 |
| Metridia lucens | 10 | | 1 | 10 | 3 | 1 | | 3 | 3 | 4 | 1 | 4 | 5 |
| Paracalanus parvus | 3 | 24 | | | | | | | | | | | |
| Pseudocalanus elongatus | 6 | 15 | 8 | 10 | 35 | 10 | 5 | 3 | 3 | 3 | 1 | | 10 |
| Rhincalanus nasutus | | | | | | | | | | | | 5 | |
| Scolecithricella minor | T | | | | | | | | | | | | |
| Temora longicornis | | | | | 20 | 5 | | | | 1 | 1 | | |
| Development stages | F | F | | | | | C | | | | | | |
| Number of adult copepods per square meter of sea surface (approximate) | 1,250 | | 1,000 | 2,500 | 50 | 130 | 2,000 | 1,000 | 370 | 5,000 | 107,500 | 77,500 | 10,000 |

*Percentages of the several species of copepods in vertical hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 20072 | 20073 | 20074 | 20075 | 20076 | 20077 | 20078 | 20079 | 20080 | 20081 | 20083 | 20085 | 20086 | 20087 | 20088 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | March—Continued | | | | | | | | | | | | | | |
| Day of month | 13 | 17 | 19 | 19 | 19 | 19 | 20 | 22 | 22 | 22 | 23 | 23 | 23 | 24 | 24 |
| Depth in meters | 75–0 | 70–0 | 150–0 | 90–0 | 200–0 | 800–0 | 110–0 | 210–0 | 60–0 | 200–0 | 65–0 | 60–0 | 170–0 | 250–0 | 75–0 |
| VERTICAL NET | | | | | | | | | | | | | | | |
| Acartia clausi | 10 | | 2 | | | 15 | | | 5 | | | 40 | | | 2 |
| Acartia longiremis | 5 | | 10 | | | 5 | | | | | | 8 | | | 2 |
| Aetidius armatus | | | | | | | | | | | | 1 | | | |
| Anomalocera pattersoni | | | | | | | | | | | | 1 | | | |
| Calanus finmarchicus | 32 | 30 | 30 | 55 | 50 | 30 | 55 | 50 | 45 | 75 | 50 | 50 | 75 | 25 | 50 |
| Calanus hyperboreus | | | 30 | 5 | 10 | 10 | 15 | 10 | 5 | 5 | | | 2 | 15 | 10 |
| Candacia armata | | | | | | 1 | | | | | | | | | |
| Centropages bradyi | | | | | | | | | | | | | | | 1 |
| Centropages hamatus | | | | | | | | | | | | | | 2 | |
| Euchæta media | | | | | | | | | | | | | | T | |
| Euchæta norvegica | | | 5 | | 10 | 4 | | 5 | 5 | 5 | | | | 10 | 10 |
| Eurytemora herdmani | | | | | | | | | | | | | | 2 | |
| Gaidius tenuispinis | | | | | | 1 | | | | | | | | | |
| Labidocera æstiva | | | | | | | | | | | | | | 1 | |
| Metridia longa | 7 | 10 | 6 | 15 | 20 | 20 | 10 | 5 | 5 | | 15 | | 7 | 15 | 20 |
| Metridia lucens | 25 | 35 | 6 | 15 | 10 | 10 | 10 | 15 | 10 | 5 | 20 | | 10 | 20 | 5 |
| Paracalanus parvus | 5 | | 6 | | | 4 | | | | | | | | | |
| Pleuromamma xiphias | 4 | | | | | | | | | | | | | | |
| Pseudocalanus elongatus | 6 | 15 | 5 | 10 | | | 10 | 10 | 20 | 10 | 15 | | 6 | 10 | |
| Rhincalanus cornutus | | | | | | | | | | T | | | | | |
| Rhincalanus nasutus | T | | | | | | | | | T | | | | | |
| Temora longicornis | | 10 | | | | | | | | | | | | | |
| Temora turbinata | | | | | | | | 5 | 5 | | | | | | |
| Undeuchæta major | 4 | | | | | | | | | T | | | | | |
| Undeuchæta minor | 2 | | | | | | | | | | | | | | |
| Number of adult copepods per square meter of sea surface (approximate) | 1,250 | 100 | 5,000 | 1,000 | 2,300 | | 25,000 | 1,250 | 375 | 5,000 | 250 | 500 | 8,750 | 27,750 | 4,750 |

*Percentages of the several species of copepods in vertical hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 20089 | 20090 | 20091 | 20092 | 20093 | 20094 | 20095 | 20096 | 20097 | 20098 | 20099 | 20100 | 20101 | 20102 | 20103 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | April | | | | | | | | | | | | | | |
| Day of month | 6 | 9 | 9 | 9 | 9 | 10 | 10 | 10 | 10 | 10 | 12 | 12 | 12 | 13 | 15 |
| Depth in meters | 60–0 | 120–0 | 30–0 | 80–0 | 160–0 | 90–0 | 90–0 | 35 | 80–0 | 90–0 | 70–0 | 225–0 | 115–0 | 60–0 | 90–0 |
| VERTICAL NET | | | | | | | | | | | | | | | |
| Acartia clausi | | | 15 | | | | 10 | 10 | 15 | 2 | 1 | 10 | 1 | 45 | 20 |
| Acartia longiremis | | | | | | | | | | 2 | 14 | 1 | 1 | 5 | 5 |
| Aetidius armatus | | | | | | | | | | | 1 | | | | |
| Anomalocera pattersoni | | | | | | | | | | | | | 1 | | |
| Calanus finmarchicus | 50 | 45 | 65 | 75 | 25 | 80 | 75 | 80 | 80 | 80 | 80 | 75 | 34 | 30 | 35 |
| Calanus hyperboreus | | 45 | 4 | 10 | 20 | 17 | 5 | 3 | 2 | 2 | 2 | 2 | 1 | 5 | 5 |
| Candacia armata | | | | | | | | | | | | | | | 1 |
| Centropages hamatus | | | | | | | | | | | | | | | 2 |
| Centropages typicus | | | | | | | | | 1 | | | | | | |
| Dwightia gracilis | | | | T | | | | | | | | | | | T |
| Eucalanus attenuatus | 2 | | | | | | | | | | | | | | 2 |
| Eucalanus elongatus | | | | | | | | | | | | | 1 | | |
| Euchæta media | | | | | | | | | | T | | | | | 2 |
| Euchæta norvegica | | 1 | | | | | | | | 2 | | 2 | | | |
| Euchirella rostrata | | | | | | | | | | | | | 1 | | |
| Gaidius tenuispinis | | | | | | | | | 1 | | | | | | |
| Halithalestris croni | | 1 | | | | | | | | | | | | | |
| Labidocera æstiva | | | | | | | | | 1 | | | | | | |
| Metis ignea | 1 | | | | | | | | | | | | | | |
| Metridia longa | 10 | 4 | 12 | | 20 | 1 | 5 | 4 | | | | 2 | 35 | 1 | 5 |
| Metridia lucens | 15 | 2 | 4 | | 20 | 1 | 3 | 2 | | | | 1 | 20 | 1 | 5 |
| Paracalanus parvus | T | | | | | | | | | 1 | | | | | 2 |
| Phyllopus bidentatus | | | | | | | | | T | | | | | | |
| Pleuromamma abdominalis | | | | | | | | | | | | | 1 | | |
| Pleuromamma gracilis | | | | | | | | | | | | | | | 1 |
| Pleuromamma robusta | 2 | | | | | | | | | 1 | | | | | |
| Pleuromamma xiphias | | | | | | | | | | | | | | 1 | |
| Pseudocalanus elongatus | 15 | 2 | | 10 | 12 | 1 | 2 | | | 10 | 1 | 5 | 4 | 10 | 10 |
| Rhincalanus cornutus | 2 | | | | | | | | | | | | | | |
| Rhincalanus nasutus | | | | | | | T | | | | | | | | |
| Scolecithricella minor | | | | | | | | 1 | | | | | | | |
| Temora longicornis | 2 | | | 5 | 3 | | 1 | | | | 1 | 1 | 1 | 1 | 2 |
| Temora turbinata | 1 | | | | | | | | | | | | | | |
| Tortanus discaudatus | | | | | | | | | | | | | | | 1 |
| Undeuchæta major | | | | | | | | | | | | | | | 2 |
| Undeuchæta minor | | | | | | | | | | | | | | | T |
| Development stages | | | | | | F | C | C | A | C | A | A | A | A | C |
| Number of adult copepods per square meter of sea surface (approximate) | 2,500 | 7,500 | 7,500 | 12,500 | 7,500 | 5,000 | 10,600 | 7,800 | 3,250 | 1,250 | 2,000 | 4,750 | 2,750 | 900 | 2,650 |

*Percentages of the several species of copepods in vertical hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 20104 | 20105 | 20106 | 20107 | 10108 | 20109 | 20110 | 20111 | 20112 | 20113 | 20114 | 20115 | 20116 | 20117 | 20119 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | April—Continued | | | | | | | | | | | | | | |
| Day of month | 15 | 15 | 15 | 16 | 16 | 16 | 16 | 17 | 17 | 17 | 17 | 18 | 18 | 18 | 20 |
| Depth in meters | 45-0 | 125-0 | 40-0 | 240-0 | 135-0 | 155-0 | 80-0 | 65-0 | 290-0 | 230-0 | 175-0 | 295-0 | 200-0 | 85-0 | 90-0 |
| VERTICAL NET | | | | | | | | | | | | | | | |
| Acartia clausi | 1 | 2 | 50 | 2 | 45 | 2 | 6 | 25 | 2 | 1 | | 4 | 20 | 20 | 15 |
| Acartia longiremis | | 1 | 4 | | | | 10 | | 10 | 1 | | 4 | 10 | 5 | |
| Aetidius armatus | | | 1 | | | 1 | | | | | | | | | |
| Calanus finmarchicus | 25 | 60 | 20 | 60 | 35 | 60 | 60 | 60 | 50 | 54 | 75 | 50 | 55 | 65 | 75 |
| Calanus hyperboreus | 1 | 7 | 20 | 5 | 5 | 10 | | | 2 | 1 | | 4 | 5 | 1 | 5 |
| Centropages typicus | 1 | | | | | | | | | | | | 1 | | |
| Dwightia gracilis | | | | | | | 5 | | | | | | | | |
| Eucalanus elongatus | | | | 1 | | | | | | | | | | | |
| Euchæta norvegica | | | | | | | | | 2 | 1 | | 4 | 2 | | |
| Eurytemora herdmani | | | | | | 1 | | | | | | | | | |
| Halithalestris croni | 1 | | | | | | | | | T | | 1 | | | |
| Metis ignæa | | | | | | | | | | | 1 | | 1 | | |
| Metridia longa | 10 | 20 | 2 | 2 | 5 | 10 | 3 | 5 | 25 | 20 | 3 | 20 | 1 | 1 | 1 |
| Metridia lucens | 16 | 6 | 1 | 20 | 5 | 10 | 3 | 5 | 3 | 15 | 15 | 1 | 2 | 2 | 2 |
| Paracalanus parvus | | | | | 2 | | 7 | | | | | 8 | | 1 | |
| Pleuromamma gracilis | | | | | | | | | | | 1 | | | | |
| Pleuromamma xiphias | | | | | | | | | | | | | | 1 | |
| Pseudocalanus elongatus | 45 | 3 | 1 | 10 | 2 | 5 | 5 | 5 | 5 | 7 | 4 | 1 | 2 | 2 | 2 |
| Rhincalanus nasutus | | | | | | | | | | | | | | 1 | |
| Temora longicornis | | 1 | 1 | | 1 | | 1 | | 1 | | 1 | | 1 | 1 | |
| Temora turbinata | | | | | | 1 | | | | | | | | | |
| Development stages | C | F | | | | | | | | | | F | C | C | A |
| Number of adult copepods per square meter of sea surface (approximate) | 2,600 | 130,000 | 6,000 | 4,800 | 47,250 | 1,000 | 2,800 | 9,000 | 8,600 | 5,600 | 20,000 | 20,000 | 28,000 | 17,500 | 5,000 |

| Station number | 20120 | 20121 | 20122 | 20123 | 20124 | 20125 | 20126 | 20127 | 20128 | 20129 |
|---|---|---|---|---|---|---|---|---|---|---|
| Month | May | | | | | | | | | |
| Day of month | 4 | 4 | 7 | 16 | 16 | 16 | 17 | 17 | 17 | 17 |
| Depth in meters | 48-0 | 55-0 | 95-0 | 55-0 | 90-0 | 140-0 | 155-0 | 145-0 | 70-0 | 160-0 |
| VERTICAL NET | | | | | | | | | | |
| Acartia clausi | 10 | 15 | 15 | 8 | 10 | 7 | 5 | 5 | 5 | 1 |
| Acartia longiremis | 5 | 2 | 5 | 8 | 1 | 1 | 5 | 5 | | 2 |
| Aetidius armatus | | | | | | | | | | T |
| Anomalocera pattersoni | 1 | | | | | | | | | |
| Calanus finmarchicus | 40 | 60 | 60 | 80 | 75 | 80 | 80 | 80 | 80 | 80 |
| Calanus hyperboreus | | | 5 | 2 | | 3 | 3 | 5 | 1 | 1 |
| Candacia armata | | | | | | | | | | 2 |
| Centropages bradyi | | 1 | | | | | | | | |
| Centropages typicus | | | | | | | | | | 1 |
| Eucalanus attenuatus | | 1 | | | | | | | | |
| Euchæta media | | | | | | 1 | | | | |
| Euchæta norvegica | 1 | | | | | | | | | 1 |
| Halithalestris croni | | | 1 | | 1 | | | | | 1 |
| Heterorhabdus spinifrons | 1 | | | | | | | | | |
| Metridia longa | 10 | 2 | 3 | 1 | 2 | 3 | 3 | 2 | 2 | 2 |
| Metridia lucens | 30 | 2 | 3 | 1 | 2 | | 1 | | 2 | 2 |
| Paracalanus parvus | | 1 | 2 | | | 1 | 1 | 2 | | 2 |
| Pseudocalanus elongatus | 1 | 15 | 5 | | 8 | 4 | 1 | 1 | 10 | 2 |
| Rhincalanus nasutus | 1 | | | | | | | | | 1 |
| Temora longicornis | | 1 | 1 | | 1 | | 1 | | | 2 |
| Development stages | A | A | C | C | F | | | | | |
| Number of adult copepods per square meter of sea surface (approximate) | 55,000 | 12,600 | 27,750 | | 14,000 | 77,000 | 21,750 | 28,750 | 28,500 | 21,250 |

*Percentages of the several species of copepods in samples from the surface hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*

| Station number | 20044 | 20045 | 20046 | 20047 | 20048 | 20049 | 20053 | 20056 | 20058 | 20059 | 20060 | 20061 | 20063 | 20064 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | February | | | | | | March | | | | | | | |
| Day of month | 22 | 22 | 22 | 23 | 23 | 23 | 1 | 3 | 4 | 4 | 4 | 5 | 11 | 11 |
| SURFACE NET | | | | | | | | | | | | | | |
| Acartia clausi | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 25 | T. | 20 | ------ |
| Acartia longiremis | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | T. | 10 | 4 | ------ |
| Asterocheres bœcki | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | T. | ------ | ------ | ------ | ------ |
| Calanus finmarchicus | 66 | 50 | 80 | 75 | 34 | 90 | 60 | 70 | 66 | 95 | 50 | 60 | 10 | 45 |
| Calanus hyperboreus | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | T. | ------ | T. | 10 |
| Halithalestris croni | ------ | ------ | ------ | ------ | ------ | ------ | 10 | 4 | ------ | 5 | T. | 4 | T. | ------ |
| Metridia lucens | ------ | 20 | ------ | 25 | 33 | 5 | ------ | ------ | ------ | ------ | 15 | 6 | ------ | ------ |
| Monstrilla serricornis | ------ | ------ | ------ | ------ | ------ | ------ | ------ | T. | ------ | ------ | ------ | ------ | ------ | ------ |
| Pseudocalanus elongatus | 34 | 30 | 20 | ------ | 33 | 5 | 30 | 22 | 17 | ------ | 10 | 20 | 66 | 45 |
| Temora longicornis | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 3 | 17 | ------ | ------ | ------ | ------ | ------ |
| Development stages | ------ | ------ | A. | A. | A. | C. | A. | C. | F. | ------ | ------ | ------ | ------ | C. |

| Station number | 20065 | 20067 | 20070 | 20071 | 20072 | 20073 | 20075 | 20077 | 20079 | 20081 | 20083 | 20084 | 20087 | 20088 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | March—Continued | | | | | | | | | | | | | |
| Day of month | 11 | 12 | 13 | 13 | 13 | 17 | 19 | 19 | 22 | 22 | 23 | 23 | 24 | 24 |
| SURFACE NET | | | | | | | | | | | | | | |
| Acartia clausi | ------ | 25 | 10 | 60 | T. | ------ | 30 | 5 | T. | 10 | 15 | 25 | 15 | 10 |
| Acartia longiremis | ------ | 5 | 5 | ------ | T. | ------ | 3 | 5 | T. | 6 | 65 | 25 | 5 | 5 |
| Calanus finmarchicus | 80 | 30 | 75 | ------ | 66 | 50 | 30 | 65 | 50 | 60 | 8 | 5 | 60 | 75 |
| Calanus hyperboreus | ------ | ------ | ------ | ------ | ------ | 5 | T. | 5 | 25 | ------ | 2 | ------ | ------ | 1 |
| Euchæta norvegica | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 6 | 25 | ------ | ------ | ------ | ------ | ------ |
| Halithalestris croni | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 1 | 2 | ------ | 5 | 1 |
| Metridia longa | 5 | 10 | ------ | ------ | ------ | 10 | ------ | 5 | ------ | 15 | 2 | ------ | ------ | ------ |
| Metridia lucens | 8 | 5 | ------ | 20 | 1 | 5 | ------ | 3 | ------ | 6 | 6 | 25 | ------ | ------ |
| Monstrilla serricornis | ------ | ------ | T. | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Paracalanus parvus | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 5 | ------ | 2 | ------ | 10 | ------ | ------ |
| Pseudocalanus elongatus | 5 | 25 | 10 | 20 | 33 | 30 | 33 | 1 | T. | ------ | ------ | ------ | 15 | 8 |
| Temora longicornis | 2 | T. | ------ | ------ | ------ | ------ | 4 | ------ | ------ | ------ | ------ | 10 | ------ | ------ |
| Development stages | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | C. | C. | A. | A. | C. |

| Station number | 20089 | 20090 | 20091 | 20092 | 20093 | 20094 | 20096 | 20099 | 20100 | 20101 | 20104 | 20105 | 20106 | 20107 | 20108 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | April | | | | | | | | | | | | | | |
| Day of month | 6 | 6 | 9 | 9 | 9 | 10 | 10 | 12 | 12 | 12 | 15 | 15 | 16 | 16 | 16 |
| SURFACE NET | | | | | | | | | | | | | | | |
| Acartia clausi | 15 | ------ | 1 | ------ | ------ | 1 | 40 | ------ | ------ | 12 | 65 | 20 | 1 | 70 | 45 |
| Acartia longiremis | 5 | ------ | 1 | ------ | ------ | 1 | 5 | ------ | ------ | 6 | 10 | 3 | 1 | 5 | 40 |
| Calanus finmarchicus | 70 | 98 | 97 | 50 | 55 | 95 | 45 | 98 | 100 | 50 | 10 | 50 | 65 | 5 | 10 |
| Calanus hyperboreus | ------ | ------ | 1 | 1 | 1 | 1 | 2 | 2 | ------ | ------ | ------ | 7 | 30 | ------ | 3 |
| Halithalestris croni | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 1 | ------ | ------ | ------ | ------ | ------ |
| Metridia longa | ------ | ------ | ------ | 25 | 16 | 1 | 6 | ------ | ------ | 20 | ------ | 15 | 1 | ------ | ------ |
| Metridia lucens | 10 | ------ | ------ | 12 | 14 | 1 | 2 | ------ | ------ | 10 | 10 | 5 | 1 | ------ | ------ |
| Monstrilla serricornis | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | T. | ------ | ------ | T. | ------ | ------ |
| Pseudocalanus elongatus | ------ | ------ | ------ | 10 | 12 | ------ | ------ | ------ | ------ | 1 | 5 | ------ | 1 | 20 | ------ |
| Temora longicornis | ------ | 2 | ------ | 2 | 2 | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 2 |

*Percentages of the several species of copepods in samples from the surface hauls, February to May, 1920, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 20109 | 20110 | 20111 | 20112 | 20113 | 20114 | 20115 | 20119 | 20120 | 20122 | 20124 | 20125 | 20127 | 20128 | 20129 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | April—Continued | | | | | | | | May | | | | | | |
| Day of month | 16 | 16 | 17 | 17 | 17 | 17 | 18 | 20 | 4 | 8 | 16 | 16 | 17 | 17 | 17 |
| SURFACE NET | | | | | | | | | | | | | | | |
| Acartia clausi | 45 | 16 | 17 | | | | | 8 | 35 | 6 | 6 | 10 | 6 | 30 | 7 |
| Acartia longiremis | 40 | 16 | 17 | | | | | 2 | 5 | 3 | | | 1 | 4 | 2 |
| Calanus finmarchicus | 10 | 60 | 33 | 100 | 100 | 98 | 80 | 87 | 60 | 90 | 90 | 75 | 65 | 60 | 90 |
| Calanus hyperboreus | 5 | 6 | | | | T. | 5 | | T. | 1 | 1 | 2 | | 2 | |
| Halithalestris croni | | 2 | | | | T. | | | | | | | | | |
| Metridia longa | | | | | | 2 | 5 | | | | | 3 | 20 | 1 | |
| Metridia lucens | | | | | | | | | | | | | 4 | 1 | |
| Paracalanus parvus | | | 20 | | | | 10 | 1 | | | | | | | |
| Pseudocalanus elongatus | | | 10 | | | | | 2 | | | 3 | 10 | 4 | 1 | |
| Temora longicornis | | | 3 | | | | | | | | | | | 1 | 1 |
| Development stages | | | | | | | F. | C. | C. | C. | A. | A. | C. | | |

*Percentages of the several species of copepods in samples from the horizontal hauls, December, 1920, and January and March, 1921, identified and tabulated by Dr. C. B. Wilson*

| Station number | 10488 | 10489 | 10490 | 10491 | 10492 | 10493 | 10494 | 210495 |
|---|---|---|---|---|---|---|---|---|
| Month | December | | | | | | | |
| Day of month | 29 | 29 | 29 | 30 | 30 | 30 | 30 | 31 |
| Depth, in meters, of major part of haul | 15 | 75 | 240 | 125 | 20 | 75 | 60 | 60 |
| HORIZONTAL NET, OPEN | | | | | | | | |
| Acartia clausi | 5 | 3 | 1 | 3 | 1 | 10 | 3 | 5 |
| Acartia longiremis | 6 | 15 | | 2 | 1 | 10 | 5 | 5 |
| Anomalocera pattersoni | T. | | | | | | | |
| Calanus finmarchicus | 65 | 30 | 90 | 55 | 55 | 55 | 75 | 25 |
| Calanus hyperboreus | | | 5 | | | | | |
| Centropages hamatus | 8 | | | | | | | 5 |
| Centropages typicus | 5 | 2 | | | | 1 | | 5 |
| Dwightia gracilis | | | | | T. | | | |
| Euchæta norvegica | | | 2 | | | | | |
| Eurytemora herdmani | 1 | | | | | | | |
| Metis ignea | 1 | | | | | | | |
| Metridia longa | 1 | 20 | | 25 | 10 | 15 | 5 | 3 |
| Metridia lucens | 1 | 20 | | 5 | 10 | 2 | 3 | 1 |
| Paracalanus parvus | | | 2 | | 2 | 2 | 2 | |
| Pseudocalanus elongatus | 5 | 10 | | 10 | 15 | 5 | 5 | 50 |
| Rhincalanus cornutus | | | | | 1 | | 1 | |
| Scolecithricella minor | | | | | T. | | | |
| Temora longicornis | 2 | | | | 5 | | 1 | 1 |

*Percentages of the several species of copepods in samples from the horizontal hauls, December, 1920, and January and March, 1921, identified and tabulated by Dr. C. B. Wilson*—Continued

| Station number | 10496 | 10497 | 10499 | 10500 | 10502 | 10505 | 10506 | 10507 | 10508 | 10509 | 10510 | 10511 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | January | | | | | March | | | | | | |
| Day of month | 1 | 1 | 4 | 4 | 5 | 4 | 4 | 4 | 4 | 5 | 5 | 5 |
| Depth, in meters, of major part of haul | 100 | 50 | 150 | 60 | 150 | 20 | 10 | 60 | 40 | 150 | 175 | 100 |
| HORIZONTAL NET, OPEN | | | | | | | | | | | | |
| Acartia clausi | ------ | 5 | 2 | ------ | 10 | 5 | 5 | 3 | 15 | 5 | 10 | 5 |
| Acartia longiremis | ------ | 2 | 1 | ------ | ------ | ------ | ------ | ------ | T. | ------ | 2 | 2 |
| Calanus finmarchicus | 65 | 35 | 75 | 35 | 10 | 45 | 45 | 50 | 50 | 70 | 30 | 70 |
| Calanus hyperboreus | 2 | 2 | 5 | ------ | ------ | ------ | ------ | ------ | ------ | ------ | 2 | ------ |
| Centropages bradyi | ------ | ------ | ------ | T. | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Centropages hamatus | 3 | 16 | ------ | 2 | 5 | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Centropages typicus | 5 | 8 | ------ | 3 | 3 | ------ | ------ | ------ | ------ | ------ | 1 | 1 |
| Eucalanus attenuatus | T. | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Euchæta norvegica | 2 | ------ | 2 | ------ | T. | ------ | ------ | ------ | ------ | ------ | 30 | ------ |
| Galdius tenuispinis | 1 | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Halithalestris croni | ------ | ------ | ------ | ------ | 5 | ------ | ------ | ------ | ------ | 1 | ------ | 1 |
| Labidocera æstiva | 1 | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Metis ignea | ------ | ------ | ------ | ------ | ------ | T. | ------ | ------ | ------ | ------ | ------ | ------ |
| Metridia longa | 10 | 8 | 10 | 30 | 25 | 5 | ------ | 20 | 10 | 15 | 15 | 10 |
| Metridia lucens | 5 | 8 | ------ | 30 | 5 | ------ | ------ | 2 | T. | 5 | ------ | 5 |
| Paracalanus parvus | ------ | 2 | ------ | ------ | 10 | ------ | 5 | ------ | ------ | ------ | ------ | 1 |
| Pseudocalanus elongatus | 5 | 14 | 5 | ------ | 10 | 45 | 45 | 25 | 25 | 3 | 10 | 5 |
| Rhincalanus cornutus | 1 | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Temora longicornis | ------ | ------ | ------ | ------ | 10 | ------ | ------ | ------ | ------ | 1 | ------ | ------ |
| Tortanus discaudatus | ------ | ------ | ------ | ------ | 7 | ------ | ------ | ------ | ------ | ------ | ------ | ------ |
| Development stages | ------ | C. | C. | C. | A. | C. | A. | C. | F. | ------ | ------ | ------ |

## Supplementary note on the copepods [60]

Since the preceding account of the copepods was written, Dr. C. B. Wilson has made a further examination of the tow nettings of 1920 and 1921 and communicates the following notes on additional species detected. Most of these appear only in very small numbers. One, however—*Oithona similis*—is plentiful enough to suggest that it will prove widespread in the gulf.

*Aegisthus mucronatus.*—A single female was obtained from a vertical haul at station 20069, March 12, 1920, southeast of Georges Bank.

*Alteutha depressa.*—About a dozen of these peculiar harpactids, which look very much like sowbugs, were taken in a vertical net at station 20117 on April 17, 1920, close to the eastern shore of Cape Cod.

*Amallophora magna.*—Three females taken in a vertical net just off the southern edge of Georges Bank, February 22, 1920, station 20044.

*Calanus minor.*—Ten of these tiny calanids were taken at the surface between the eastern end of Georges Bank and Nova Scotia, April 16, 1920, station 20106.

*Calanus tonsus.*—Six females were taken in a vertical net off the eastern end of Georges Bank, April 16, 1920, station 20107.

*Candacia norvegica.*—Three females were captured at the surface off the southern edge of Georges Bank, May 17, 1920, station 20129.

*Chiridius armatus.*—Eight specimens, including both sexes, were taken in a vertical net southeast of Nova Scotia, March 19, 1920, station 20077.

[60] Communicated by Dr. C. B. Wilson.

*Chiridius obtusifrons.*—Three females were captured in a vertical net southeast of Cape Sable, March 19, 1920, station 20075.

*Chirundina streetsii.*—Two females were found in a vertical haul just south of Georges Bank, February 22, 1920, station 20045.

*Clytemnestra rostrata.*—A single female was taken in a vertical haul south of Georges Bank, February 22, 1920, station 20044.

*Cornucalanus magnus.*—A single female of this large calanid was found in a vertical haul southeast of Nova Scotia, September 6, 1915, station 10313.

*Corycæus carinatus.*—Eight specimens, including both sexes, were taken in a vertical net just north of Georges Bank, February 23, 1920, station 20048.

*Corycæus elongatus.*—Ten specimens, including both sexes, were found in the same haul with the preceding species, station 20048.

*Corycæus ovalis.*—Two females were taken with the preceding species.

*Corycæus speciosus.*—Two females were captured in a closing net north of Georges Bank, March 1, 1920, station 20053.

*Dwightia gracilis.*—Ten specimens, including both sexes, were taken in a vertical net just north of Georges Bank, February 23, 1920, station 20048 (see also p. 226).

*Dwightia oculata.*—Six females and three males of this beautifully colored species were taken in a vertical haul southeast of Nova Scotia, March 19, 1920, station 20076.

*Euchæta marina.*—A single male of this species was taken in a vertical haul northeast of Cape Cod, August 31, 1915, station 10307.

*Euchirella curticauda.*—Six specimens, including both sexes, were taken in a vertical net southeast of Nova Scotia, September 6, 1915, station 10313.

*Euchirella pulchra.*—Three females were captured in a vertical haul south of Georges Bank, February 22, 1920, station 20044.

*Gætanus miles.*—A single female was taken in a vertical net in deep water southeast of Nova Scotia, March 12, 1920, station 20069.

*Gaidius brevispinus.*—Three females were taken in a bottom net at a depth of 150 meters south of Georges Bank, February 22, 1920, station 20045.

*Heterorhabdus norvegicus.*—Six specimens, including both sexes, were captured in a vertical haul south of Georges Bank, February 22, 1920, station 20044.

*Metridia brevicauda.*—Fifteen specimens, including both sexes, were taken at the surface northeast of Cape Cod, April 18, 1920, station 20115.

*Metridia princeps.*—A single female was taken in a vertical haul off the southern edge of Georges Bank, February 22, 1920, station 20044.

*Microthalestris forficula.*—About 50 specimens of both sexes of this tiny harpactid were obtained at the surface north of Georges Bank, station 20114.

*Oithona atlantica.*—Thirty males and females were taken at the surface southeast of Nova Scotia, March 19, 1920, station 20075.

*Oithona plumifera.*—Three females were captured at the surface at station 10511, March 5, 1921.

*Oithona similis.*—Several hundred specimens of both sexes were obtained at various stations in vertical nets and at the surface.

*Oncæa conifera.*—Twelve specimens, including both sexes, were taken at the surface in the Eastern Channel, April 16, 1920, station 20107.

*Oncæa minuta.*—Fifteen males and females were captured in a vertical haul in deep water southeast of Georges Bank, March 12, 1920, station 20069.

*Oncæa venusta.*—Twenty-five males and females were found in a vertical haul south of Georges Bank, February 22, 1920, station 20044.

*Scolecithricella obtusifrons.*—Three females were captured in a vertical net in deep water southeast of Nova Scotia, March 19, 1920, station 20077.

*Scolecithricella ovata.*—Twenty females were taken in a vertical net south of Georges Bank, February 22, 1920, station 20044.

*Temora stylifera.*—A single female was captured in a vertical net southeast of Nova Scotia, September 6, 1915, station 10313.

*Tisbe furcata.*—A single female was taken at the surface just outside Boston Harbor, April 6, 1920, station 20089.

## Daphnids (Cladocera)

These little crustaceans are often extremely plentiful in the coastwise waters of boreal seas, especially of the North Sea region. It is probable that they are an important element in the plankton of estuarine situations all around the coast line of the Gulf of Maine, for McMurrich found the genera Podon and Evadne regularly at St. Andrews during the summer months, often in abundance, while to the south of our area Fish (1925) reports both Evadne and Podon in abundance at Woods Hole and in Long Island Sound. The group as a whole, however, is so strictly neritic that it hardly figures in the planktonic communities of the open gulf more than a few miles out from land, except at rare intervals for brief periods, and is only accidental outside the 100-meter contour.

Only one cladoceran genus—Evadne—has yet been noted in our catches, and because of its slight importance in the natural economy of the offshore waters of the Gulf of Maine no attempt was made to list the occurrence in the towings of 1912 to 1914. A preliminary survey of the surface towings for 1915 located it at stations 10287, 10302, 10303, 10313, 10317, 10318, and 10319 and in Shelburne Harbor, Nova Scotia. In 1916 Evadne was recorded at only one Gulf of Maine station—10398. All these localities, as I have already stated (p. 35), lie within 15 miles of land. It did not appear in the samples of the catch at the other summer stations, which were passed under the microscope, but as examination of larger amounts of the plankton might have disclosed occasional specimens of Evadne, the most that can be said is that it was certainly scarce if not actually absent at the stations where it was not recorded (also on Georges Bank, August 13, 1926).

Evadne was not found at all in the spring towings of 1920 or during the winter and early spring of 1920–1921, but in August, 1922, it appeared at several stations in Massachusetts Bay (10636, 10637, 10638, 10640, 10641, 10643, and 10644). Up to that time we had found it in large numbers on only two occasions, namely, near Cape Elizabeth, September 20, 1915 (station 10319), and Cape Cod Bay, August 24, 1922 (station 10644), most of the other records being based on only a scattering. On August 18, 1924, however, after this report was ready for the press, surface tows

yielded a great abundance of Evadne off Gloucester, 1 to 10 miles out in Massachusetts Bay. It was less abundant 16 miles out and scarce or absent over the northern end of Stellwagen Bank. A tow made that same day close to the extremity of Cape Ann yielded only a fraction as many Evadne as off the mouth of Gloucester Harbor, and only a scattering was taken two days later in Provincetown Harbor, though young herring seined there were full of Podon and Evadne.

In the North Sea region Evadne is definitely seasonal in its occurrence. The two species whose occurrence there has been plotted—*spinifera* and *nordmani*—are both most plentiful in August. The entire stock of the former produces resting spores in autumn; then dies off. This is likewise the fate of most of the *nordmani*, though some few of these survive and continue to reproduce parthogenetically during the winter. The spores of the two species winter on the bottom, hatch in May, and by rapid asexual multiplication the stocks are again built up to their summer plurimum.[61]

Specific identification of the Evadne of the Gulf of Maine has not been attempted as yet, but our few records of the genus as a whole, with McMurrich's data for Podon and Evadne at St. Andrews, show a corresponding seasonal periodicity in the Gulf of Maine, all falling within the period June 8 to September 20, with the largest offshore catches in August and September. At Woods Hole, Fish (1925) found *Evadne nordmani* most plentiful in November, least so in spring, but *E. tergestina* at its maximum during the summer and early autumn.

Cladocera are one of the most important items in the diet of many species of larval and post-larval fishes in British waters (Lebour 1919 and 1920). Judging from the general similarity between the planktonic communities in general, probably this applies also to the inshore waters of the Gulf of Maine. The various young fishes that are in shoal water there in summer will probably be found to consume Evadne and Podon regularly—herring, for instance, as just noted.

## WORMS

### Glass worms (chætognaths)[62]

Four species of chætognaths are known from the Gulf of Maine, one of which—*Sagitta elegans*—is a regular member of the local endemic plankton while the others enter its limits as immigrants only.

#### Sagitta elegans

If I were asked to name three animals as most characteristic of the plankton of the offshore waters of the Gulf of Maine I should unhesitatingly select the copepods *Calanus finmarchicus* and *Pseudocalanus elongatus* and the chætognath *Sagitta elegans*.[63] Throughout the year and in every part of the Gulf of Maine, as well as over the offshore banks which inclose it on the south, this large, active, and voracious worm is so nearly universal that it has been taken at practically every station and in the great majority of our hauls. To the east and north of our limits,

[61] See Apstein (1910) for an account of the seasonal cycle.

[62] Identifications follow von Ritter-Záhony (1911) and Huntsman (1919).

[63] I follow Huntsman (1919) in treating as a unit the several "subspecies" of *S. elegans*, a species comparable to the herring, among fishes, in its tendency to develop local races in different physical environments.

too; it is a regular inhabitant of the whole continental shelf off Nova Scotia (Bigelow, 1917, and Huntsman, 1919), likewise over the Grand Banks of Newfoundland and in the Gulf of St. Lawrence, where the Canadian fisheries expedition found it at many localities and in large numbers (Huntsman, 1919). Generally speaking, the Gulf of Maine is the most southerly important center of regular reproduction and constant abundance for *S. elegans*, as it is for various other boreal planktonic animals. West and south of Cape Cod this chætognath is less plentiful, less regular in its occurrence, and more or less seasonal, ranging southward as far as Chesapeake Bay in cold summers (e. g., 1916) but rare beyond Nantucket in warm (e. g., the year 1913), as I have elsewhere remarked (Bigelow, 1922, p 152). At Woods Hole it is fairly plentiful from December to June, but decidedly rare or lacking entirely in summer (Fish, 1925, fig. 34). Probably it occurs farthest to the southward in winter, but the limit to its distribution in that direction is not yet known for the western Atlantic.

It has been well established, both by our own records and by those of the Canadian fisheries expedition of 1915 (Huntsman, 1919), that *S. elegans* (though not dependent on the bottom at any stage of development) is a creature of coast and not ocean waters. This, indeed, its occurrence in other seas would suggest. Broadly speaking, the outer edge of the continental shelf is its offshore boundary west of Cape Sable at all seasons, a fact illustrated by its rarity at our deep stations over the continental slope[64] both in the cold months and in the warm. East of this, however, Huntsman has shown that its outer limit fluctuates with the seasons, spreading out to the eastward to cover the great oceanic triangle between the Nova Scotian and Newfoundland Banks in spring, to contract again to the general contour of the continental edge as far as the tail of the Grand Banks (including the Laurentian Channel, however) in midsummer. The high temperature, or high temperature combined with high salinity, of the inner edge of the so-called Gulf Stream is an impassable offshore barrier to it along the North American coast.

Only a preliminary survey has yet been made of the collections of this species gathered during the Gulf of Maine cruises; enough, however, to show that its range covers the offshore parts of the gulf. We have seldom found it in any abundance over the deep basin, however, as appears clearly from the accompanying chart (fig. 86) showing the numbers of *S. elegans* per square meter of sea area as calculated from the catches of the vertical nets for the summer seasons of 1913, 1914, 1915, and 1916. Out of a total of about 80 such hauls, only seven have yielded more than 50 *S. elegans* per square meter anywhere in the gulf outside the general 100-meter contour, and these seven stations were all located close to that contour line. With these few exceptions, all our rich hauls of *S. elegans* have been in shallow water, either in the coastal zone (in July, 1912, we found *S. elegans* in some numbers in Casco Bay) or on the offshore banks. But the localization of the rich and poor catches show that not all parts of the peripheral zone of the gulf offer an equally favorable habitat for *S. elegans*,

[64] None were taken at station 10220 in 1914, station 10352 in 1916, stations 20044 and 20129 in 1920, nor at any of the deep stations on the slope west and south of Cape Cod either in 1913 or in 1916, but a few were detected in the vertical haul from 500 meters off Georges Bank, July, 1914 (station 10218).

the "rich" hauls (50+ and especially 400+ per square meter) being definitely concentrated in three chief centers of abundance—viz., in the Massachusetts Bay region and the waters immediately to the north and south of it on Georges Bank, which would

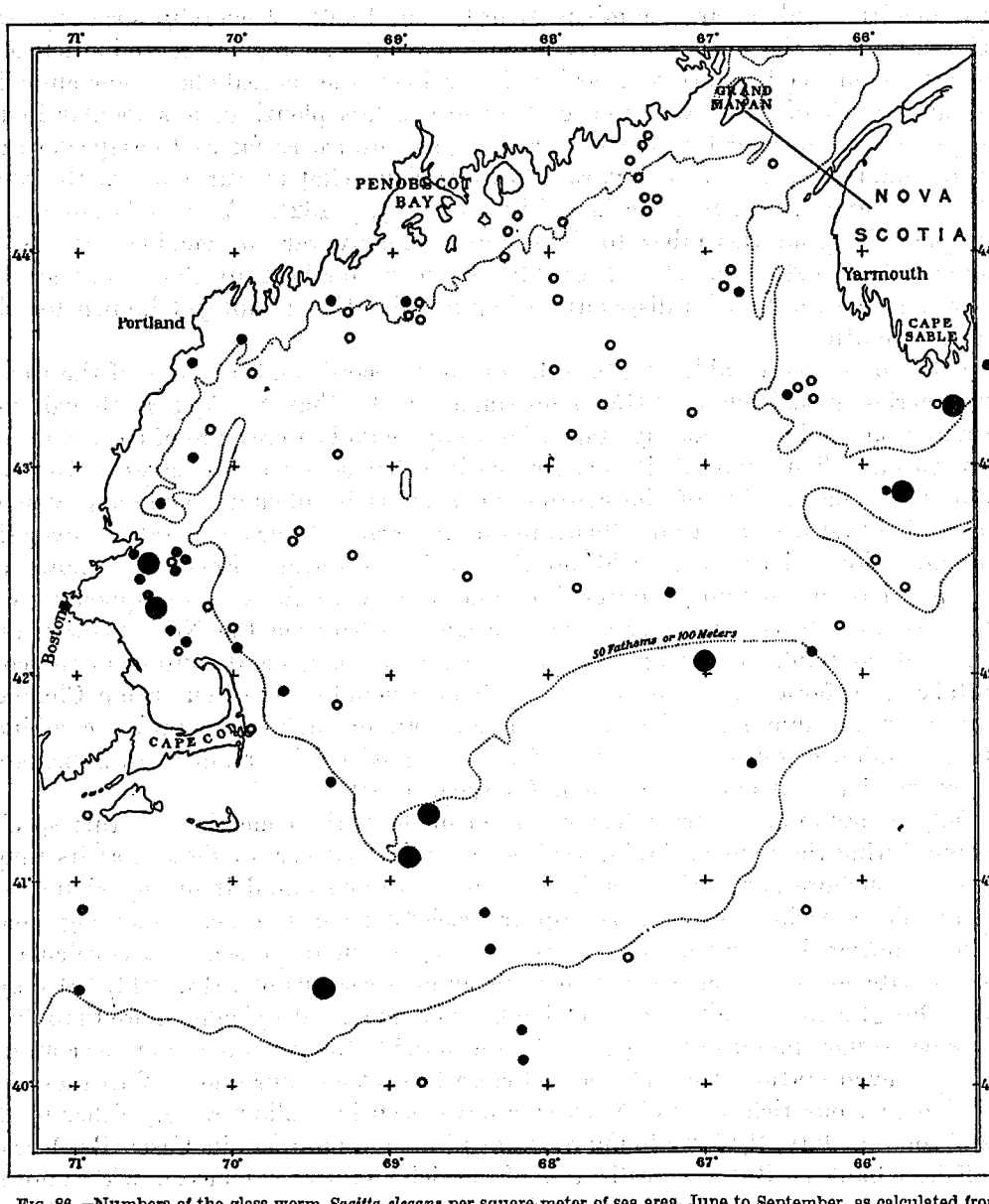


FIG. 86.—Numbers of the glass worm *Sagitta elegans* per square meter of sea area, June to September, as calculated from the vertical hauls. ○, less than 50, including stations where it was so scarce that none were taken in the verticals; •, 50 to 1,000; ●, 1,000+

probably apply equally to Nantucket Shoals, and in the neighborhood of Cape Sable in the eastern side of the gulf. It is only in these regions that we have made catches of 1,000 and more to the square meter.

The most abundant congregation of *S. elegans* so far encountered in the gulf was approximately 5,000 per square meter (young stages) over the outer part of the shelf off Nantucket on July 25, 1916 (Station 10354). *S. elegans* is far less abundant along the coast of Maine east of Cape Elizabeth, and off western Nova Scotia it is often so rare that the vertical nets failed to take it, though it might occur in the horizontal hauls. It is frequently as numerous as 50 per square meter in the Bay of Fundy, however, as Huntsman and Reid (1921) have pointed out.

*Approximate numbers of individuals of Sagitta elegans per square meter of sea surface, based on the catches of the vertical nets*

| Station | Date | Number | Station | Date | Number |
|---|---|---|---|---|---|
| 10213 | July 19, 1914 | 10 | 10329 | Oct. 9, 1915 | 230 |
| 10214 | do | 10 | 10336 | Oct. 26, 1915 | 10 |
| 10215 | July 20, 1914 | 1,380 | 10337 | do | 0 |
| 10216 | do | 860 | 10338 | Oct. 27, 1915 | 100 |
| 10219 | July 21, 1914 | 20 | 10339 | do | 385 |
| 10223 | July 23, 1914 | 170 | 10341 | July 19, 1916 | 2,500 |
| 10224 | do | 2,000 | 10342 | do | 1,750 |
| 10225 | do | 260 | 10344 | July 22, 1916 | 60 |
| 10226 | July 24, 1914 | 260 | 10345 | do | 810 |
| 10227 | do | 50 | 10346 | do | 445 |
| 10229 | July 25, 1914 | 1,340 | 10347 | July 23, 1916 | 2,500 |
| 10230 | do | 2,140 | 10349 | July 24, 1916 | 470 |
| 10243 | Aug. 11, 1914 | 70 | 10354 | July 25, 1916 | 5,000 |
| 10244 | Aug. 12, 1914 | 40 | 20048 | Feb. 23, 1920 | 65 |
| 10245 | do | 10 | 20049 | do | 50 |
| 10246 | do | 20 | 20050 | Mar. 1, 1920 | 30 |
| 10247 | do | 0 | 20053 | Mar. 3, 1920 | 25 |
| 10248 | Aug. 13, 1914 | 0 | 20054 | do | 15 |
| 10249 | do | 10 | 20055 | do | 50 |
| 10250 | Aug. 14, 1914 | 10 | 20058 | Mar. 4, 1920 | 5 |
| 10253 | Aug. 22, 1914 | 50 | 20060 | do | 5 |
| 10255 | Aug. 23, 1914 | 30 | 20061 | Mar. 5, 1920 | 15 |
| 10266 | May 4, 1915 | 10 | 20062 | do | 0 |
| 10267 | May 5, 1915 | 0 | 20064 | Mar. 11, 1920 | 204 |
| 10269 | May 6, 1915 | 10 | 20065 | do | 5 |
| 10270 | do | 15 | 20066 | do | 50 |
| 10271 | May 7, 1915 | 40 | 20067 | Mar. 12, 1920 | 150 |
| 10272 | May 10, 1915 | 25 | 20068 | do | 0 |
| 10278 | May 14, 1915 | 5 | 20069 | do | 0 |
| 10279 | May 26, 1915 | 0 | 20074 | Mar. 19, 1920 | 180 |
| 10282 | June 10, 1915 | 0 | 20075 | do | 50 |
| 10283 | do | 5 | 20079 | Mar. 22, 1920 | 150 |
| 10284 | June 11, 1915 | 0 | 20080 | do | 60 |
| 10286 | June 14, 1915 | 10 | 20082 | Mar. 23, 1920 | 10 |
| 10287 | do | 0 | 20086 | do | 5 |
| 10288 | June 19, 1915 | 20 | 20087 | Mar. 24, 1920 | 0 |
| 10290 | do | 20 | 20089 | Apr. 6, 1920 | 10 |
| 10291 | June 23, 1915 | 585 | 20090 | Apr. 9, 1920 | 40 |
| 10296 | June 24, 1915 | 0 | 20094 | Apr. 10, 1920 | 0 |
| 10298 | June 25, 1915 | 5 | 20095 | do | 65 |
| 10299 | June 26, 1915 | 0 | 20100 | Apr. 12, 1920 | 50 |
| 10303 | July 7, 1915 | 70 | 20102 | Apr. 13, 1920 | 5 |
| 10304 | Aug. 7, 1915 | 25 | 20105 | Apr. 15, 1920 | 50 |
| 10306 | Aug. 31, 1915 | 15 | 20107 | Apr. 16, 1920 | 20 |
| 10307 | do | 10 | 20108 | do | 10 |
| 10309 | Sept. 1, 1915 | 25 | 20109 | do | 10 |
| 10310 | Sept. 2, 1915 | 0 | 20110 | do | 490 |
| 10311 | do | 20 | 20111 | Apr. 17, 1920 | 85 |
| 10313 | Sept. 6, 1915 | 15 | 20112 | do | 10 |
| 10315 | Sept. 7, 1915 | 410 | 20113 | do | 5 |
| 10316 | Sept. 11, 1915 | 10 | 20115 | Apr. 18, 1920 | 20 |
| 10318 | Sept. 16, 1915 | 15 | 20116 | do | 15 |
| 10319 | Sept. 20, 1915 | 455 | 20118 | Apr. 20, 1920 | 90 |
| 10320 | Sept. 29, 1915 | 130 | 20120 | May 4, 1920 | 0 |
| 10321 | do | 145 | 20121 | do | 0 |
| 10323 | Oct. 1, 1915 | 45 | 20122 | May 8, 1920 | 20 |
| 10324 | do | 130 | 20123 | May 16, 1920 | 100 |
| 10325 | Oct. 4, 1915 | 115 | 20124 | do | 95 |
| 10326 | do | 5 | 20125 | do | 5 |
| 10327 | Oct. 9, 1915 | 5 | 20128 | May 17, 1920 | 1,000 |
| 10328 | do | 25 | 20129 | do | 100 |

We have encountered one or more centers of abundance for *S. elegans* on every cruise, and on such occasions the numbers actually present in the water may be very great (for so large an animal), as illustrated by the following examples:

| Date | Station | Approximate number of S. elegans per square meter | Date | Station | Approximate number of S. elegans per square meter |
|---|---|---|---|---|---|
| July 19, 1916 | 10341, Massachusetts Bay | 2,500 | July 25, 1916 | 10354, off Nantucket | 5,000 |
| Do | 10342, Massachusetts Bay | 1,750 | July 23, 1914 | 10224, Georges Bank | 2,000 |
| July 23, 1916 | 10347, Georges Bank | 2,500 | July 25, 1914 | 10330, near Cape Sable | 2,140 |

In every case, however, we have found these swarms limited to areas so small that the neighboring stations have yielded only a fraction as many Sagittæ. Thus, in July, 1913, hauls off northern Cape Cod and on the western end of Georges Bank each yielded upwards of 1,000 large *S. elegans*, but an intermediate station of about the same temperature and salinity yielded only 28, while a month later the Sagitta stock at the first of these localities had dwindled nearly to the vanishing point (Bigelow, 1915, p. 298). Variations in the local abundance of this species were no less striking on August 15 of the same year, when we found it abundant off Cape Elizabeth and near the Isles of Shoals but extremely rare at a station halfway between those two localities. Again, on July 23, 1914, we found the waters over the northeast edge of Georges Bank (station 10224) alive with *S. elegans*, though there were very few at a neighboring station (10223) on the bank to the south or over the deep a few miles to the north. Similarly, *S. elegans* swarmed a couple of days later near Cape Sable and in the Northern Channel (stations 10229 and 10230), but was so rare over Browns Bank (station 10228) that our tow nettings yielded only one or two examples; and in July, 1916, we found *S. elegans* in multitudes in Massachusetts Bay on the 19th (station 10342) but much less common off Cape Cod only a few miles away (station 10344).

The data gathered on the spring cruises of 1913 and 1920 show that *S. elegans*, like most other large planktonic animals, becomes very scarce in most parts of the Gulf in early spring shortly after the water has cooled to its winter minimum, and falls to its lowest numerical ebb during the vernal flowering period of the diatoms. Thus in Massachusetts Bay in 1913 *S. elegans* dominated the tow in mid-February, with a catch of about 125 cubic centimeters in the horizontal haul on the 13th (Bigelow, 1914a, p. 405); but it had become so scarce by March 4 that the total catch in the large net (half hour's haul) was only 12 individuals, and no Sagittæ at all were taken on April 3, when diatoms were swarming. In 1920 *S. elegans* persisted in some numbers in the bay until the diatom flowerings were well advanced, vertical hauls on April 6 and 9 (stations 20089 and 20090) still yielding Sagittæ at the rates of 10 and 40 specimens, respectively, per square meter; but shortly thereafter they became so scarce in that general region that none were taken in the vertical haul and only occasional specimens in the horizontals on May 4 (station 20120). In this respect

Passamaquoddy Bay closely parallels Massachusetts Bay, for Saggittæ do not appear at all in Doctor McMurrich's plankton lists for St. Andrews between the first week in April and the first week in June. Our spring cruises in 1915 and 1920 suggest

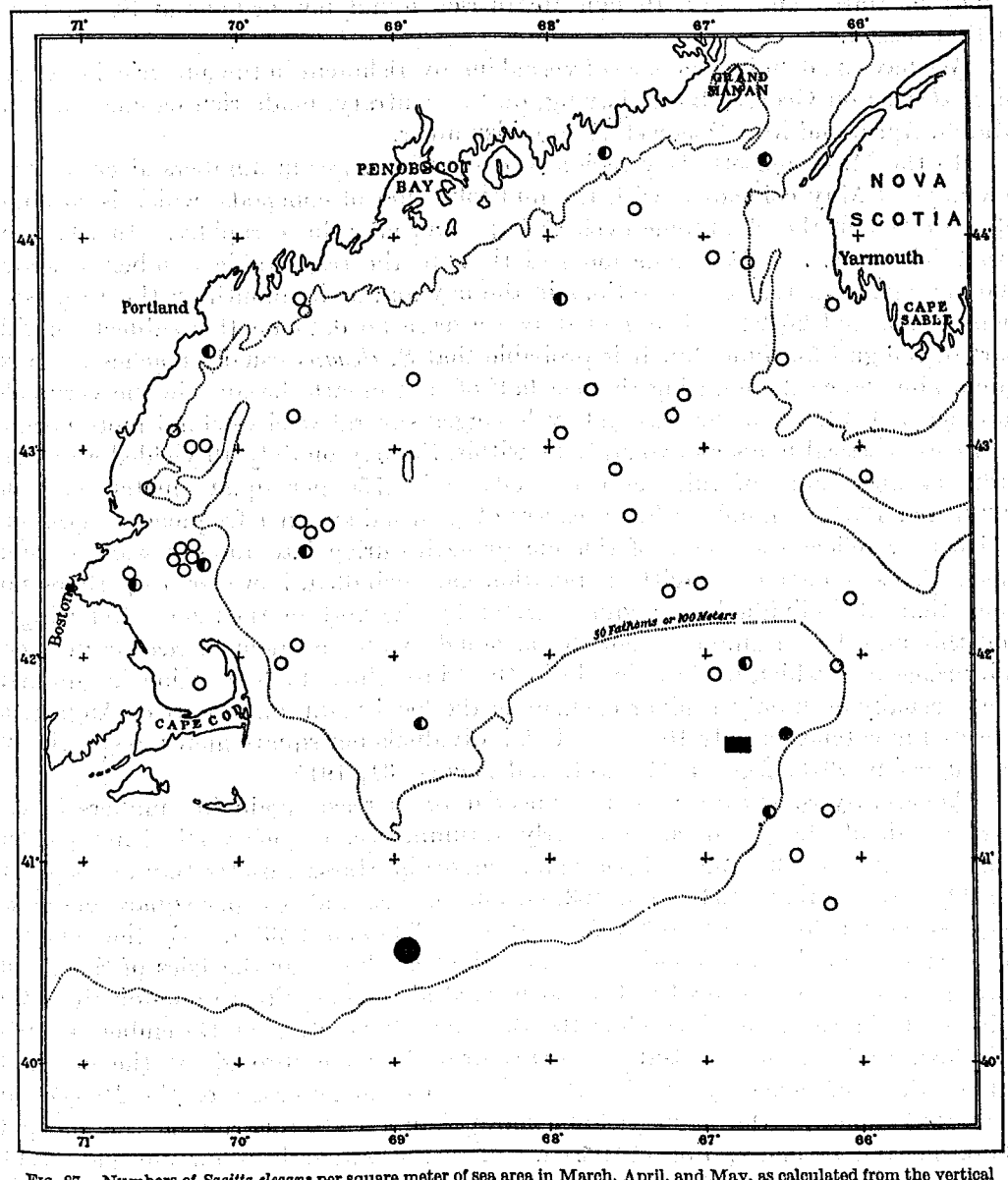


FIG. 87.—Numbers of *Sagitta elegans* per square meter of sea area in March, April, and May, as calculated from the vertical hauls. ○, less than 50, including stations where none were taken in the verticals; ◐, 50 to 400; •, 400 to 1,000; ●, 1,000+; ▬, stations where the horizontal haul yielded a swarm, but where no vertical haul was made

that the stock of *S. elegans* is at its lowest ebb over the inner parts of the gulf as a whole at about the same season (that is, end of April and beginning of May) as it is in Massachusetts and Passamaquoddy Bays (fig. 87) but does not fall to so low an

ebb offshore, having proved sufficiently plentiful in April and May for the vertical net to pick up at least a few specimens at almost every station. Similarly, Huntsman and Reid (1921) record considerable numbers of Sagittæ in the open Bay of Fundy in March and May, though McMurrich found few or none at St. Andrews at that season.

We have no definite evidence of vernal impoverishment in the numerical strength of *S. elegans* on Georges Bank, having, on the contrary, made rich catches there in March, April, and May [65] as well as in midsummer.

In the Massachusetts Bay region *S. elegans* increases in numbers after the first few days of May coincident with the multiplication of copepods, which is so notable an event in the planktonic cycle (p. 41), and may do so rapidly. In 1920, for example, the *S. elegans* population had risen to the respectable number of about 100 per square meter at two stations in the bay and at its mouth on the 16th (stations 20123 and 20124). Unfortunately we have no data on this subject for this part of the gulf for June, but it is probable that *S. elegans* usually reaches its maximum abundance there during the last half of that month, because in the very cold summer of 1916, when the seasonal cycle lagged several weeks behind more normal summers, vertical hauls at two stations within the bay on July 19 yielded an extraordinary abundance of this Sagitta—2,500 and 1,750 per square meter (stations 10341 and 10342)—numbers far in excess of its usual summer frequency there, and which may reflect the status of this chætognath during late June of warmer summers. This tremendous Sagitta population had dwindled, however, to perhaps not more than 50 individuals per square meter by the 29th of the month following; [66] and this may be an annual event, for although we have taken *S. elegans* in every subsurface haul which we have made in the Massachusetts Bay region in summer, it has usually been only a minor element in the local plankton in July or August, as reflected in catches of only 10, 50, and 15 individuals per square meter, respectively, on August 9, 1913, August 22, 1914, and August 31, 1915.

Apparently *S. elegans* may be expected to increase again in numbers in the western side of the gulf during the early autumn, because our vertical net yielded it at the rates of 130 and 145 per square meter in Massachusetts Bay on September 29, 1915 (stations 10320 and 10321), and of 100 and 385 per square meter at neighboring localities on October 27 (stations 10338 and 10339). By the evidence of horizontal hauls it was perhaps as abundant as this near the Isles of Shoals on November 1, 1916 (station 10400), and formed about one-fifth to one-fourth of the volume of the catch in Massachusetts Bay, off Gloucester, on December 4, 1912 (Bigelow, 1914a, p. 404). But *S. elegans* proved scarce throughout the northern half of the gulf generally on the December to January cruise of the *Halcyon* in 1920–1921, none of the hauls yielding more than a scattering among the copepod plankton, and at one station (10493) we missed it altogether—an unusual event. Our data on the status of *S. elegans* during the later winter are confined to the

[65] On the eastern part of the bank *S. elegans* dominated the horizontal catch on March 11, 1920 (station 20066), though the vertical haul indicated only about 50 per square meter, which illustrates the unreliability of the latter method when dealing with animals so large and so active. There were 490 per square meter at a neighboring location on April 16 (station 20110), and on the southwest part of the bank 1,000 per square meter on May 17 (station 20128).

[66] Judging from the scanty yield of the horizontal haul at station 10298. No vertical haul was made.

Massachusetts Bay region. Here we found it constituting from one-fourth to one-half of the rather scanty tow in January, 1913, and it dominated the planktonic community off Gloucester on February 13.

*Sagitta elegans* certainly is endemic in the Gulf of Maine. Huntsman and Reid (1921, p. 104), to whom we owe the only local record of its eggs (this for the Bay of Fundy), found from examination of ovarian eggs that in the Bay of Fundy the "spawning season is a long one, extending from the end of March or the beginning of April to September at least. September 4 would seem to be near the end of the season." Corresponding to this, they found eggs (identified by comparison with large series of eggs and young Sagittæ from the southern part of the Gulf of St. Lawrence, an important breeding ground) in the Bay of Fundy plankton from April to October, numerous or rare locally according to the abundance of the adult Sagittæ. Huntsman and Reid further point out that the proportional abundance of eggs at different stages in development proves that they do not develop properly in the Bay of Fundy until September, the warmest month of the season, nor did they find the young Sagittæ in any numbers in the plankton until that time. However, the young proved to be even more widely distributed than their parents, occurring not only in the open bay but also up the estuaries, where the adults are not to be found; and in general the younger stages were most plentiful at locations where the water was stratified vertically as to its temperature and density, and least so where vertical circulation was most active.

Huntsman and Reid concluded (and I believe justly) that the Bay of Fundy is such an unfavorable environment for the reproduction of *S. elegans* that the stock raised there locally is small and that the Sagitta population is kept up by immigration from the Gulf of Maine.

Sagitta eggs have not been detected (perhaps because not especially sought) in our plankton hauls in the open gulf, nor has the probable spawning season, as revealed by the state of the ovarian eggs, yet been established except for the Bay of Fundy, a region so peculiar in its hydrography as to be a law unto itself. Statistical study of the relative sizes of the Sagittæ captured in our hauls, from which much information about the seasons and localities of reproduction may be hoped, is likewise a task for the future. However, I may point out that catches of *S. elegans* made prior to mid-May during the springs of 1915 and 1920 consisted chiefly of very large individuals, such as might be expected toward the end of a period of growth. In 1915 it was not until June 14 that Sagittæ less than 10 millimeters in length were recognized among the plankton of the gulf. In 1920, however, equally young *S. elegans* (8 millimeters long) were taken in Massachusetts Bay as early as May 16 (station 20123), with still smaller stages (5 to 12 millimeters long) on the western part of Georges Bank on the 17th (station 20128), and from June on through the summer, until the last of October, specimens smaller than 10 millimeters have been detected at a considerable proportion of our stations.[68]

On the whole, then, it is safe to say that *S. elegans* is a late spring and summer breeder in the Gulf of Maine, in so far as any considerable production is concerned, but probably it reproduces more or less throughout the entire year. Fish's (1925)

[68] Oct. 31, 1916, is our latest date for specimens of 10 millimeters or shorter (station 10399).

records suggest that its most active breeding season commences earlier to the westward of Cape Cod, for he found them with ripe eggs at Woods Hole as early as March, and many eggs in the plankton during the latter part of April. He first observed the young on May 2 and found them in abundance throughout May and June. Thus the season of active reproduction falls later and later from southwest to northeast along the coast, as it does for many other animals.

It is likely that with sufficient search the young would be found to be as widely distributed as the adults over the open gulf, just as is the case in the Bay of Fundy, but definite records of them from outside the 100-meter contour are still so few (as a rule based on few individuals and invariably greatly outnumbered by larger sizes) that the importance of coastwise and shoal banks waters as the breeding ground of this species appears very clearly on the chart (fig. 88). Georges Bank in particular serves as a nursery for Sagittæ, witness the notable concentration of young Sagittæ, accompanied by a few larger (15 to 20 millimeters) specimens, over its western end on May 17, 1920 (station 20128). Specimens ranging in size from 4 millimeters upwards abounded over a considerable area at about the same general locality in mid-July, 1916 (stations 10347, 10348, and 10354). Slightly older specimens, 5 to 15 millimeters long, were also plentiful a few miles farther east on the 20th of the same month in 1914 (about 430 per square meter at station 10216) and occurred sparingly among the hosts of adults on the eastern part of the bank three days later (station 10224). Other notable catches of young *S. elegans* were made near Cape Sable among a swarm of adults on July 25, 1914 (station 10230), and off Shelburne, Nova Scotia, June 23, 1915 (about 200 small ones of 6 to 10 millimeters in a total of about 600 Sagittæ of all sizes per square meter at station 10291). I may also mention the presence of young *S. elegans* in Casco Bay in July, 1912, as an example of its propagation close in to the land. Probably it is simply because the adults are more abundant, not because physical conditions are more favorable to reproduction, that more young Sagittæ are produced within the 100-meter contour than over deeper water. At any rate we can regard it as established that *S. elegans* is not only endemic in the Gulf of Maine but breeds there in sufficient numbers to maintain the abundant stock by local production, quite apart from any additions this may receive by immigration from other rich centers of reproduction.

The general relationship of *S. elegans* to temperature and salinity, and its bathymetric status, is well established by Huntsman's (1919) exhaustive analysis, which our Gulf of Maine data generally confirm. Broadly speaking, it is a creature of low temperatures and comparatively low salinities, and wherever its range spreads out from the coastal banks over parts of the oceanic basin high salinities act as a barrier to its downward migrations. It is not likely, however, that this applies to any part of the Gulf of Maine, unless it be to the deepest stratum of water in the extreme southeastern corner. On the other hand, judging from the occurrence of *S. elegans* in the Baltic, no part of the gulf, not even the larger estuaries, is too fresh for some local variety of it to survive. Consequently, its local presence or absence in the Gulf and its concentration at one or other level there can not be ascribed to the precise salinity of the water, but its bathymetric distribution as it varies from season to season is just what might be expected of any planktonic animal preferring

low temperature and tending to shun strong light. Thus in late February and March of 1920, while the water was still near its annual minimum in temperature, with the surface nowhere warmer than 3.6° in the inner parts of the gulf or 4° to

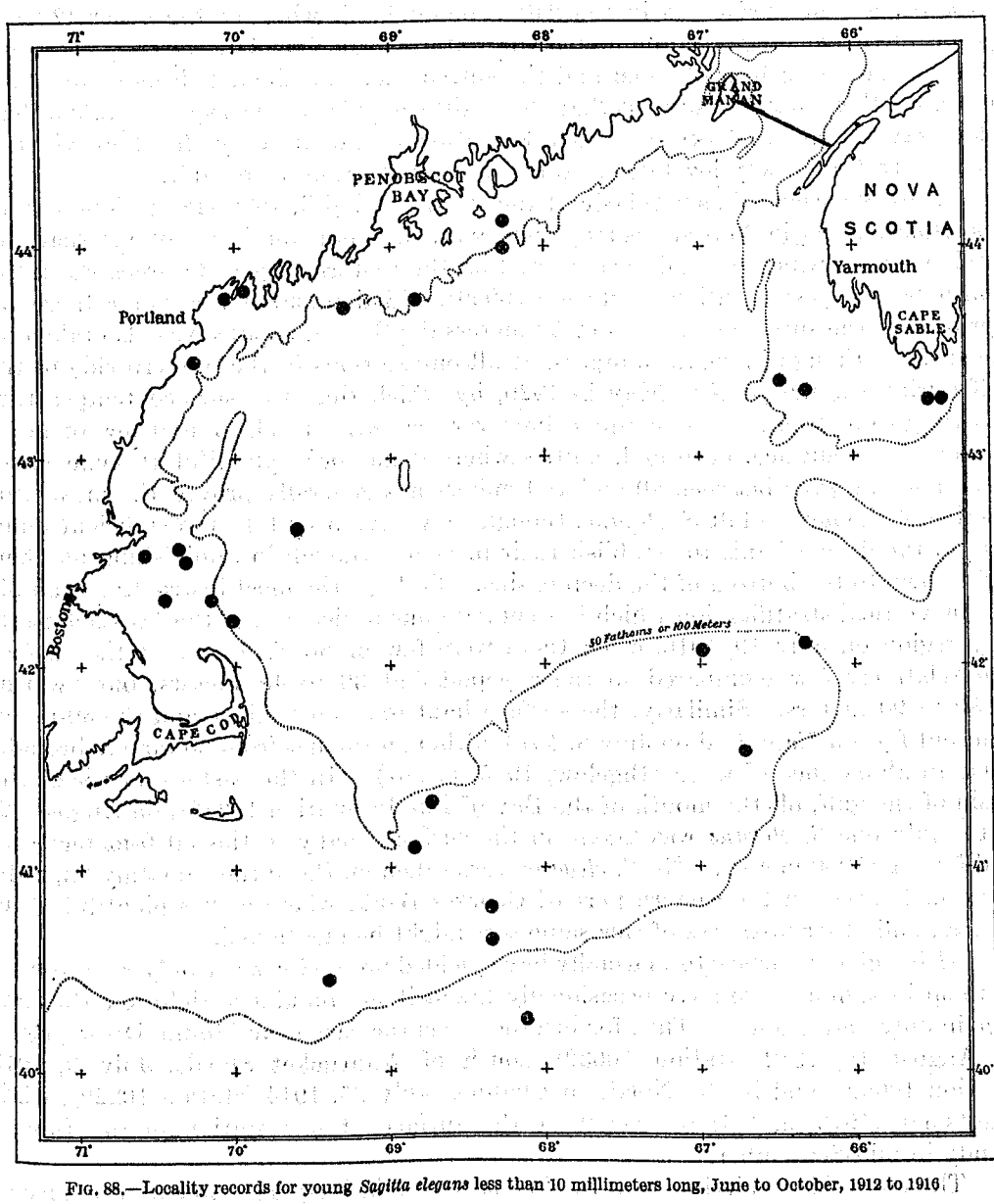


FIG. 88.—Locality records for young *Sagitta elegans* less than 10 millimeters long, June to October, 1912 to 1916.

5° over the seaward slope of Georges Bank, and with the vertical range of temperature less than 4° at most of the stations, we found large *S. elegans* indifferently at all the depths at which we towed and almost as regularly at the surface as at any other

level,[69] but the numbers caught at the surface were usually small compared to the deep hauls. The two stations at which moderately rich surface catches were made were both occupied after dark; at one of them (20049) there were nearly as many *S. elegans* on the surface as in the 240–0 meter haul, while at the other (20066) swarms of this chætognath dominated the water at the time, but the deep haul captured upwards of a liter of them and the surface net but about half as many. On the whole, these stations suggest that the sagitta population was sparser above than below, say, 10 meters depth in March, but below that depth they afford no evidence of concentration at any level down to the deepest stratum of the gulf.

*S. elegans* occurred as regularly at the surface in April, 1920 (18 stations out of a possible 22), as in March; usually, however, in small numbers, except that the notable swarm which we had encountered on the eastern part of Georges Bank the month before, just mentioned (station 20066), still dominated the water there on April 16, at the surface as well as at 50 meters depth. *S. elegans* was also taken on the surface, though in small numbers, at all our stations in the western side of the gulf during the first half of May in 1920, by which time the surface temperature had risen to 6° to 9.7°. In summer, however, we have usually found few or no *S. elegans* at the surface, even at localities where it has been plentiful at some lower level, and the zone between 40 and 100 meters has generally proved the most productive of the large adult *S. elegans*, though they have been taken in sufficient numbers in the deeper hauls to establish their presence, though in diminishing number, right down to the bottom of the deep basins. Perhaps the most instructive example of this vertical stratification which has come to our notice was in the Massachusetts Bay region on July 19, 1916, when there were few or no *S. elegans* at the surface and relatively few (compared to the copepods) at 30 to 40 meters, but swarms at 80 to 90 meters. Similarly, the surface haul took no Sagittæ and the 30-meter haul but few off Cape Cod on July 8, 1913, although the net from 60 meters brought back an abundance of them (Bigelow, 1915, p. 267). In the eastern corner of the basin of the gulf, off the mouth of the Bay of Fundy (station 10246), on August 12, 1914, only one *S. elegans* was taken on the surface, many in the 50–0-meter haul, and few at 150–0 meters. No *S. elegans* were taken on the surface on July 23, 1914 (station 10224), on the eastern part of Georges Bank, where it was plentiful at 40 meters, and other instances of this same sort might be mentioned.

Although our surface tows usually have yielded no *S. elegans* or only a scattering of them in summer, we have occasionally taken it in abundance right on the surface in July and August. This, for instance, was the case near Mount Desert Rock on August 16, 1912 (station 10032), south of Nantucket Shoals, July 9, 1913 (station 10060), and in the Northern Channel, July 25, 1914 (station 10229), while Huntsman (1919, p. 464) records it at the surface at one station in the Bay of Fundy in mid-September.

The large-sized individuals of *S. elegans* were relatively as scarce at the surface in the western half of the gulf at the end of October and during the first days of November in 1916,[70] when the surface temperature had fallen to 8.3° to 10.2°, as they

[69] *S. elegans* taken in 20 surface tows out of a possible 27.

[70] No large ones taken in the surface hauls, stations 10399 to 10404.

are in summer, though moderately plentiful at deeper levels in temperatures of 4 to 7°; but the small sizes were taken in all the surface hauls on that cruise, once in some numbers (station 10399). With the continued cooling of the water the adults must spread through the superficial stratum of water at some time during the late autumn and winter to attain the distribution just described for March (p. 317), but the horizontal hauls at our winter stations have not been adapted to show just when this takes place.

The data just outlined for the Gulf of Maine are directly in line with Huntsman's (1919, p. 465) observations based on the collections made by the Canadian fisheries expedition, that off Nova Scotia the large *S. elegans* rise to the surface by night during May and June while the surface temperature is still low, sinking again during the hours of bright daylight, but are virtually absent from the surface during July and August, night as well as day.

The primary cause for this seasonal variation in the vertical distribution of *S. elegans* is to be found in the temperature of the water, which, being uniformly low during the early spring, then imposes no barrier to upward dispersal; but when the vernal warming of the surface has proceeded to a certain degree, which may tentatively be set at 10 to 12°, most of the Sagittæ remain below the warm superficial layer. The diurnal migration described by Huntsman (1919), together with the fact that when *S. elegans* rises to the surface in the Gulf of Maine in July or August this usually takes place at night, makes it probable that bright light as well as high temperature to some extent limits its dispersal upwards. But, judging from its vertical distribution in March and April, when it is at the surface day and night indifferently, this is not the case until the sun attains a comparatively high declination, the inference being that while *S. elegans* is negatively tropic to light of more than a certain intensity, its movements are little influenced by a paler illumination. This warrants the following working hypothesis. In winter and early spring all levels in the Gulf are sufficiently cool for *S. elegans*, and the illumination by the sun is not so bright but what a certain number may regularly be found at the surface by day as well as by night; but in late spring and early summer it is daily driven downward for some meters by the sun, and by July and August the high temperature renders the uppermost stratum of water unsuitable for its permanent presence, an unfavorable condition from which it can and does escape by sinking. Occasionally it rises to the surface in summer, irrespective of temperature or of illumination. We found an abundance of medium-sized specimens south of Nantucket Shoals, July 9, 1913 (station 10060), at 6 p. m., in a surface temperature of 16.1°, but it is not likely that such upward incursions endure for more than a brief period, perhaps only for a few hours.

Huntsman and Reid (1921) have pointed out for the Bay of Fundy (and our own observations corroborate them) that the young *S. elegans* tend to congregate nearer to the surface than the adults.

In the deeper strata of the gulf, below 20 meters or so, where the physical state of the water is apparently favorable for the existence of *S. elegans*, the local variations in its abundance at different depths may be governed by quite a different

factor—that is, the supply of available food—for this chætognath is both extremely voracious and an active swimmer and hence would tend to gather at the levels, and probably to some extent to congregate in the regions where the copepods on which it chiefly preys are most abundant. Furthermore, it would naturally grow fastest and breed most actively where food was most plentiful, tending to produce and maintain an abundant local stock.

It seems more probable that it is the dependence of *S. elegans* on the calanoid copepod plankton which, as remarked above (p. 30), is most plentiful in the mid-levels, which accounts for the comparatively sparse sagitta population of the deepest levels in the Gulf of Maine and not the comparatively high salinity at these depths, for it thrives in still higher salinities in the North Sea region (Apstein, 1910).

Temperature not only governs the distribution of *S. elegans* but also the size to which it grows, a fact that has long been recognized. Indeed, three varieties or subspecies of this species, one of them a large northern ("*arctica*"), another a smaller boreal-temperate ("*elegans*"), have been recognized by von Ritter-Záhony (1911); but Huntsman (1919) points out that these are not distinct, being connected by intermediates. In fact, the Gulf of Maine collections suggest that the difference in size between them probably is not hereditary at all, but the result of a direct physiological influence of the environment on the individual, for the adults average decidedly larger (up to 35 millimeters long) in March and April, when the temperature is near its lowest for the year, than in summer. This is not the maximum size for the Gulf of Maine, however, Huntsman (1919, p. 446) having recorded specimens of this length with ovaries still immature, and he describes *S. elegans* up to 52 millimeters long from the still colder waters of parts of the Gulf of St. Lawrence. He has also pointed out that it matures sexually at a smaller size in high temperatures than in low, as is the case with sundry other boreal planktonic animals—for example *Aglantha digitale*.[71]

### Sagitta serratodentata Krohn

The fact that *S. serratodentata* is an annual immigrant to the Gulf of Maine and not endemic there has been brought out in an earlier chapter (p. 58), and its tropical origin and lines of dispersal have been discussed. It is safe to say there are no *S. serratodentata* in the inner parts of the gulf in late winter or early spring, the visitors of the previous summer all having perished, because our February and April cruises of 1920 did not yield it anywhere within the continental edge except for a single specimen in the southeastern part of the basin on March 11 (station 20064). It is probably to be found in the warmer water along the slope abreast of the gulf, however, throughout the year, for odd specimens were detected at our outer stations off the southwest face of Georges Bank on February 22 (station 20044), and off Cape Sable on March 19 (station 20077).

In the year 1915 *S. serratodentata* had penetrated the eastern side of the gulf as far as the neighborhood of Lurcher Shoal and the northeastern part of the basin by May 10 (stations 10272 and 10273; Bigelow, 1917, p. 296), and by the last of that month and first days of June the Canadian fisheries expedition found it at two

[71] For a discussion of other differences between the races of *S. elegans* living in high temperatures and in low see Huntsman (1919).

stations on the outer part of the shelf off Halifax and generally distributed over the deep oceanic triangle into which the Laurentian Channel debouches, but not

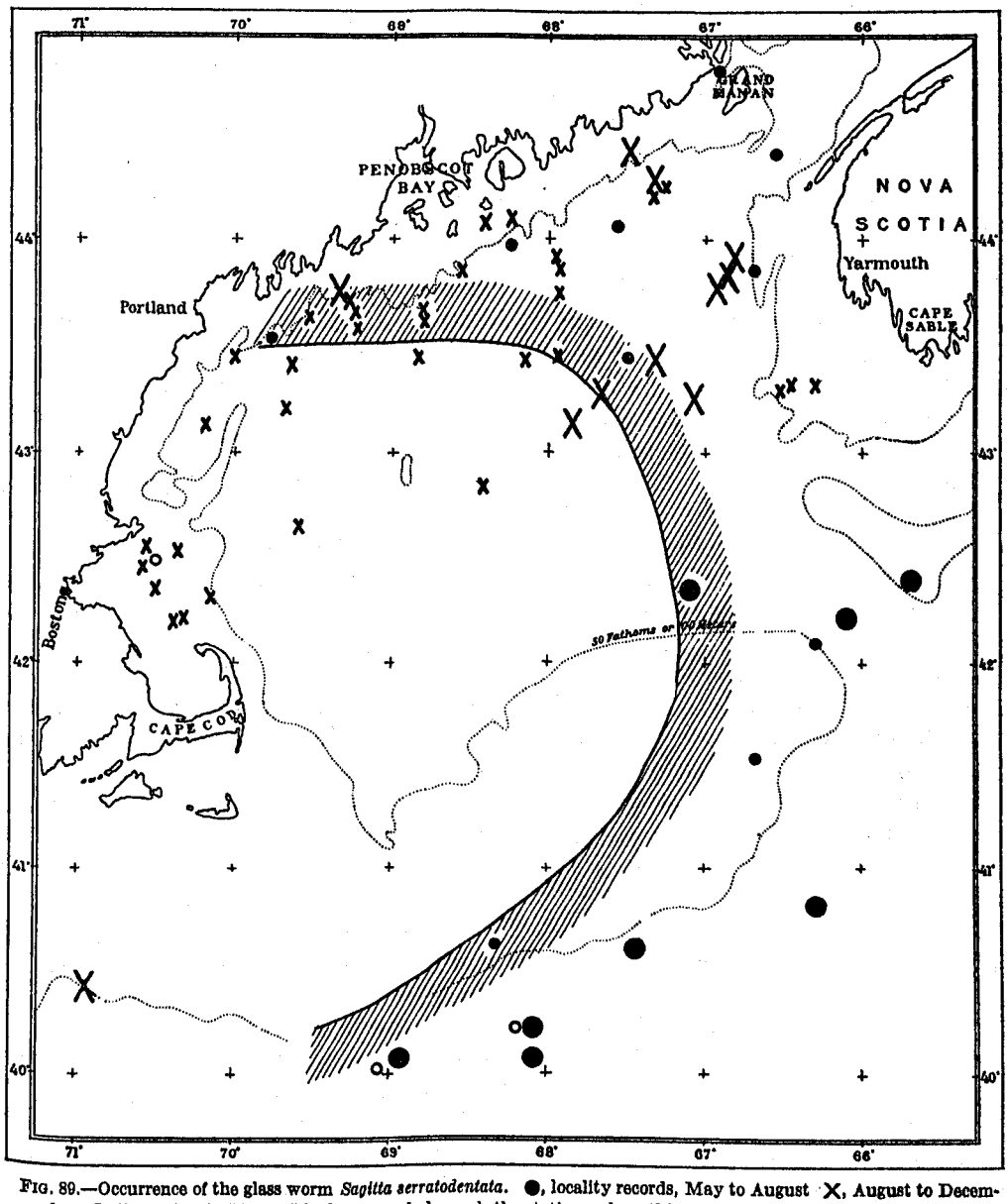


FIG. 89.—Occurrence of the glass worm *Sagitta serratodentata*. ●, locality records, May to August X, August to December; ○, December to May. The large symbols mark the stations where this species has predominated notably over *S. elegans*. The hatched curve is the approximate limit to its area of occurrence up to August

nearer shore in Scotian waters (Huntsman, 1919, p. 442, fig. 5). During June of that year *S. serratodentata* spread generally over the eastern side of the gulf with locality records on Browns Bank, in the Fundy Deep, in the Grand Manan Channel,

off Mount Desert Island, and in the eastern basin, as well as on the outer edge of the continental shelf and over the slope off Shelburne, Nova Scotia (stations 10281, 10282, 10286, 10294, 10295, and 10296). By the 1st of August it may be expected anywhere over the southern and eastern parts of Georges Bank, in the eastern channel, on Browns Bank, in the eastern side of the gulf generally, and as far westward along the coast as outlined on the accompanying chart [72] (fig. 89). As the summer advances *S. serratodentata* continues to spread westward, until by August we have found it very generally distributed over all parts of the gulf where we have towed during that month, right across from Massachusetts to the Nova Scotian Bank, though still with a decided preponderance of locality records for the eastern side (p. 58), reminiscent of the fact that it enters the gulf chiefly between the eastern part of Georges Bank and Cape Sable, perhaps not in the western side at all. The Canadian fisheries expedition likewise found it plentiful on the banks off southern Nova Scotia late in July; also at most of the stations along and outside the continental edge and in the trough of the Laurentian Channel, marking a considerable expansion in its range in this general region since May, but not at all on the banks off Cape Breton or on the Newfoundland Banks.

Judging from captures in 1915, it continues as widespread in the gulf during September and probably throughout October, also, when we found it at localities as widely separated as off Machias, Me., off Mount Desert Island, Massachusetts Bay (two stations), and the continental edge off Marthas Vineyard.

*S. serratodentata* reaches its maximum expansion and greatest abundance in the gulf during the late summer and early autumn, the precise date no doubt varying from year to year. Later in the autumn it disappears. In some years it seems that this happens as early as the first week in November, for we did not find it at any of the stations in the western side of the gulf from October 31 to November 8 in 1916 (stations 10399 to 10404); but in 1912 there were a few in Massachusetts Bay on November 20 (station 10047; Bigelow 1914a, p. 403). Although *S. serratodentata* was not detected anywhere in the inner part of the gulf during the December to January, 1920–1921, cruise of the *Halcyon*, the fact that odd specimens were towed off Gloucester on December 14, 1912 (station 10048), and January 16, 1913 (station 10050), and none on December 23 (station 10049) suggests that a scattering may continue to exist in Massachusetts Bay for a month or two after they have vanished from other parts of the gulf.

No attempt has been made to estimate the numerical strength of *S. serratodentata* in the gulf, but, as I have previously remarked (Bigelow, 1917, p. 297), we have always found it subordinate to *S. elegans* early in the season—that is, until August—and in the western part of the gulf at all seasons. In fact, most of the Gulf of Maine records from west of Penobscot Bay and north of the continental edge have been for odd individuals or at most for a few dozens per haul; but during August and September we have found it predominant over *S. elegans* at the several stations in the eastern side of the gulf marked on the chart (fig. 89), and once swarming (station 10032, August 16, 1912). In July and August, 1914, "*Sagitta serrato-*

[72] For station records for 1912 to 1915, on which this statement is based, see Bigelow, 1914, p. 121; 1914a, p. 403; 1915, p. 297; and 1917, p. 294.

*dentata* was much the more numerous of the two in the deep hauls in the eastern and southeastern parts of the gulf (stations 10225, 10245, 10246, 10249), in the eastern channel (station 10227)" (Bigelow, 1917, p. 295), and on the southern edge of Georges Bank.

Along the continental edge abreast of the gulf, *S. serratodentata* has usually predominated over *S. elegans* at most of our stations irrespective of the season of the year, or at least equaled the latter in numbers (stations 10218, 10219, 10220, 10233, 10260, 10261, 10295, 10349, 10351, 20044, 20077, and 20129).

From New York southward *S. serratodentata* is the prevalent chætognath right in to the shore during warm summers such as that of 1913 (Bigelow, 1915), but in cooler years, such as 1916, *S. elegans* is the dominant member of the pair over the inner part of the shelf as far south as Delaware Bay and perhaps still farther, but with *S. serratodentata* outnumbering it farther offshore and along the continental edge generally, as I have pointed out in a previous report (Bigelow, 1922, p. 152).

The strong probability that *S. serratodentata* is not able to reproduce successfully in boreal water, though it not only grows to a larger size there than in higher temperatures but attains sexual maturity, as evidenced by the large size of the reproductive organs (Huntsman, 1919, p. 482), lends interest to the wide range of temperature in which it occurs both in the Gulf of Maine and off southern Nova Scotia. In the gulf its presence is definitely established in water as cold as 3.9° (station 10272, May 10, 1915) and 4.4° to 7.5° (stations 10281, 10282, and 10286, June 4, 10, and 14, 1915), and the Canadian fisheries expedition likewise had it in 4° to 5°; but most of the Gulf of Maine records (also the Canadian) have certainly been from temperatures upwards of 7° to 8°, though there is no positive evidence of its presence in the gulf in water warmer than 13.9° (station 10032, August 16, 1912; Bigelow, 1914, p. 122), most of the captures having been in subsurface hauls, or if at the surface in regions of low surface temperature (stations 10030, 10229, and 10247). However the occurrence of *S. serratodentata* elsewhere forbids the assumption that high temperatures are *per se* unfavorable to it, for it has been taken in great abundance off the continental edge in Gulf Stream temperatures (station 10070, surface 23.33°; a few at stations 10071, 10073, and 10074 in temperatures of 24.44° and 23.9°), as well as off southern Nova Scotia in 19.7° (Huntsman, 1919, *Acadia* station 44, surface).

Uncertainty as to the depth of the captures makes it impossible to establish the precise salinity for the Gulf of Maine records of *S. serratodentata* except in the following instances:

| | Salinity, per mille |
|---|---|
| Station 10025, closing net, 30 fathoms | 32.9 |
| Station 10027, closing net, 30 fathoms | 33.3 |
| Station 10030, surface | 32.7 |
| Station 10032, surface | 32.5 |
| Station 10229, surface | 32.01 |
| Station 10247, surface | 32.52 |

It is not likely that it would be altogether barred from the surface by salinities considerably lower than this, for Huntsman (1919) found it repeatedly in eastern

Canadian waters on the surface in 31 to 32 per mille when a few fathoms sinking would have carried it into much more saline water.

From the data just outlined it would appear that the whole column of water in the offshore parts of the Gulf of Maine offers an environment favorable for the existence if not for the reproduction of *S. serratodentata* during the season (July to September) when it is most widespread there, but probably it could not long survive water much less saline than about 31 per mille or colder than 6° to 8°, and Huntsman (1919) has suggested that low salinity may be the factor that bars it from the Gulf of St. Lawrence.

Neither temperature nor salinity offers an explanation for the disappearance of *S. serratodentata* from the gulf in autumn, for the water is considerably warmer in November than when it first enters the gulf in spring, and the salinity is not very different from that of late summer. Neither does its immigration into the gulf in spring parallel the vernal warming of the water, but is not at its height until long after the gulf is warm enough for its support. It is therefore likely that the increase in its numbers with the summer chiefly mirrors an accumulation of the stock within the gulf, where it finds good feeding ground and conditions favorable for growth and prolonged existence. Apparently no more enter after early autumn, a phenomenon probably connected with the seasonal reproductive cycle of the species, and as the visitors of summer die off during the autumn from one cause or another or are devoured by other animals without leaving progeny to take their places, *S. serratodentata* disappears from the gulf, not to reappear there until with the earliest immigration of the succeeding spring.

Our data do not allow a statement as to the vertical distribution of *S. serratodentata* in the Gulf of Maine more definite than that it has seldom been detected there at the surface, though most often in hauls from shoaler than 100 meters. If it is actually as uncommon right at the top of the water in the gulf as now appears to be the case, the food supply may be as effective a factor as any of the physical features of its surroundings in holding so rapacious an animal at lower levels.

There is no evidence that this chætognath ever succeeds in reproducing itself in the gulf.

### Sagitta maxima Conant

In a previous chapter (p. 64) I have discussed the geographical distribution of this species and of the next within the gulf from the standpoint of their routes of entrance and dispersal. What demands chief emphasis here is that both *S. maxima* and *S. lyra* are distinctly seasonal in the inner parts of the gulf, like *S. serratodentata*. During all our cruises we have found only a single specimen of *S. maxima* within the offshore banks during the summer or early autumn months (eastern basin, September 2, 1915, station 10310), our failure to find it there in July and August, 1914, being specially significant because it occurred then off the seaward slope of Georges Bank (station 10220). Neither have we any early winter records for it in the gulf; this, however, may be an accident, for we have tried only two tows in the deep trough in December or January, which may simply have missed the *S. maxima*. However, this large chætognath was detected at 12 stations within the gulf as well as over the deeper parts of the continental shelf off southern Nova Scotia during March, April,

and early May of 1920, and at all four of the stations on the continental slope. The localities for the gulf proper (fig. 90) are all from the deepest trough, as is the one autumn record for the eastern basin just mentioned, and most of the captures have been in hauls from considerable depths, as follows:

| Station | Depth in meters | Number of specimens | Station | Depth in meters | Number of specimens |
|---|---|---|---|---|---|
| 20044 | 250–0 | 1 | 20081 | 40–0 | 1 |
| | 750–0 | 13 | 20086 | 150–0 | 2 |
| 20055 | 180–140 | 1 | 20087 | 200–0 | 2 |
| 20066 | 60–0 | 1 | 20107 | 140–0 | 2 |
| 20069 | 1,000–0 | 9 | 20112 | 100–0 | 1 |
| 20074 | 125–0 | 5 | | 200–0 | 3 |
| 20076 | 200–0 | 15 | 20013 | 130–0 | 2 |
| 20077 | 800–0 | 20 | 20015 | 200–0 | 3 |
| 20079 | 180–0 | 1 | 20129 | 100–0 | 2 |

The single September specimen was from a tow at 130–0 meters, while the June specimens off southern Nova Scotia (station 10295) were from 500–0 meters. The reader will note that there are only two records (a total of two specimens) from tows shoaler than 100 meters, one of which was taken over much deeper water and may have been brought up from its normal habitat by some local upwelling; the other was on Georges Bank.

Associated with the considerable depth of the records, we have usually found *S. maxima* in water of the relatively high salinity of 33.5 to 34 per mille, or more, though on the rare occasions when it is swirled up toward the surface it may stray into less saline strata of water (32.36 per mille at station 20081; 32.6 per mille on Georges Bank). Its general distribution farther north, and especially its failure to colonize the Gulf of St. Lawrence (Huntsman, 1919), suggests that it is unable to survive in water of low salinity, irrespective of temperature.

*S. maxima* is at home only in comparatively low temperatures. We have never found it in temperatures warmer than about 6.5° within the gulf, but, on the other hand, it usually lies below the coldest level in waters of 3.5 to 5°, the only records from temperatures lower than 3° being its sporadic appearances in the upper levels, in about 1.63° at station 20081 and about 2.6° at station 20066. The captures of *S. maxima* along the continental slope have been in temperatures of 3 to 6° and salinities of 34 to 34.9 per mille. It occurred under about these same conditions over the continental shelf abreast of Shelburne in March, 1920 (stations 20074 and 20076). Occasionally, however (whether or not as a result of upwelling is not clear), we have taken it in decidedly warmer water at our outermost stations; for example, in 7 to 8° temperature at station 20129 and one specimen in 9° or warmer at station 20044.

In north European seas *S. maxima* is equally characteristic of cold but highly saline water layers (Apstein, 1911), and probably it is this rather precise relationship to the physical state of the water which bars it from the Gulf of Maine in summer but allows it access there in winter; for while the trough of the gulf is sufficiently salt for it throughout the year and cold enough—say, 5° to 6° below 100 meters—in winter and early spring, the bottom water may well be too warm for it in some summers if not in all. At such times any *maxima* that drift inward through the eastern channel

probably perish shortly, whereas during the cold months they survive long enough to spread generally along the trough of the gulf. There is no reason to suppose that *S. maxima* ever breeds successfully in the Gulf of Maine.

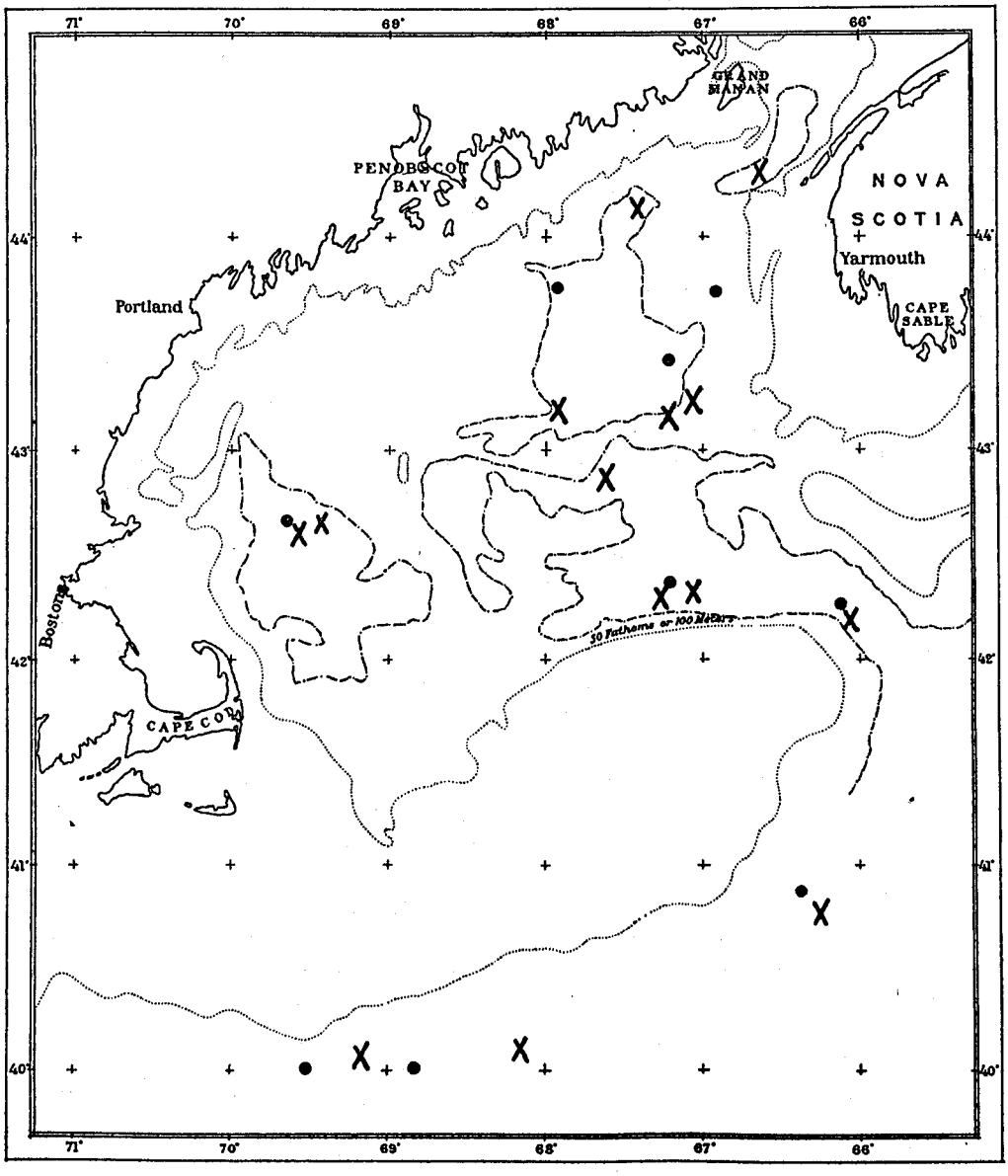


FIG. 90.—Occurrence of the glass worms *Sagitta lyra* and *S. maxima*. ●, locality records for S. lyra; X, locality records for *S. maxima*. Contours for 100 and 200 meters.

*Sagitta maxima* is as cosmopolitan on the high seas as Eukrohnia (von Ritter-Záhony, 1911) but reaches its maximum abundance at a rather deeper level. Only in high latitudes does it normally rise near the surface, then usually in the persons of young specimens, and it is on such that most of our Gulf of Maine records are based.

Inasmuch as the planktonic communities of the deeper levels of the Atlantic never penetrate the gulf *in toto* (p. 67), it can hardly be questioned that such examples of *S. maxima* as appear there come via the northeastern route in the band of cold mixed water along the edge of the continent, not from the much greater depths which they inhabit off the slope. Very likely the chief source of supply for this species in the Gulf of Maine is the deep oceanic triangle between the Nova Scotian and Newfoundland Banks, where the Canadian fisheries expedition found *S. maxima* in great abundance in a haul from 200 meters on the 1st of June, 1915 (Huntsman, 1919, p. 429). In short, it is as a distinctively northern visitor and as such alone that *S. maxima* reaches the Gulf of Maine, but our experience so far has been that but few individuals find their way in through the eastern channel, which is the only line of ingress sufficiently deep to be normally open to it.

*S. maxima* is an extraordinarily voracious animal and as such must occupy an important position in the natural economy of the plankton of the deepest waters of the gulf if it ever enters the latter in any abundance.

### Sagitta lyra Krohn

This chætognath is as distinctly a summer visitor as is its larger relative, *S. maxima*, a winter one to the inner parts of the Gulf of Maine, where it has been detected on six occasions in three distinct years—all in July and August. These records are as strictly confined to the deep trough as are those of *S. maxima* (p. 325), and whether within or without the gulf the depths of capture are about the same as for that species.

| Station | Depth in meters | Specimens | Station | Depth in meters | Specimens |
|---|---|---|---|---|---|
| 10031 | 100–0 | 2 | 10227 | 180–0 | 1 |
| 10093 | 155–0 | 2 | 10246 | 150–0 | 2 |
| 10226 | 225–0 | 2 | 10254 | 225–0 | 1 |

*S. lyra* occurs side by side with *S. maxima* over the continental slope in late winter and early spring as well as in summer.

| Station | Date | Depth in meters | Specimens of S. lyre |
|---|---|---|---|
| 20129 | May 17, 1920 | 50–0 | 2 |
| 10295 | June 24, 1915 | 750–0 | 10 |
| 10220 | July 22, 1914 | 400–0 | 5 |
| 10061 | July 10, 1913 | 73–0 | 1 |

Being a summer visitor to the gulf, *S. lyra* occurs there in rather higher temperatures than does *S. maxima*. About 6° is the lowest in which our records establish its presence, and the upper temperature limit for the captures so far made within the gulf is at least as warm as 8.17° (station 10031). Our records for it over

the continental slope have been in temperatures ranging from about 6 to 10.8° (station 10061).[73]

The salinities have been even higher for *S. lyra* than for *S. maxima*, ranging from 34.3 per mille to about 35 per mille within the gulf and about the same along the slope outside. Thus, on the whole, our observations corroborate Huntsman's (1919, p. 432) conclusion that *S. lyra* is associated with rather higher temperatures than is *S. maxima*, though equally cosmopolitan in the mid-depths of the high seas.

### Sagitta hexaptera D'Orbigny

The claim of *S. hexaptera* to mention here rests on a single specimen, since lost, taken near Lurcher Shoal on August 12, 1914, in a tow from 100 meters (Bigelow, 1917, p. 297). Outside the gulf it is a regular inhabitant of the intermediate strata of the oceanic basin, occurring at all the outermost Canadian stations (Huntsman, 1919, p. 423) and at one of our own (station 20044). We likewise found it over the slope abreast of Delaware and Chesapeake Bays in July, 1913 (Bigelow, 1915, p. 297). Huntsman (1919, p. 424) has described its faunistic status, saying that it belongs to the Gulf Stream coming up from the south off the northeastern American coast, not to the cold boreal water coming down from the north. In the former it is characteristic of the intermediate depths from 100 to 200 meters, and it occurs so regularly 50 to 60 miles out beyond the continental edge that careful watch should be kept for it within the Gulf of Maine as an indicator of tropical water.

### Eukrohnia hamata Möbius

The general status of this glass worm has been discussed in an earlier chapter (p. 63) as an immigrant in the Gulf of Maine. Only a few notes need be added here on the actual record of its local occurrences. Eukrohnia being, beyond question, a creature of the deeper strata of water in these latitudes, the precise depths of the captures are of interest. So far as I can learn it has only once been found on the surface within the limits of the gulf—viz, a single specimen recorded by Huntsman (1919, p. 476) from Friar Roads in the Bay of Fundy. No doubt, as he suggests, vertical currents were responsible for bringing this lone Eukrohnia up to the surface there from its normal habitat deeper down, the local tides being "of such magnitude that the water forms whirlpools and the boiling up of the deep water to the surface can be seen constantly." At this locality three Eukrohnia were also taken at 20 meters on the same occasion. For the open gulf our shoalest records for it are from 40 meters (stations 10095 on German Bank, 10099 close to Mount Desert Island, and 10102 off Penobscot Bay, one or two examples at each, all in August, 1913, and several taken near the eastern Maine coast on March 22, 1920, station 20080), 50 meters (one specimen, station 10497, near Mount Desert Rock, January 1, 1921, and odd specimens from Browns Bank, June 24, 1915, station 10296), and 60 meters (off Cape Elizabeth, December 30, 1920, station 10494; near Lurcher Shoal; and over the deep trough to the northeast on August 12 and 13, 1913, at stations 10096 and 10097).

[73] At station 10295 the specimens may have come from water as cold as 4.9°, but equally from the warmer strata penetrated by the net on its journey down and up.

That Eukrohnia should so seldom have been captured in the many tows that have been made between the surface and 60 meters in different years and seasons and in various parts of the gulf is sufficient evidence that it is only an accidental visitor to the upper strata of water there; so much so, indeed, that we have learned not to expect it shoaler than 75 meters except on rare occasions.

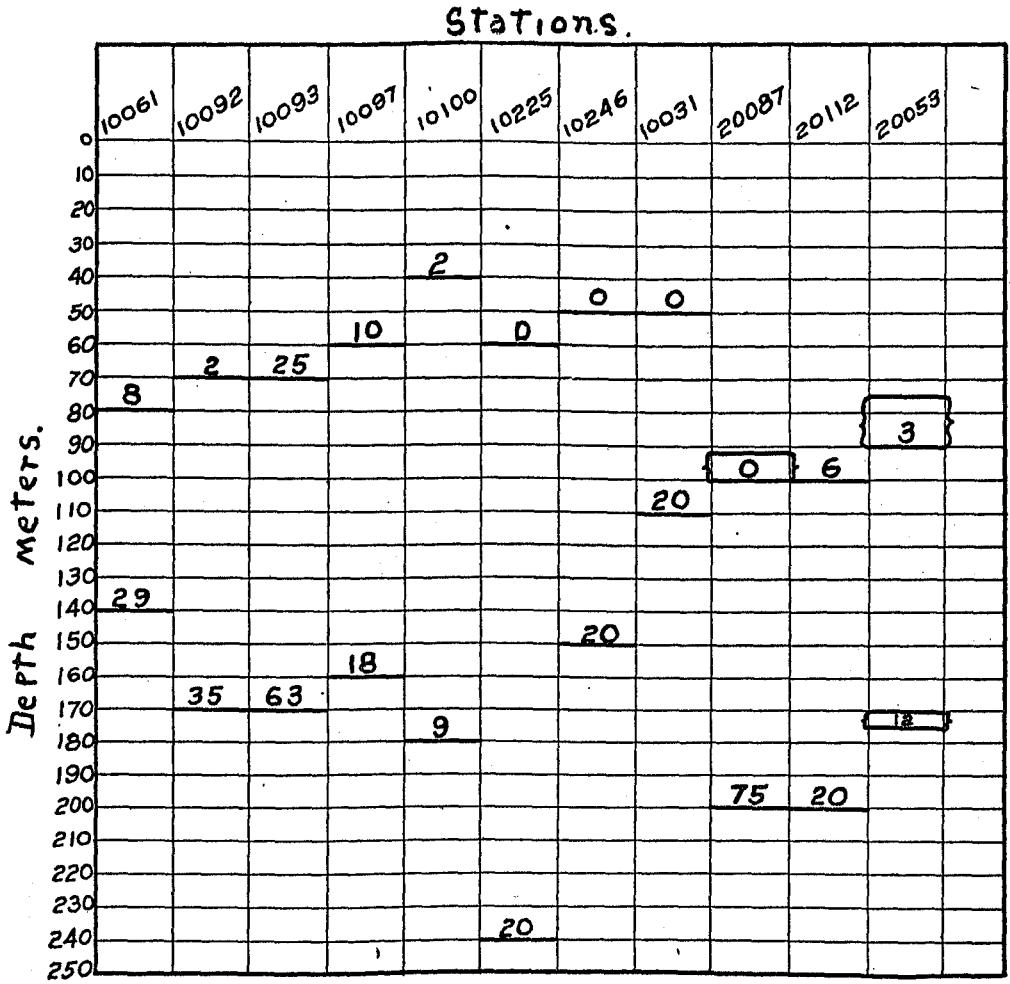


FIG. 91.—Numbers of specimens of *Eukrohnia hamata* taken in hauls from different depths at selected stations. In the case of closing-net hauls the depth zone is bracketed

Its scarcity at 60 to 100 meters, contrasted with its comparative abundance in deeper water, illustrated by the accompanying diagram of the catches of Eukrohnia at representative stations where two deep horizontal tows were made at different levels (fig. 91) points to the 100-meter level or thereabouts as about the upper limit to its common and regular occurrence. Below 100 meters, however, it has been de-

tected in something like 50 per cent of our horizontal tows,[74] irrespective of season or general situation in the gulf. The average depth of the trough of the gulf being about 250 meters, it follows that the bulk of its Eukrohnia population is confined to a

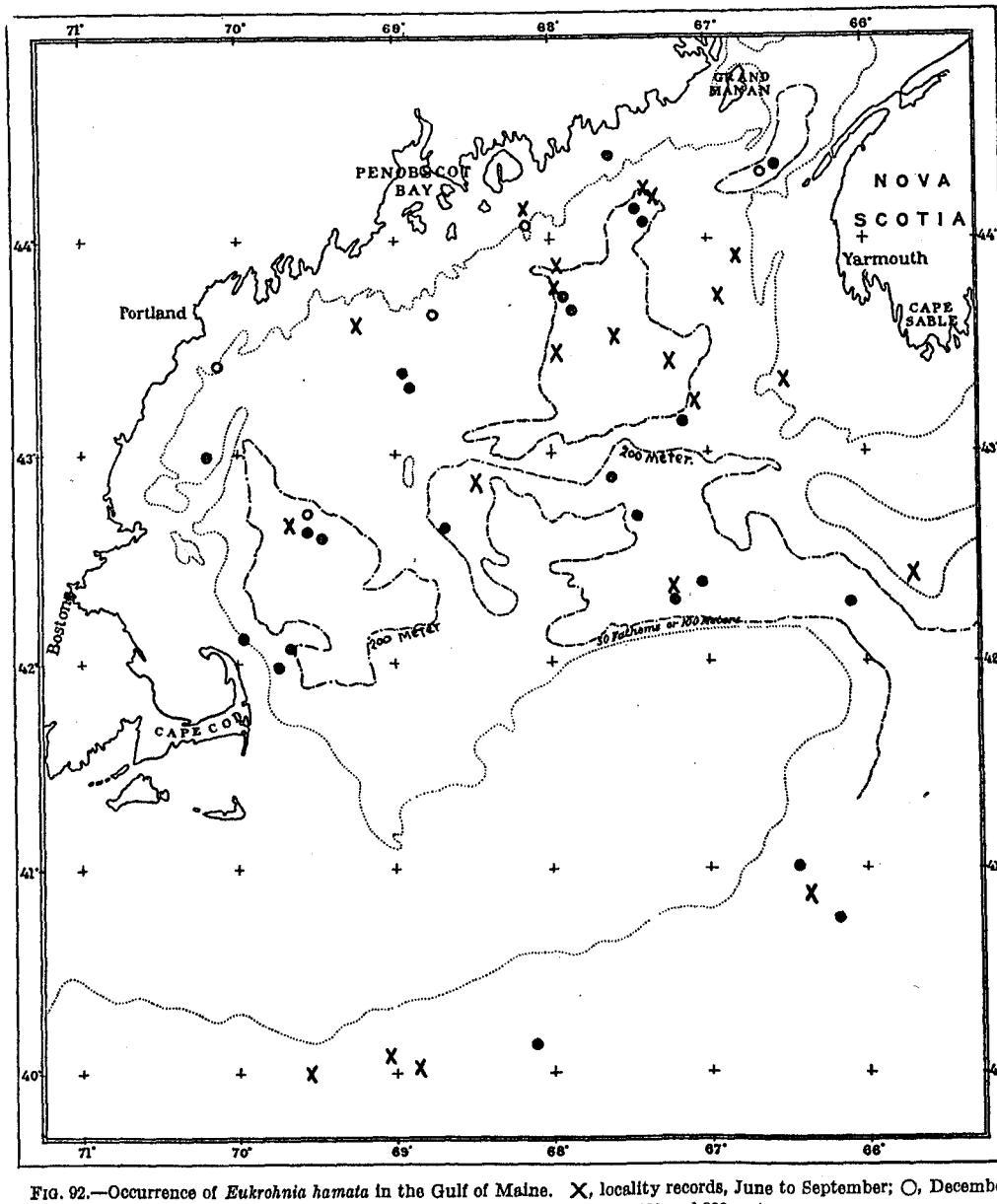


FIG. 92.—Occurrence of *Eukrohnia hamata* in the Gulf of Maine. X, locality records, June to September; ○, December to January; ●, February to May. Contour for 100 and 200 meters

stratum hardly more than 150 meters in thickness; but whether it is usually concentrated in the deepest water within this stratum is still to be learned, for up to the

[74] Eukrohnia usually occurs in numbers so small that its presence or absence in vertical tows is not significant, with nets as small as we have employed for that purpose. Contours for 100 and 200 meters.

present time we have made only 9 horizontal tows at depths of 200 meters or more within the gulf, in six of which Eukrohnia occurred.

It follows from the bathymetric status of Eukrohnia, as just outlined that this worm is practically confined to the offshore parts of the gulf (fig. 92), occurring only very rarely between the 100-meter contour and the coast; and while it may be expected anywhere in tows of appropriate depth, the actual localities of capture have been concentrated along the eastern, northern, and western margins of the deep

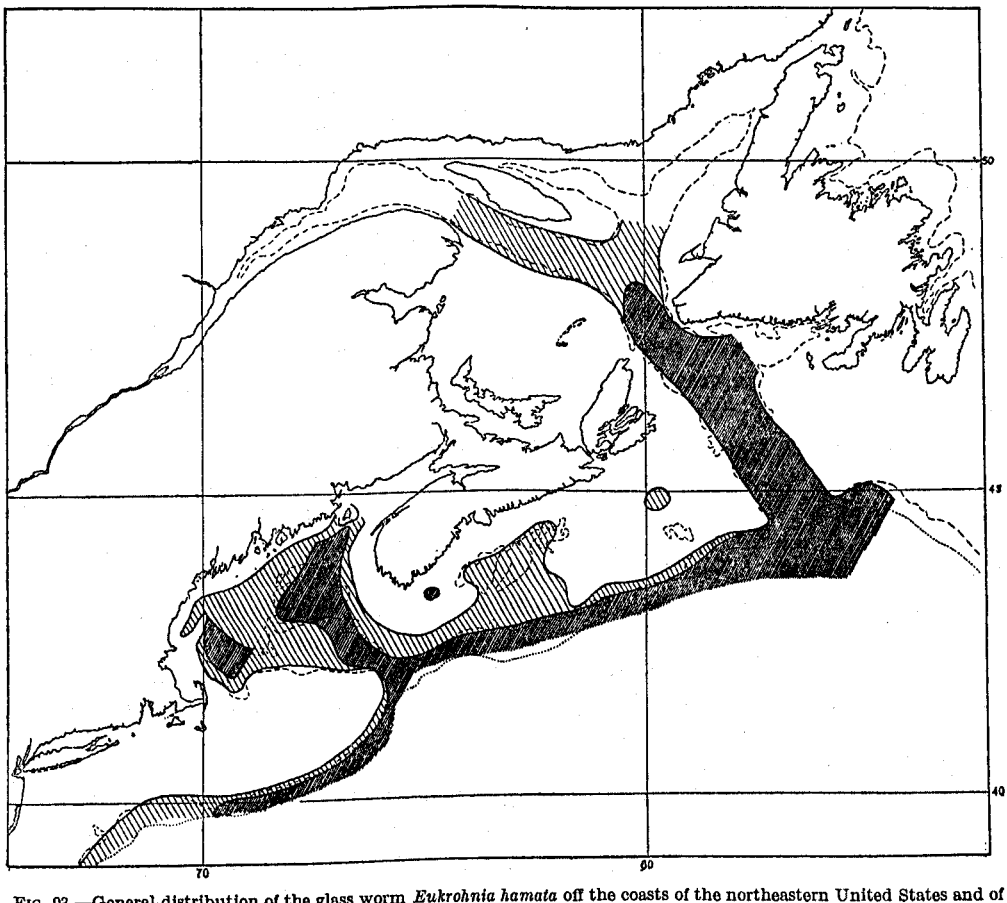


FIG. 93.—General distribution of the glass worm *Eukrohnia hamata* off the coasts of the northeastern United States and of eastern Canada. A half hour's tow with a net 1 meter in diameter, at the appropriate depth, may be expected to yield up to 20 specimens in the lightly hatched areas, and more than 20 in the heavily hatched area. The chart east of longitude 63° is based on the published records of the Canadian fisheries expedition (Huntsman, 1919)

basin, a reflection of its immigrant origin and of the anticlockwise eddy current with which it drifts once it is within the gulf. It has usually proved far more numerous along the eastern side of the basin from the Eastern Channel right up to the entrance of the Bay of Fundy on the one side of the gulf, and in the northern half of the western trough on the other, than in the intervening deep waters. In these two rich areas half an hour's tow with a meter net at any level deeper than 100 meters will usually yield at least 20 Eukrohnia if it occurs at all (fig. 93); elsewhere it is usually

represented in the tow by occasional examples only, even though the water be well over 100 meters deep. Its apparent rarity in the southeastern deep of the gulf—I say apparent because we have made few tows there—is interesting in connection with the probable route which it follows in its journeyings (p. 64). Eukrohnia occasionally reaches the trough between the Isles of Shoals and Jeffreys Ledge, where we have found it at one station (20093, April 9, 1920); but apparently it never finds its way into the sink at the mouth of Massachusetts Bay, or at least so rarely that we have never taken it there, though we have towed repeatedly at various seasons of the year [75].

The largest catch of Eukrohnia actually counted so far from any one of our tow-net hauls has been 63 specimens (station 10093, haul from 85–0 fathoms, August 12, 1913). Possibly other hauls may have yielded more, but, if so, very rarely. We have no reason to suppose that it ever occurs anywhere in the gulf in numbers to compare with *S. elegans* or even with *S. serratodentata*.

A catch of 20 to 50 individuals in half an hour's towing (which may be stated as a fair average of the more prolific horizontal hauls, whether made with the 1-meter open net or with the slightly smaller closing net) means a very sparse population, indeed, when translated into terms of actual density of aggregation in the water—say one Eukrohnia to every 30 to 70 cubic meters of sea water. To make this more graphic let us say not more than one Eukrohnia in a space the size of an ordinary room.

There is no direct evidence that Eukrohnia breeds within the gulf at any time of year, sexually mature specimens never having been found there. Hence the local stock is maintained chiefly if not entirely by immigration from centers of production elsewhere, but a few large Eukrohnia (up to about 45 millimeters in length) with well-developed ovaries were taken among the more numerous immature specimens in the deep haul over the slope abreast of Cape Sable on March 19, 1920 (station 20077).

Eukrohnia is never absent from the gulf at any time of year, but our records, if they can be taken at face value, point to the late spring and early summer as a period of decided scarcity, for only one specimen was taken at our May stations in 1920 (station 20125), and none at all during May or June in 1915.

The stock of Eukrohnia present in the Gulf of Maine fluctuates unmistakably and widely from year to year. The summer of 1913, when it occurred in all but one of the horizontal hauls deeper than 100 meters and at a total of 10 stations in July and August, was the best summer for it in our experience, while the summers of 1912 [76] and 1915 stand at the other extreme. In March and April, 1920, Eukrohnia was detected in 60 per cent of all the horizontal hauls deeper than 100 meters, and at 21 stations scattered far and wide over the gulf; likewise in the deep water along the continental slope.

[75] For records of Eukrohnia, 1912 to 1916, see Bigelow, 1914, p. 123; 1915, p. 294; 1917, p. 298; and 1922 pp. 138 and 155. During the spring of 1920 it was recognized at stations 20044, 20053, 20055, 20057 ,20064 ,20068 ,20069 ,20074 ,20075, 20077, 20079, 20080, 20081 20086, 20087, 20088, 20093 20097, 20098, 20107, 20112, 20113, 20114, 20116, and 20125, and during the winter of 1920–1921 at stations 10490, 10494, 10496, 10497, and 10499.

[76] Found only once in 1912 (Bigelow, 1914, p. 123), three times within the gulf, in July and August, 1915, once on Browns Bank and once over the continental slope abreast of Shelburne, Nova Scotia (Bigelow, 1917, p. 298).

Thanks to the confinement of Eukrohnia to considerable depths, where seasonal variations in the physical state of the water are slight, it is easy to establish the temperatures and salinities in which it most often occurs in the gulf, the former ranging from 1.3° to upward of 9°, the latter upward of 32.16 per mille, with most of the Eukrohnia living in water more saline than 32.5 per mille. Assuming Eukrohnia to occur close to the bottom, the maximum salinity in the gulf would be about 34.8 per mille.

Our largest summer catches of this worm have been made in water of about 6 to 8° temperature and of 33 to 34 per mille salinity, with an extreme range from about 5.9° to about 9.3° temperature and from about 32.6 per mille to about 35 per mille salinity. In spring we have taken it in 1.3 to 6.7°. The seasonal data thus show that Eukrohnia can survive in the gulf through a considerable range of temperature, from the coldest up to 9° or so, or even slightly warmer, and in water varying in salinity from slightly more than 32 to 35 per mille; that is, in all but the warmest and least saline locations. This is interesting, for with both the salinity and the temperature of the surface waters within these limits over most of the gulf in winter and spring, and with the water as cool and as saline as this only a few meters down even in midsummer, neither temperature nor salinity but probably light is the factor that bars Eukrohnia from the upper layers of water at all seasons.

With Eukrohnia occurring in the gulf only as an immigrant and not as a permanent and endemic inhabitant, a few words as to its distribution in the waters to which the gulf is tributary will be germane. Originally supposed to be an Arctic animal, this glass worm is now known to be cosmopolitan in the high seas from Arctic to Antarctic; but except in high latitudes it is confined to waters so deep that it probably never reaches the Gulf of Maine from the oceanic basin abreast of it. Hence, as Huntsman (1919, p. 476) points out, the Eukrohnia living in the upper 500 meters or so (and this includes practically all the representatives of the species collected either by the Gulf of Maine or by the Canadian fisheries expeditions) may be considered as distinctly northern. It is known to be common in the cool, heavy, mixed water all along the continental slope from the Grand Banks of Newfoundland on the north to the latitude of Chesapeake Bay to the south (fig. 93) in depths of 300 to 500 meters. For records of it east of Cape Sable see Huntsman (1919). How universal it is along this zone abreast the mouth of the Gulf of Maine and thence westward and southward in considerable depths will appear from the fact that it has been detected in the towings from 250 to 1,000 meters at 9 out of 12 *Grampus* and *Albatross* stations from 1913 to 1920, irrespective of the time of year (stations 10076, 10220, 10233, 10352, 10368, 10384, 10393, 20044, and 20077).

Outside the Gulf of Maine it is probably more numerous below 400 meters than above, for on February 22, 1920 (station 20044), none were found at 250–0 meters when a number were taken in a haul from 750–0 meters. Again, on the slope abreast of Cape Sable more Eukrohnia were taken in the haul from 800–0 meters on March 19, 1920 (station 20077), than from 500–0; and on July 21, 1914, none were taken in a horizontal haul at 300 meters off the slope of Georges Bank at station 10218, but several were had at 400–0 meters at a neighboring station (10220) at about

the same relative position on the slope. Farther offshore, where the warm surface stratum is thicker, Eukrohnia probably tends to keep still deeper.

From this main area of distribution it works into the Gulf of St. Lawrence via the Laurentian Channel, and into the Gulf of Maine via the eastern channel. It likewise reaches the deep sinks between the Nova Scotian fishing banks, as Huntsman (1919) showed, recent examples of which are its occurrence at two stations off Shelburne (20074 and 20075) in March, 1920. Generally speaking, the farther in from the continental slope, the less plentiful is Eukrohnia.

### Other chætognaths

The species just mentioned completes the list of glass worms so far recorded from the inner parts of the Gulf of Maine, nor are any others to be expected there unless as rare and accidental stragglers; but it would be no surprise to find any of the chætognaths known from any part of the North Atlantic at one level or another in the oceanic basin abreast of the gulf. In fact, *Sagitta enflata*, a tropical species common in waters of southern origin off the east coast of North America "appeared, with other tropical organisms, in the tows over the continental slope in 1914 [stations 10218 and 10220]; off Marthas Vineyard in 1915 [station 10333, one specimen]" (Bigelow, 1917, p. 298). *Pterosagitta draco*, similarly tropical in origin, was represented by about 50 specimens in the 60-meter haul off the slope of Georges Bank on July 21, 1914 (station 10218). Previous to that time we had taken it over the slope abreast of Delaware Bay and Chesapeake Bay in July, 1913 (Bigelow, 1915, p. 299), and Huntsman (1919) has since recorded it at the outer stations of the Canadian fisheries expedition off Cape Sable and off the mouth of the Laurentian Channel in July and August, 1915. Along the American littoral and off the Grand Banks region these two species are among the most reliable of tropical indicators. Watch should therefore be kept for them in the Gulf of Maine, where it is not likely that they could long survive the low temperature.

## TOMOPTERIDS

### Tomopteris catharina (Gosse) [77]

The curious pelagic worm, Tomopteris, not uncommonly appears in the plankton of the Gulf of Maine, though never forming an important constituent of it, quantitatively speaking. So far the well-known *T. catharina* is the only species of the genus which has been detected regularly within the southern rim of the gulf.

In the western Atlantic this species is Arctic-boreal, having been recorded in abundance on the Newfoundland Banks (Apstein, 1900) and in the Laurentian Channel (Huntsman, 1921); southward, also, over the continental shelf about to latitude 39° 30′ (station 10069, July 19, 1913; Bigelow, 1915, p. 301); but it does not occur in the Gulf of St. Lawrence, except as carried thither in the inflowing current around the northern side of Cabot Strait or via the Strait of Belle Isle.

[77] This Tomopteris has usually been called *T. helgolandica* (e. g., by Apstein, 1900; by Reibisch, 1905; and by Southern, 1911), but Rosa (1908) and Southern (1911) have shown that the common Tomopteris of the North Sea region was first described under the specific name *catharina*, which consequently was adopted by Huntsman (1921). For accounts of Tomopteris and diagnoses o its several species see Apstein (1900), Reibisch (1905), and Huntsman (1921).

In the eastern Atlantic it is widely distributed in the North Sea (not, however, in the Baltic, from which it is probably barred by low salinity), around Ireland, and in the English Channel. It is also recorded from the Sargasso Sea and from off the mouth of the Amazon (Apstein, 1900); but, as Huntsman (1921) points out, it seems so unlikely that *T. catharina* should normally occur at these tropical stations that the records call for confirmation.

Slight differences have been described between the American and European races of this worm (Huntsman, 1921), interesting because of a possible physiological difference in their relation to the salinity of the water.

*T. catharina* has been taken here and there in the Gulf of Maine in every month of the year, including midsummer (the warmest season), on the one hand, and late winter and early spring (the coldest), on the other. As the chart (fig. 94) shows, it is very generally distributed north of a line from Cape Cod to Cape Sable. For example, it appeared at about 60 per cent of our stations in August, 1913; at about 50 per cent of the stations in the waters thus limited during February to May, 1920; at 5 stations (out of a possible 13) in the northern half of the gulf during December and January, 1920–1921; and occasionally off Gloucester during the winter of 1912–13.[78]

Thus, it is constantly present in the gulf throughout the year, with no definite fluctuations in abundance from season to season except an apparent scarcity in late autumn and early winter, evidence for which is our failure to find it at any of our stations in the western part of the gulf in October and November, 1916, or in Massachusetts Bay during November and December of 1912. We have also found it occupying the same geographic range in the cold season as in the warm, which is also the case around Ireland (Southern, 1911).

Although Tomopteris is so large and conspicuous that one is not apt to overlook it in the catch, it occurs so sparsely (usually from one to half a dozen individuals per haul) that it may well have been missed by the net at other stations, though actually present in the immediate neighborhood.

As appears from the chart, *T. catharina* has been taken with about equal frequency in the coastwise belt and over the deeper basin of the gulf. It is also recorded (once only) from St. Andrews in Doctor McMurrich's plankton lists (p. 12) and in the Bay of Fundy by Huntsman (1921), but we did not find it in Casco Bay in July, 1912, when it was taken at several stations along the coast from Massachusetts Bay to Mount Desert (Bigelow, 1914, p. 121). As we have never taken it in any harbor (e. g., Gloucester, Portland, Southwest, or Eastport, etc.) it is to be looked upon as occurring chiefly outside the outer islands and headlands and rarely in the estuarine waters tributary to the gulf. On the other hand, we have never taken *T. catharina* anywhere on Georges Bank or Browns Bank at any season, nor at any of our deep stations along the continental slope. Thus, while not

[78] For records of *T. catharina* (as "*T. helgolandica*") 1912 to 1913, see Bigelow, 1914 p. 121; 1914a, pp. 403–405; 1915, p. 301. Since then it has been detected at the following stations: In 1914 at 10213, 10214, 10225, 10245, 10246, 10247, 10248, 10249, 10250, and 10255; at stations 10267, 10270, 10290, and 10317 in 1915; 10398 in 1916; at stations 20048, 20050, 20052, 20055, 20056, 20057, 20059, 20060, 20062, 20079, 20080, 20081, 20084, 20085, 20087, 20092, 20093, 20096, 20097, 20098, 20100, 20107, 20113, 20114, 20115, 20116, 20119, 20125, 20126, and 20127 in the spring of 1920; and at stations 10489, 10490, 10494, 10495, 10499, 10510, and 10511 in the winter and early spring of 1920 and 1921.

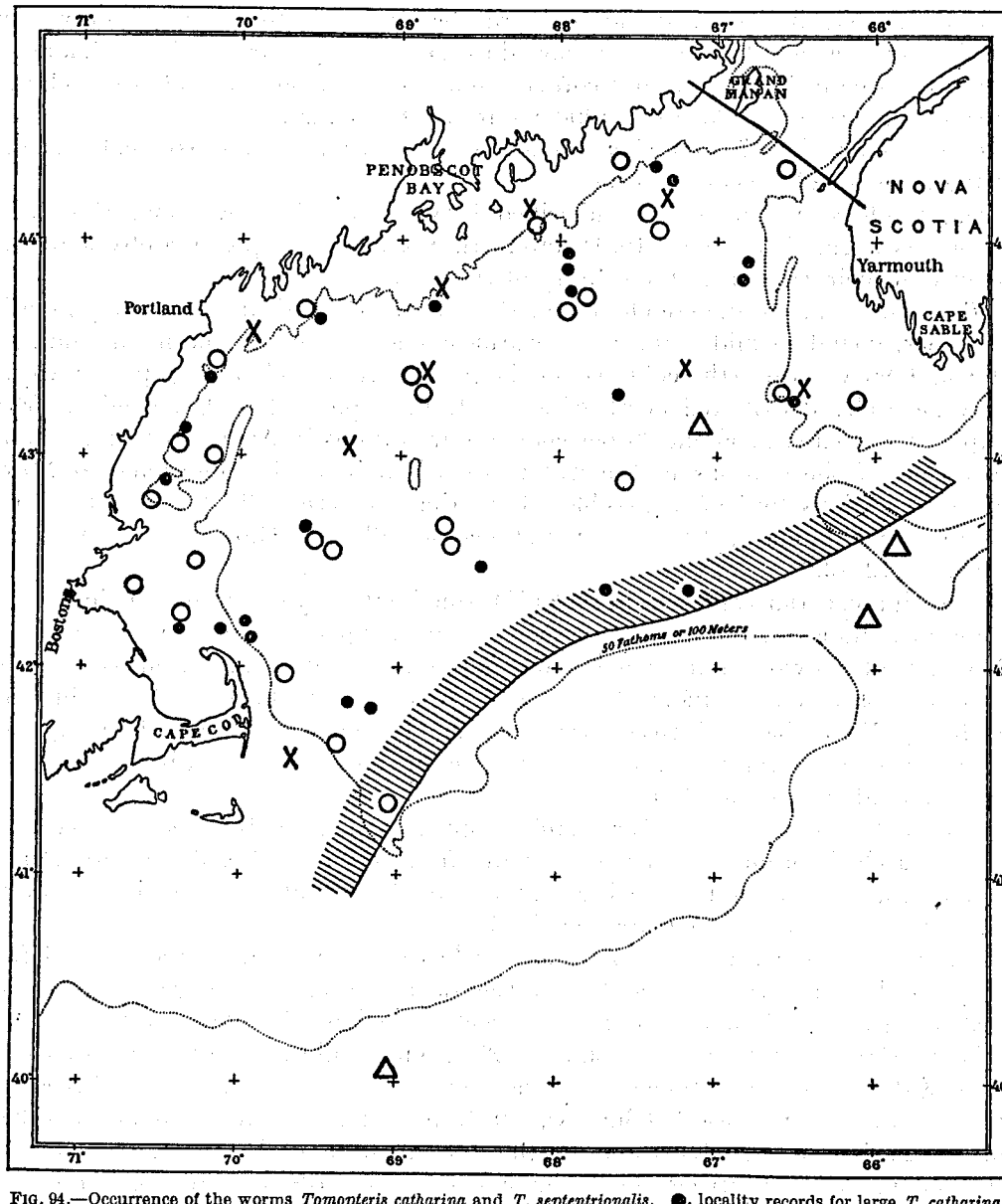


FIG. 94.—Occurrence of the worms *Tomopteris catharina* and *T. septentrionalis*. ●, locality records for large *T. catharina*, July and August; X for young *T. catharina*, July and August; ○, for large *T. catharina*, March to May; △, for *T. septentrionalis*, March to May. The hatched curve includes the parts of the Gulf of Maine where *T. catharina* has been taken in summer

actually neritic (witness its rarity or absence under estuarine conditions), *T. catharina* is clearly a creature of the coastwise waters, as it occurs within the limits of the Gulf of Maine.

The bathymetric range of *T. catharina* in the gulf is considerable. We have taken it on the surface at four stations in August, two in March, and three in April.[79] In connection with the relationship of Tomopteris to temperature, discussed below, it is interesting that the surface captures in summer have all been in the northeast part of the gulf—that is, on German Bank, near Lurcher Shoal, and off the eastern coast of Maine—whereas the localities where we have taken it on the surface in early spring include Massachusetts Bay and the general neighborhood of the Isles of Shoals in the western side as well as German Bank in the eastern.

At the other extreme *T. catharina* certainly occurs as deep as 180 meters (closing-net haul at station 20079, March 22, 1920), and probably down to 200 meters, if not still deeper, though the majority of captures have been in open-net hauls from 40 to 150 meters depth. When the actual depths of the individual hauls yielding Tomopteris are classified by months, its bathymetric distribution appears decidedly uniform from season to season, as illustrated by the following partial list of the captures for midsummer as compared with early spring:

*Partial list of the captures of Tomopteris for midsummer, as compared with early spring*

MIDSUMMER

| Station | Date | Depth in meters | Station | Date | Depth in meters |
|---|---|---|---|---|---|
| 10011 | July 17, 1912 | 110–0 | 10103 | Aug. 14, 1913 | 55–0 |
| 10014 | July 24, 1912 | 40–0 | 10213 | July 19, 1914 | 70–0 |
| 10030 | Aug. 14, 1912 | (1) | 10214 | do | 100–0 |
| 10032 | Aug. 16, 1912 | (1) | 10225 | July 23, 1914 | 240–0 |
| 10057 | July 8, 1913 | 55–0 | 10245 | do | (1) |
| 10058 | do | 73–0 | 10246 | Aug. 12, 1914 | 50–0 |
| 10088 | Aug. 9, 1913 | 146–0 | 10247 | do | (1) |
| 10091 | Aug. 11, 1913 | 37–0 | 10248 | Aug. 13, 1914 | 50–0 |
| 10095 | Aug. 12, 1913 | 36–0 | 10249 | do | 175–0 |
| 10097 | Aug. 13, 1913 | 146–0 | 10250 | Aug. 14, 1914 | 120–0 |
| 10099 | do | 36–0 | 10255 | Aug. 23, 1914 | 150–0 |
| 10100 | do | 165–0 | | | |

EARLY SPRING

| | | | | | |
|---|---|---|---|---|---|
| 20050 | Mar. 1, 1920 | 75–0 | 20086 | Mar. 23, 1920 | 150–0 |
| 20052 | Mar. 2, 1920 | 100–0 | 20087 | Mar. 24, 1920 | 200–0 |
| 20055 | Mar. 3, 1920 | [2] 180–140 | 20092 | Apr. 9, 1920 | (1) |
| 20056 | do | 75–0 | 20093 | do | (1) |
| 20057 | Mar. 4, 1920 | 75–0 | 20096 | Apr. 10, 1920 | 35–0 |
| 20059 | do | 60–0 | 20097 | Apr. 11, 1920 | 80–0 |
| 20060 | do | (1) | 20098 | do | 90–0 |
| 20062 | Mar. 5, 1920 | 30–0 | 20100 | Apr. 12, 1920 | 100–0 |
| 20072 | Mar. 13, 1920 | 75–0 | 20107 | Apr. 16, 1920 | 140–0 |
| 20079 | Mar. 22, 1920 | [2] 180–0 | 20113 | Apr. 17, 1920 | 130–0 |
| 20080 | do | 40–0 | 20114 | do | 110–0 |
| 20081 | Mar. 23, 1920 | 140–0 | 20115 | Apr. 18, 1920 | 200–0 |
| 20084 | do | 30–0 | 20116 | do | 100–0 |
| 20085 | do | 60–0 | 20119 | Apr. 20, 1920 | (1) |

[1] Surface net. [2] Closing net.

Although *T. catharina* has not yet been detected in the bottom water of the deepest trough of the gulf, it is to be expected there, for off Ireland it occurs indifferently from the surface down to more than 1,000 meters depth (Southern, 1911). Our surface catches, like Huntsman's (1921, p. 87) were with one exception between 6 p. m.

[79] The surface records are as follows: Stations 10030 and 10032, Aug. 14 and 16, 1912; stations 10245 and 10247, Aug. 12 and 13, 1914; stations 20060 and 20085, Mar. 4 and 23, 1920; stations 20092, 20093, and 20119, Apr. 9 and 20, 1920.

and 6 a. m., corroborating his view that *T. catharina* comes to the surface most often by night.

As a rule, Tomopteris has been represented in our hauls by large adults or medium-sized specimens 15 to 40 millimeters long, with from 15 to 21 parapods, and Doctor Huntsman informs me that he has invariably found this to be the case in the Bay of Fundy. But during our August cruise of 1913 we took a considerable number of its young in the northern and western parts of the gulf, including specimens as small as 4 to 8 millimeters in length, with only 6 to 8 parapods (but identifiable as this species by the tail, already visible, and by the number and location of the rosette organs), at about the stage figured by Apstein (1900, pl. 10, fig. 2), as follows:

| Locality | Station | Number of specimens | Stage of development |
|---|---|---|---|
| German Bank | 10095 | (1) | 6 millimeters upward, 8 to 12 parapods. |
| Northeast corner off Grand Manan | 10097 | 1 | 6 millimeters, 12 parapods. |
| North of Cashes Ledge | 10089 | 2 | 8 and 11 parapods. |
| Near Mount Desert Island | 10099 | 2 | 10 millimeters, 12and 14 parapods. |
| Off Penobscot Bay | 10101 | 2 | Do. |
| Eastern basin | 10093 | 1 | 5.5 millimeters, 13 parapods. |
| Off Penobscot Bay | 10091 | 1 | 7 millimeters, 11 parapods. |
| Off Cape Elizabeth | 10103 | (1) | 4 millimeters upward, 6 parapods and upward. |
| 15 to 18 miles southeast from Chatham, Cape Cod | ---------- | (1) | 6 millimeters upward, 8 to 14 parapods. |

[1] Several.

Judging from the early stage in development represented by these specimens, it appears that *T. catharina* reproduced itself in some numbers in the Gulf of Maine during the summer in question, proving that it is actually endemic there and not restricted as a breeder to more northern seas. Although young specimens have not been detected in our tow nettings before or since at any season (evidence that it would be quite exceptional for Tomopteris to breed in any abundance within the gulf), what little reproduction does take place there may be enough to maintain the rather sparse stock of this worm.

Of course, this does not negative the possibility that more or less immigration takes place into the gulf from the north (p 339); but the distribution of *T. catharina* in eastern Canadian waters, as outlined by Huntsman (1921), suggests rather that the Gulf of Maine colony is to some extent isolated and separated from the more abundant stock of this worm in Newfoundland waters and in the region of the Laurentian Channel by a considerable gap, for it was taken at only one station inside the continental edge along Nova Scotia by the Canadian fisheries expedition of 1915. Our scanty data point to an early summer breeding season, which agrees with Southern's (1911) discovery—based on the occurrence of females with eggs as well as of young—that it breeds from May until August in Irish waters.

*Relation to temperature and salinity.*—The highest temperature in which we have positively established the presence of *T. catharina* in the Gulf of Maine is 14.44° (surface haul, Station 10245, August 12, 1914), and the great majority of captures have been from water colder than 8°. At the other extreme it has been taken in

temperatures between 0 and 1° at several stations along the coasts of Maine and Massachusetts in March (e. g., stations 20056, 20059, and 20062), frequently in water of 2 to 4°, and the specimens taken by the Canadian fisheries expedition over the Newfoundland Banks and in the Laurentian Channel in May, 1915, were probably in water colder than 0° (see Huntsman, 1921, p. 86, for these records) and very likely fractionally colder than −1°. Thus this worm finds its optimum in comparatively low temperatures. Perhaps 15° might be stated as its absolute upper limit in the Gulf of Maine, and, in fact, it is doubtful whether it could long survive water warmer than 10 to 12°.

On three occasions we have taken *T. catharina* in salinities as low as 31 to 32 per mille,[80] but the great majority of captures have been in water of 32 to 33 per mille. The highest salinity in which our records positively establish its occurrence in the Gulf of Maine (closing-net hauls at stations 20052 and 20055) is 33.7 to 33.8 per mille, and although we took Tomopteris at one station (10225) where the net worked for a time in water as saline as 35 per mille, it is more likely that the odd specimens that it brought back were picked up on its journey up or down through the lower salinities of the superficial strata of water.

Thus, these additional records obtained during 1920 and 1921 corroborate Huntsman's (1921, p. 90) conclusion that a salinity of approximately 33 to 34 per mille is the upper limit for *T. catharina* off North America. On the other hand, it seems well established that it never occurs in water much less saline than 32 per mille except when it makes brief excursions to the surface, and our records thus support Huntsman's (1921, p. 90) suggestion that low salinity is the factor that prevents it from colonizing estuarine situations. In north European waters, as he remarks, the relationship which *T. catharina* bears to salinity is quite different, for around Ireland Southern (1911) found it only in water more saline than 34 per mille. Of course, it is possible that this is a physiological difference between the American and European races of this species; but the question also naturally occurs whether high salinity, *per se*, acts anywhere as a bar to its dispersal, and whether it is not high temperature, quite independent of salinity, which lays down a definite offshore bound for *T. catharina* just outside the American continental edge as far northward as the Nova Scotian banks. The rarity of *T. catharina* over the continental shelf along Nova Scotia (Huntsman, 1921) is especially interesting in this connection, because the temperatures and salinities there both fall within the limits in which it exists either to the south or to the north.

The most reasonable explanation for its peculiar distribution is that *T. catharina* occurs chiefly in the immediate neighborhood of its centers of production, of which there are but two in the seas under discussion—a major on the Grand Banks and a minor in the Gulf of Maine. It does not breed in the intervening stretch of waters because it requires a closer balance in its physical environment for successful breeding than for vegetative existence. This, we may assume, it does not find in the Gulf of St. Lawrence.

It is therefore likely that when the geographic limits within which *T. catharina* breeds successfully are better known, specimens taken elsewhere will prove to be

[80] Station 20092, surface, 31.01 per mille; station 20093, surface, 31.92 per mille; station 20119, surface, 31.43 per mille.

among the most reliable of indicators of ocean currents. Huntsman (1921, p. 89) has remarked that failure to find it more frequently along Nova Scotia "indicates the smallness of the contribution given by the water covering the Newfoundland Bank to the mass of water passing southwestward over the Breton and Scotian Banks." In fact, the evidence so far at hand suggests that it is exceptional for Tomopteris of Newfoundland Bank origin to stray southwestward much beyond 60° longitude, much more so for it to reach the Gulf of Maine by this route.

What rôle *T. catharina* plays in the economy of the planktonic community is still to be learned.

### Tomopteris septentrionalis Apstein

*Tomopteris catharina* is the only species of the genus which so far has been recognized anywhere in the inner parts of the Gulf of Maine at any season, but during March, 1920, a second and much smaller tailless Tomopteris, provisionally identified as *T. septentrionalis*,[81] was taken over the outer edge of the continental shelf off Cape Sable (stations 20076 and 20077), on Brown's Bank (station 20072), and in the southeastern part of the Gulf basin (station 20086); also in the Eastern Channel (station 20107) in April and off the southwest slope of Georges Bank in May (station 20129), one or two specimens on each occasion (fig. 94).

These records are interesting as extending the known range of this species southward along America to the Gulf of Maine. It was found off Halifax and at the mouth of the Laurentian Channel by the Canadian fisheries expedition of 1915 (Huntsman, 1921); has been taken at many localities in the Labrador current from the Grand Banks northward; along the west coast of Greenland; right across the North Atlantic to the Hebrides (Apstein, 1900); off Ireland, where Southern (1911) described it as common; and as far south as the region of the Canaries and as the Mediterranean near Gibraltar (Malaquin and Carin, 1911). It is likewise recorded from the South Pacific off Chile (Rosa, 1908).

Unlike *T. catharina*, *T. septentrionalis*, is characteristically oceanic, but its status in regard to temperature is not yet understood.

## PELAGIC CŒLENTERATES

The Gulf of Maine supports many species of cœlenterates, which live pelagic for at least part of their lives. Most of them, however (medusa stages of hydroids), are strictly neritic animals, which find their most favorable environment in the sheltered bays and among the islands and on the offshore banks, and which so seldom stray more than a few miles away during the brief period during which they are afloat that they are of practically no importance in the plankton of the gulf basin. Animals belonging to this category need not concern us here, since they have seldom if ever dominated in our offshore catches. Most of the local species have been described and beautifully illustrated by Alexander Agassiz (1865), to whom I refer

[81] The distinguishing characters of this species are its lack of tail, of rosette organs, or of first cirri; the development of sex organs only in the dorsal branches of the parapodia; and the presence of one glandular organ in each ventral branch of the latter. There is no danger of confusing *septentrionalis*, with the much larger *catharina*, specimens of the former, sufficiently adult to bear 21 parapods, being only 12 millimeters long, according to Reibisch (1905). Our largest with 17 parapods was 7.5 millimeters. The separation from *T. planktonis*, which depends on the parapodial glands, requires specimens in good condition.

any reader who may desire knowledge of them.[82] The few species of hydroid medusæ which do drift out more or less frequently into the open basin are among the most valuable indicators of coast water. Two of the local species of scyphomedusæ, which are of similarly neritic habit, are of still greater interest in this connection because of their large size (p. 33). In the following pages the reader will find notes on the occurrence of most of the species which we have found in any number in the deeper parts of the gulf.

The ctenophores (p. 365) are much more important in the natural economy of the plankton community than either of the groups just mentioned, for they are not only exceedingly abundant at times and locally in the gulf, but they are among the most voracious of pelagic animals (p. 108). Only one species of siphonophore (p. 377) is a regular inhabitant of the Gulf of Maine.[83]

## Hydroid medusæ

Only a few of the many species of hydroid medusæ assume any numerical importance in the planktonic communities of the open Gulf of Maine outside the outer headlands and islands, except over the offshore banks.

### Melicertum campanula (Fabricius)

This boreal neritic species is common on the North American coast from eastern Newfoundland southward to Cape Cod, and it occasionally occurs as far south as Woods Hole, whence Nutting (1901) recorded it once. It is represented in the northeastern Atlantic by a form (*M. octocostatum*) so closely allied that it may prove identical when the two are compared critically. The European Melicertum is known from Iceland and from many localities around southern Norway, from the Skager-Rak, all around Scotland, and along the northeast coast of Iceland.[84]

The hydroid stage of *M. campanula* was grown from the egg by Alexander Agassiz (1865) many years ago, hence there can be no question of its neritic nature, while the medusa stage is so large, so easily recognized, and so closely confined to the immediate vicinity of the land that it is one of the most valuable of neritic indicators. Hence, its distribution in the gulf deserves more attention than its slight importance in the natural economy of the plankton might suggest.

The youngest medusæ of Melicertum so far recognized were found by Alexander Agassiz in Massachusetts Bay toward the end of spring. Older stages are common all along the western and northern coasts of the gulf in June (Mayer, 1910, p. 208), and the sexually mature adults swarm in harbors and bays from Cape Cod to the Bay of Fundy during the late summer. It has been found plentiful, for example, in Salem Harbor, in Gloucester Harbor, about Nahant, and off Cohasset in Massachusetts Bay; equally at the mouth of the Piscataqua River below Portsmouth; in Penobscot Bay, where I have seen processions of these beautiful medusæ drifting with the tide in late July and early August; at Southwest and Northeast Harbors

[82] See also Fewkes, 1888; Mayer, 1910. I have elsewhere (Bigelow, 1914b) listed all the positive records of the pelagic cœlenterates on the New England coast.

[83] For lists of the cœlenterates collected during the summers of 1913 and 1914, see Bigelow 1915, pp. 308 and 316, and 1917, p. 302.

[84] Its occurrence is charted by Kramp, 1919, p. 54, chart 5

on Mount Desert Island; and in the bays of Grand Manan, where Fewkes found it one of the commonest medusæ in the summer of 1886 and I, myself, in August, 1910. Its breeding period endures from mid-July throughout August or even later, both in Massachusetts Bay and in Penobscot Bay, hence is no doubt uniform along the whole coast line of the gulf. The eggs are shed freely, are easily fertilized artificially, and the early stages in development can be followed without difficulty.

I have not seen Melicertum after August, but A. Agassiz (1865, p. 181) describes it as plentiful in Massachusetts Bay "in the fall at the time of spawning." How late in the season its medusæ may survive is not known. Perhaps it appears and dies earlier in the southwestern than in the northeastern part of the gulf, like Staurophora.

It is probable that the hydroid stage of Melicertum is invariably passed in the immediate neighborhood of the coast, there being no evidence that this ever takes place on Georges or Browns Banks or even on offshore ledges within the gulf, such as Cashes and Platts. And while the adult medusæ occasionally drift out to sea (for we have taken odd specimens over the western basin on August 9, 1913 (station 10088) and near Mount Desert Rock (station 10248) on August 13, 1914), it is very seldom that one strays beyond the 100-meter contour; nor have we ever found Melicertum in numbers anywhere outside the bays, river mouths, or harbors, except off Cape Cod and near Browns Bank (p. 33, footnote).[85]

### Staurophora mertensii, Brandt

This is a boreal Arctic species, circumpolar in its distribution, ranging widely over the Arctic Ocean and adjacent parts of the North Atlantic, and also in the North Pacific. In the eastern side it is known from many localities about Iceland, from Spitzbergen, Nova Zembla, the White Sea, all along the west coast of Norway, between Scotland and Iceland, and from the northern part of the North Sea.[86] In the western Atlantic and its tributaries Staurophora has been recorded from the west coast of Greenland, from the east coast of Newfoundland, from many localities in the Gulf of Maine, as detailed below, at Woods Hole, and as far westward along the south shore of New England as Newport (Mayer, 1910) and Fisher's Island Sound (Verrill, 1875, p. 43). Its known range in the North Pacific area includes Bering Sea, the Aleutian Islands, and the coast of Alaska on the east, and Japan on the west; and if Kramp's (1919, p. 41) contention that the *S. falklandica* of Browne (1902) from the Falkland Islands is actually *S. mertensii* proves correct, it is bipolar.

This large hydromedusa is a very conspicuous member of the plankton of the Gulf of Maine during its periods of plenty, for it attains a diameter of upwards of 200 millimeters at maturity and is made easily recognizable by its white central cross. It has not been actually demonstrated that Staurophora passes through a hydroid stage, but its systematic relationships and its seasonal history, outlined below, make it practically certain that such is the case.

[85] For locality records of Melicertum during the summer cruises of 1912 to 1914 see Bigelow, 1914, p. 125; 1915, p. 316; and 1917 p. 303.

[86] Kramp (1919, p. 44), who has plotted its distribution in the northeastern Atlantic, has shown that the young "Staurophora" described by Hartlaub (1899) from Helgoland probably was not this genus, but that the *S. discoidea* described by Kishinouye (1910) from Japan is not distinguishable from *S. mertensii*.

The young medusæ of Staurophora appear off Cape Cod and probably elsewhere along the coast farther north during the last half of April.[87] In 1920, for

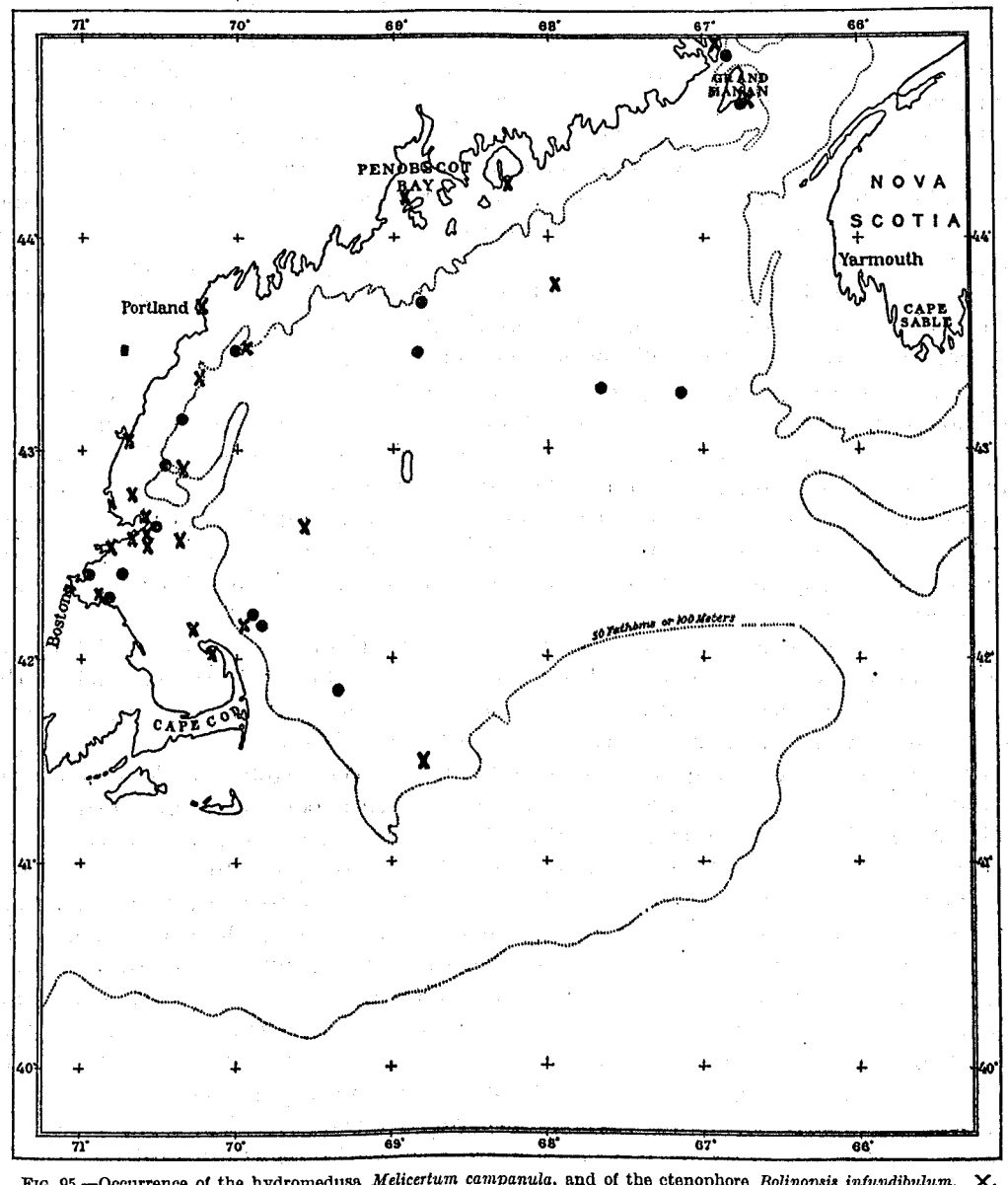


FIG. 95.—Occurrence of the hydromedusa *Melicertum campanula*, and of the ctenophore *Bolinopsis infundibulum*. X, locality for Melicertum; ●, locality records for Bolinopsis

example, we noted them first off the northern end of Cape Cod on the 17th of that month (station 20117) and found the tiny medusæ (about 5 to 15 millimeters in diameter) plentiful on the surface in Massachusetts Bay on the 20th (station 20119).

[87] According to Mayer (1910) this takes place early in the month, but such has not been our own experience.

Small specimens were again found there on May 4 (station 20120), in Ipswich Bay on the 7th and 8th (station 20122); less numerously at the Massachusetts Bay station (20124) and along Cape Cod (stations 20125 and 20126) on the 16th, and one of 40 millimeters on Georges Bank on the 17th (station 20127). It is probable that most of the Staurophora of that region are set free and reach recognizable dimensions during the last week in April and the first week of May, for in 1913 we found great numbers of the youngest stages in Gloucester Harbor on May 3 (Bigelow, 1914a, p. 407). In favorable years a tremendous production of Staurophora takes place in Massachusetts Bay, and the distribution of the adults suggests that this is true of the western coasts of the gulf as a whole, if not for its whole shore line. As yet, however, no search has been made for it in early spring anywhere north of Cape Ann in the inshore waters where the medusæ first appear, nor is it mentioned in Doctor McMurrich's plankton lists from St. Andrews.

Staurophora rivals the still larger scyphomedusæ in the rapidity of its growth, a fact long ago commented upon by Alexander Agassiz (1865) and more recently by Hartlaub (1899), who kept the young medusæ under observation for some weeks.

By the middle of May the medusæ attain a diameter of about 2 inches in the Massachusetts Bay region, and during the last week of that month I have seen specimens 3 to 4 inches in diameter cast up on the beaches of Cape Cod Bay in great numbers. Staurophoræ as large as 5 to 6 inches may be found early in June in Massachusetts Bay, and they attain a diameter of 6 to 9 inches there during the following month.

Staurophora reaches sexual maturity later, and the medusæ live until later in the season in the northern part of its range than in the southern, paralleling the differences of temperature with latitude. Thus, Mayer (1910) records mature individuals in Newport Harbor as early as the 5th to the 9th of June, 1895, while it is in spring that Staurophora appears most commonly at Woods Hole. In Massachusetts Bay it does not mature until early July, and our own experience corroborates Alexander Agassiz's statement (1865, p. 137) that Staurophora vanishes thence by the middle of that month, for we have found none there subsequent to that date. They occurred very generally, however, and often in large numbers over the northern half of the gulf, in deep water as well as shoal, during the last half of July and the whole of August of 1912, a year of plenty (Bigelow, 1914, p. 123), while Fewkes records it as common and of large size at Grand Manan during July and August, 1886, particularly in sheltered bays near the north end of the island (Fewkes, 1888, p. 233), and at Eastport until October. However, as we have not found it in September or later, it is probable that few if any of the medusæ of Staurophora survive much later than the end of August in the open gulf. Thus Staurophora disappears from most parts of the Gulf of Maine at least a month earlier in the season than either Aurelia or Cyanea; and it is probable that when specimens are seen in the southwestern part of the gulf as late as mid-August—for example, we noted it off Cape Ann and off Cape Cod on the 24th and 29th in 1912 (stations 10042 and 10043)—they are not the product of the shallows nearby but have drifted thither from the northern part of the gulf with the general eddylike circulation.

Staurophora fluctuates greatly in abundance in the Gulf of Maine from year to year. According to Willey and Huntsman (1921, p. 2) it was common in the channels leading into Passamaquoddy Bay in 1910. As just noted, also, the summer of 1912 was one of plenty. For example, great numbers were seen floating on the surface and a fathom or so down off Cape Elizabeth on July 29 and August 7; over Jeffrey Bank and near Monhegan Island on August 8; it swarmed off Penobscot Bay on the 13th; again a few miles off Seguin Island on the 22d; and 20 large medusæ, upwards of 8 inches in diameter, were taken in a haul from 30 meters a few miles north of Cape Ann on the 24th (Bigelow, 1914, p. 123). Staurophora occurred at more than one-third of our stations for 1912 (16 locality records), distributed very generally over the western and northern parts of the gulf, including Platts Bank, the Grand Manan Channel, and Eastport.[88] Willey and Huntsman (1921) also mention its presence in Passamaquoddy Bay and at St. Andrews during that summer.

If our hauls gave a true picture, the years subsequent to 1912 saw a progressive decrease in the numbers of Staurophora living in the Gulf of Maine. Thus, it was at only two localities that we found it in any numbers in 1913—in the southwest part of the gulf on July 8 and over Jeffreys Ledge off Cape Ann on August 11—with the other locality records based on occasional specimens only or on fragments, although it occurred at ten localities[89]—that is, at about the same proportion of our stations as in 1912. Straurophora proved even scarcer in the gulf in 1914, when we found it at only three stations in all (10214, 10224, and 10249), although we visited the same general localities as in the two previous summers and at about the same season.

In 1915 this medusa was so rare that we took only three specimens at as many stations (stations 10272, 10282, and 10290), although we towed in the coastwise waters of the gulf as well as offshore on many occasions from May onward throughout the summer; nor did we find it at all at our Gulf of Maine stations from Massachusetts Bay to Georges Bank in July or August, 1916. From that time forward the war caused a suspension of our work until the spring of 1920, hence nothing is known of the status of Staurophora for the years 1917, 1918, and 1919 except that none were seen at St. Andrews during that period (Willey and Huntsman, 1921). But young Staurophora were once more plentiful in Ipswich Bay, Massachusetts Bay, and along Cape Cod during the spring of 1920 (stations 20117, 20119, 20120 to 20122, and 20124 to 20126); and since it was found very generally in Passamaquoddy Bay and its tributaries during that July and August (Willey and Huntsman, 1921, p. 2), it had evidently reestablished itself in the gulf in its former abundance.

Although Staurophora, like the scyphomedusan genera Aurelia and Cyanea, and like the various smaller hydromedusæ (p. 340), is neritic, it is much less closely confined to the coastal zone in its medusan stage than is either of the former or than are most of the latter (p. 341), but occurs widely over the triangle between Nova Scotia and the Maine coast in its summers of plenty, offshore as well as in the coastal zone, and out to the 100-meter contour off the Massachusetts Bay region (fig. 96). But it seems to be wholly absent from the south-central and southeastern

[88] For these stations see Bigelow, 1914, p. 123.
[89] Stations 10057 and 10058 in July; stations 10089, 10090, 10091, 10093, 10100, 10103, and 10104 in August.

parts of the basin of the gulf, and it is only near shore or over comparatively shoal water that we have encountered it in any abundance (p. 345).

Staurophora, like Cyanea, breeds on Georges Bank as well as in the coastal zone—witness the young medusa taken there by Mr. Douthart in April, 1913 (Bigelow, 1914a, p. 414), and the specimen of 40 millimeters mentioned above at station 20127. Very likely it is commoner and more widespread there than the actual records suggest, its seasonal history in Massachusetts Bay suggesting that it may grow to maturity on Georges Bank and die there in the seasonal interval (late May to mid July) between the dates of our visits. Our failure to find it at all over the coastal bank west of Nova Scotia, including Browns Bank, may have been equally accidental. The preponderance of records for this medusa in the western side of the gulf, as contrasted with the eastern, evident on the chart (fig. 96), can not be explained away in this manner, however, but suggests that its chief center of abundance is in the zone between Cape Cod and Penobscot Bay.

*Vertical distribution.*—The youngest medusæ recognizable as Staurophora swarm on top of the water, as do the medium-sized specimens so often cast up on the beach, but although the large adults of midsummer occasionally rise to the top (most often at night and in regions of active vertical circulation—e. g., in the Grand Manan Channel) they are usually at least a meter or more below the immediate surface at this season, a fact that has been noted elsewhere (Bigelow, 1914, p. 124). On calm days they may often be seen from the ship's side as deep down as the limit of visibility, but, on the other hand, we have no evidence that Staurophora ever descends to any considerable depth, most of the records being from hauls shallower than 100 meters. As our largest catches have been made at 40 meters or less it is probable that this is the lowest level of its common occurrence and that the occasional Staurophoræ taken in the deep hauls have been picked up by the net on its way down or up through the water.

I should emphasize that the status of Staurophora as a regular endemic inhabitant of the Gulf of Maine is thoroughly established; was, indeed, to all intents and purposes by Alexander Agassiz (1865) many years ago. Inasmuch as its geographic range when it is in the medusa stage covers the whole of the inner waters of the gulf from Massachusetts Bay to the Bay of Fundy, no doubt it breeds successfully all along the New England coast north of Cape Cod and perhaps farther west as well, for the medusæ appear in most years both at Woods Hole (Hargitt, 1905a) and at Newport (Fewkes, 1888).

It is certain that many Staurophora pass through their hydroid stage in water as shallow as that of Gloucester Harbor, where we found the very young medusæ in great numbers in 1913 and 1920 (p. 43; Bigelow, 1914a, p. 407). In fact, it is probable that the majority of the stock live through their attached stage within 20 to 30 meters of the surface within a few miles of the coast line, as is the case in Massachusetts Bay. The wide distribution of Staurophora in the offshore parts of the gulf, however, and especially the fact that its medusæ are set free on Georges Bank suggest that it may also pass through its development in considerably deeper water. How deep is not yet known. Probably Platts Bank, Cashes Ledge, and Jeffreys Ledge are also nurseries for it.

The large Staurophora no doubt takes a very heavy toll of Calanus and smaller copepods, which are often to be found entangled along the elongated lips of its cruci-

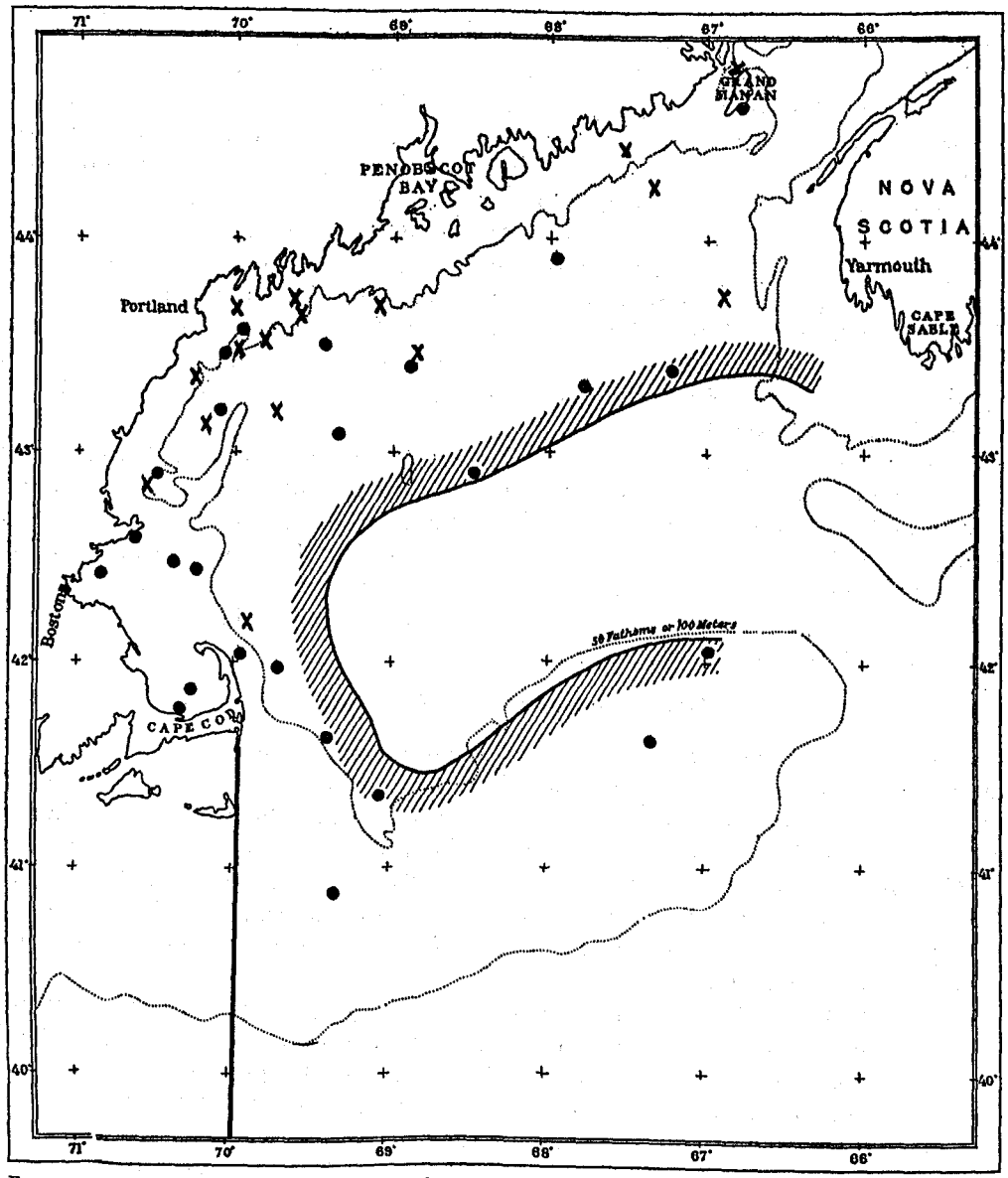


FIG. 96.—Occurrence of the hydromedusa *Staurophora mertensii*. X, locality records, summer of 1912; ●, subsequent years. The hatched curve includes its chief zone of occurrence within the Gulf of Maine

form mouth opening, and since the young Staurophora also feed on them greedily, according to Hartlaub (1899), this medusa must play an important rôle in the natural economy of the animal plankton wherever it is plentiful.

### Ptychogena lactea, A. Agassiz

The importance of this Arctic hydroid medusa in the Gulf of Maine as an indicator of water from the north has been emphasized in an earlier chapter (p. 59). I need merely list here the following records of its occurence:

Massachusetts Bay at Nahant, "where they have only been found during a single fall, and then only for a few days, when they seemed quite abundant" (A. Agassiz, 1865, p. 139); eastern basin of the gulf, May 6, 1915 (station 10270); German Bank the next day (station 10271), one specimen at each station; and several examples near Lurcher Shoal on the 10th of the month (station 10272).

The presence of this Arctic medusa in Massachusetts Bay in the autumn of 1863, as recorded by Agassiz, contrasted with the fact that we have since found it only in spring at the time the Nova Scotian current is at its maximum, and in the opposite side of the gulf, is an interesting phenomenon and one yet to be accounted for.

The nearest locality record for Ptychogena to the northward with which I am acquainted is from the neighborhood of Halifax, Nova Scotia, where it was taken by the *Challenger* (Haeckel, 1881).

*Ptychogena lactea* is Arctic and circumpolar. It has been recorded from several localities along the west coast of Greenland and in Barents Sea between northern Norway and Spitzbergen, from Franz Josef Land, from the Kara Sea near Nova Zembla, from Bering Sea, and from the Sea of Okhotsk. Its most southerly records are the Gulf of Maine in the western side of the Atlantic, between Scotland and Iceland in the eastern side, and the east coast of Hokaido, Japan, in the Pacific (Bigelow, 1913; Kramp, 1919, p. 37).

### Mitrocoma cruciata (A. Agassiz)

*Mitrocoma cruciata*, Staurophora, and Phialidium are the only hydroid medusæ that we have found generally distributed in the open gulf at any season. Mitrocoma is further interesting because it was not seen from the time it was first described by Alexander Agassiz (1865) from Nahant, Mass., many years ago, until the *Grampus* rediscovered it in the gulf in July, 1913 (Bigelow, 1915, p. 316). Although the development of this species has not been traced, there is every reason to suppose that its hydroid stage, like that of its close relative, the Mediterranean *M. annæ*, is a Cuspidella.

In the Gulf of Maine Mitrocoma is a spring species. In 1920 the *Albatross* towed specimens occasionally from February 23 (our earliest seasonal date for it) until May 4 (stations 20048, 20091, 20105, 20106, and 20120). In 1915 we found it not uncommonly in May and June (stations 10270, 10271, 10278, 10282, 10286 to 10288, 10290, 10291, and 10293). A. Agassiz's record was also for June. We have one July record of it in 1913, just noted, one in 1915 for July 15 (station 10301), one for August 4 (station 10303) and others for the 12th and 14th in 1914 (stations 10246 and 10250); but the middle of August apparently marks the end of its season of occurrence, for we have not found it on any of our cruises later in the season. Thus, its period of abundance precedes and somewhat overlaps that of Phialidium. The localities of capture are widely distributed in the

western, northern, and eastern parts of the gulf, over deep water as well as shallow, and include Browns Bank (fig. 97). We have not found Mitrocoma on Georges Bank, though a specimen was towed in the basin between the latter and

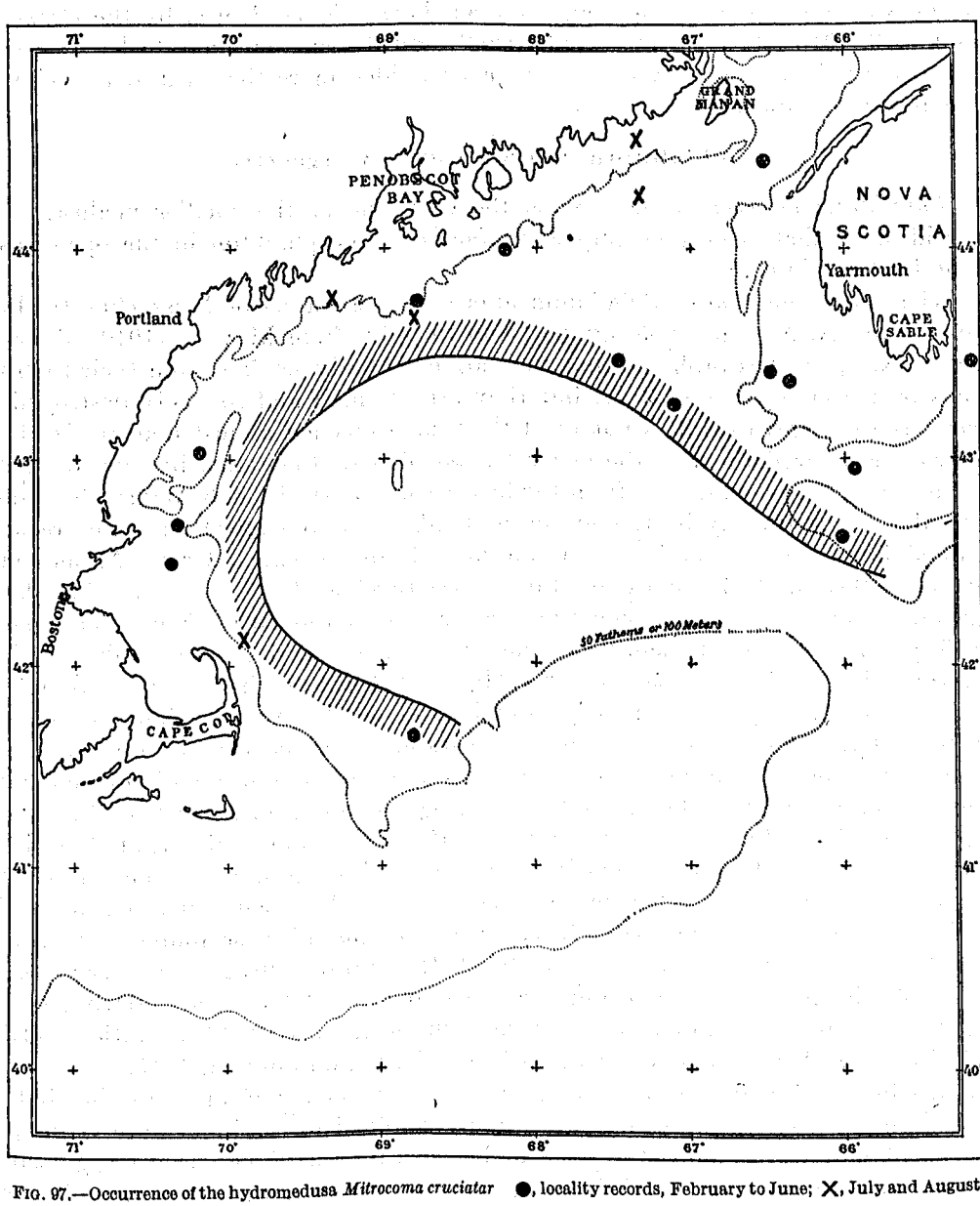


FIG. 97.—Occurrence of the hydromedusa *Mitrocoma cruciatar* ●, locality records, February to June; X, July and August

Cape Cod on July 8, 1913. Thus, the few locality records for Mitrocoma roughly parallel those for Phialidium (p. 350) in their geographic distribution, and so large a percentage of the captures have been made over one part of the basin or another

that Mitrocoma, like Phialidium, probably passes through its hydroid stage over rather a wide range of depth and perhaps down to 100 meters or more.

Up to the present time all known captures of *M. cruciata* have been from the Gulf of Maine except for a few taken off Shelburne, Nova Scotia, by the *Grampus* on June 23, 1915 (stations 10291 and 10293), and it seems nowhere to be abundant even in the gulf, for our tow nets have never yielded more than a dozen specimens or so at any one station.

### Phialidium languidum[90] (A. Agassiz)

*Phialidium languidum* (fig. 98) is the only one of the smaller medusæ with hydroid stage that is ever an important factor in the plankton in the open basin of the Gulf of Maine.[91]

The young medusæ of Phialidium appear in the waters of Massachusetts Bay late in May (A. Agassiz, 1865, fig. 96), and to judge from Mayer's (1910) observations at Newport it is probable that they are constantly set free from their hydroid stocks from that time until July, but they are so small and so easily destroyed in their earliest stages that it is not until they have reached almost mature size that we have recognized them in the general mass of plankton taken by our tow nets. The adults are most numerous from the last week of July through August, to vanish from Massachusetts Bay by the end of September, and our latest autumnal records of Phialidium are for October 9 in the coastal zone between Grand Manan and Penobscot Bay in 1915 (for list of stations see Bigelow, 1917, p. 304). The abundance in which these medusæ sometimes occur was mentioned by Alexander Agassiz (1865, p. 73), who found them "in immense shoals on warm, sunny, still days" in Massachusetts Bay during September. Mayer (1910), too, observes that from July until September they are extremely abundant along the New England coast, particularly at Eastport, where they crowd the water of the harbor, and my own more recent experience has been similar. For instance, we found Phialidium common in every harbor and bay that we entered during the month of August in 1912, especially so in Gloucester Harbor, at the mouth of the Piscataqua River, at Boothbay, and at Eastport. I had previously seen this medusa in myriads both at Grand Manan during August, 1910 (whence Fewkes (1888) also records it), and along the southern shores of Massachusetts Bay. The *Grampus* likewise found it swarming near Mount Desert Rock on August 16, 1912 (station 10032), and near Seguin Island off the mouth of the Kennebec River on the 22d of that month (station 10040); even as far offshore as the eastern basin on August 13, 1914 (station 10249), and also in the Piscataqua River and off Rye, N. H., on July 23, 1915.

We have no record of Phialidium out in the open gulf prior to the first of August, either because the young medusæ are confined to the immediate vicinity of their shallow nurseries along the coast or because they have not been recognized in the tow, but during that month it occurs very generally right across the gulf north of a line from Cape Cod to Cape Sable.[92]

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[90] For description and figures see A. Agassiz, 1865, p. 71; Mayer, 1910, p. 269.

[91] Other species are plentiful locally on Georges Bank.

[92] For locality records, summers of 1912 to 1915, see Bigelow, 1914, p. 125 1915 p. 273 and 1917 pp. 303 and 304.

Although we have taken Phialidium over the basin as well as near shore, it occurs most regularly within a comparatively short distance of the land, as might be expected of any neritic animal that passes the greater part of the year attached

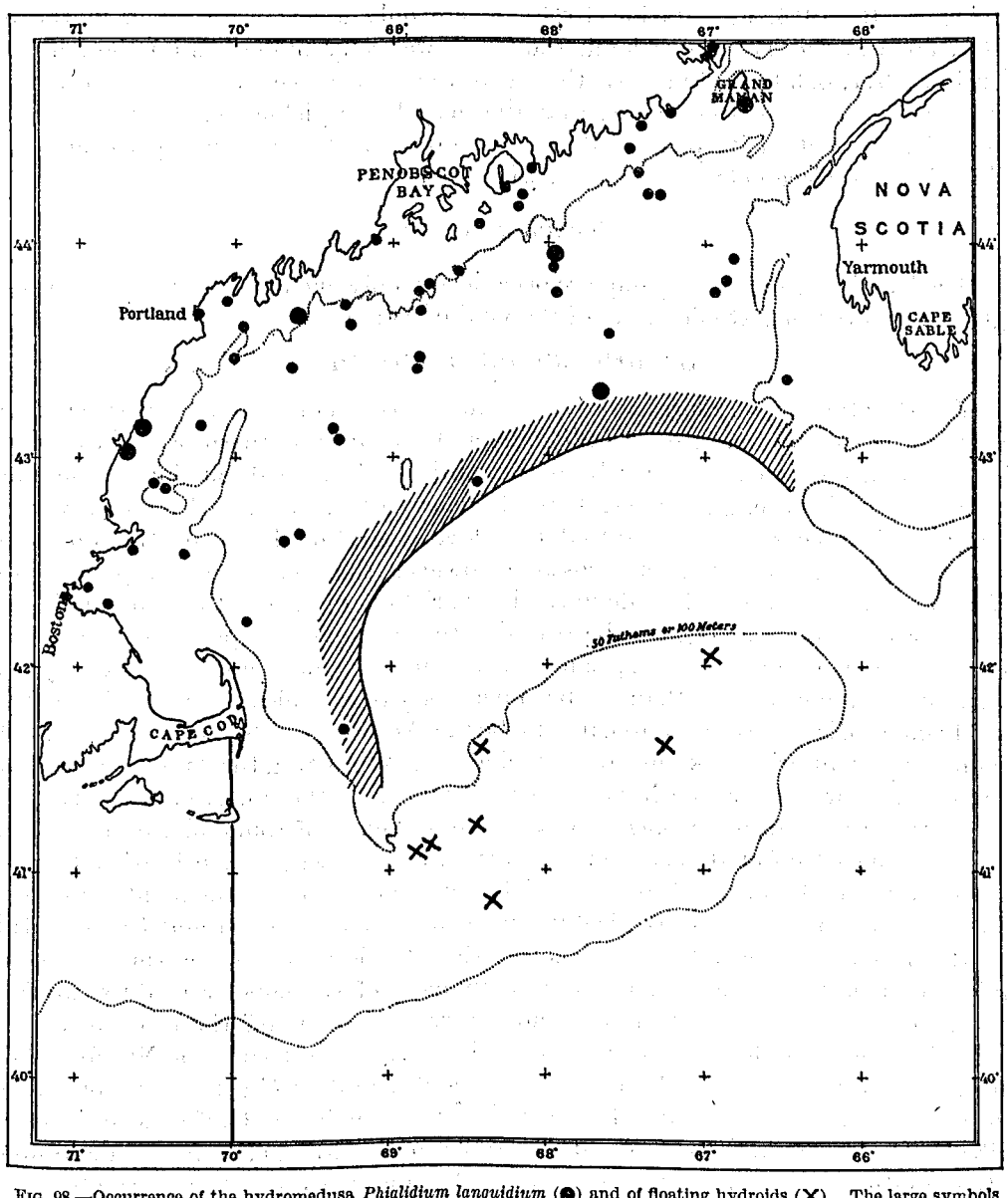


FIG. 98.—Occurrence of the hydromedusa *Phialidium languidium* (●) and of floating hydroids (X). The large symbols mark the swarms of Phialidium; the hatched curve its approximate offshore boundary

to the bottom in shoal water. There is evidence that Georges Bank and Browns Bank serve as nurseries for it, for we found it on the northwestern part of the former on August 13, 1926. We have no record for it in the southeastern part of the basin or in the Eastern Channel.

Our experience has been that the medusæ of Phialidium are always most numerous at the surface or a meter or so down at most, no matter what the precise locality in the gulf or the time of day, a fact well illustrated in the eastern basin on August 13, 1914, at "station 10249, where only a few were taken in the 50-meter, none in the 175-meter haul, though it was very numerous on the surface" (Bigelow, 1917, p. 305). Similarly, the offshore swarms twice encountered in August, 1912, were so close to the surface that the deep hauls yielded very few (no doubt caught by the net in its passage down and up through the rich superficial zone), although the surface nets were clogged with them.

## Trachomedusæ

The Trachomedusæ as a group are oceanic and only one of them is known to enter regularly into the planktonic fauna of the Gulf of Maine.

### Aglantha digitale (Fabricius)

Whether the known representatives of the genus Aglantha represent two species, a large northern with four otocysts (*digitale*) and a smaller southern (*rosea*) with eight of these organs, or only one, has been the subject of much discussion. The most recent observations (e. g., Mayer, 1910; Bigelow, 1911, 1913, and 1915) favor the latter view, it having been proved that the older separation, based on the number of otocysts, can not stand. It is still possible, however, that the genus is represented in different seas by more or less definite size varieties, of which the geographic and seasonal relationships are still to be traced. In the following pages all Aglanthas, large and small, are treated as a specific unit because they have not yet been subjected to examination more critical than has been necessary to establish their generic identity.

*Aglantha digitale* is circumpolar and boreal-Arctic. In the northeastern North Atlantic and tributaries its known range includes the White Sea, the Arctic Ocean about Spitzbergen, Barents Sea, the Norwegian Sea, and the northern part of the North Sea. It penetrates thence into the Skager-Rak, which is a center of abundance for it (Kramp, 1913), and has been found very plentiful in the Bay of Biscay in depths of 50 fathoms or more (Browne, 1906, as "*A. rosea*"). The collections made by the plankton expedition show that Aglantha is practically universal between Iceland and Greenland; in fact this probably applies to the whole North Atlantic north of the isotherm of 60° surface temperature. Aglantha is the commonest of the smaller medusæ in West Greenland waters (Vanhöffen, 1897), and the records for it off the coast of eastern North America include the east coast of Labrador, the east coast of Newfoundland (Bigelow, 1909a), the Grand Banks, and the continental shelf generally along Nova Scotia (Bigelow, 1917, p. 303). It occurs far and wide in the Gulf of Maine, as described below, and follows the cool water over the continental shelf as far west and south as the mouth of Chesapeake Bay in winter (Bigelow, 1918, p. 388); sparingly to the latitude of Delaware Bay even in summer. The high temperature of the inner edge of the Gulf Stream forms an insurmountable offshore barrier to Aglantha off the American littoral, as it does for so many other boreal members of the plankton.

Although the early development of Aglantha has not yet been traced, it is probable that it is direct, like that of its close ally, the genus Aglaura—that is, without

hydroid stage—and consequently that the medusa is independent of the coast line and of the bottom at all stages in development. Its distribution is therefore wholly independent of distance from land or from shoal water.

Aglantha, like many other medusæ, was first recorded from the Gulf of Maine by Alexander Agassiz (1865), who detected both large, sexually mature medusæ and young ones at Nahant, Mass., during the summers of 1863 and 1864, since when it has been reported both by Hargitt (1905) and by Mayer (1910) as common in spring off the shores of southern New England. Consequently it was no surprise to find it in our plankton hauls at many stations in the Gulf of Maine. The localities of capture, as appears on the chart (fig. 99), are concentrated in a peripheral zone 40 to 60 miles broad, paralleling the coast from Cape Cod to Cape Sable and spreading thence southward and westward across Browns Bank, the Eastern Channel, and following the southern half of Georges Bank westward; but we have never taken a single specimen of Aglantha in the central waters of the Gulf or over the northern part of Georges Bank.

The reader need but compare the chart of Aglantha with the corresponding chart for Beroë (fig. 102) or for *Pseudocalanus elongatus* (fig. 83), animals equally pelagic at all stages and of similar temperature affinity but regularly and constantly endemic in the Gulf of Maine, to note the sharp contrast between the definite localization of the records for Aglantha [93] and the universality of the others.

Although we have never found Aglantha with sufficient regularity (and seldom in sufficient abundance) to regard it as a characteristic member of the plankton of the gulf, it has occurred often enough and at stations indifferently enough spaced to show that it may be expected anywhere and at any season in the area inclosed by the curve on the chart. Within this area the locality records show no definite concentration in one side of the gulf or the other, nor do they correspond to the depth of water, and our experience has been that the local presence or absence of Aglantha in the gulf at any particular time is as independent of precise temperature or salinity as it is of depth, the close neighborhood of land, or the contour of the bottom. Its distribution closely mirrors the anticlockwise circulation of the upper strata of water in the gulf. The natural inference from this is that the continued presence of Aglantha within the gulf depends more on immigration from the east and north than on local reproduction. Once such immigrants have passed Cape Sable they follow right around the gulf, first north then west, southwest, and south in their involuntary journey, with little more tendency to spread toward the center of this great eddy than have the various fish eggs or other animals of neritic nature that are set free near the coast line. In this its distribution in the gulf parallels (though it does not exactly reproduce) that of the chætognath *Eukrohnia hamata*, another common visitor from colder seas to the east and north, which occurs far more regularly around the periphery of the deep basin than in its center and spreads southward along the slope of Georges Bank but at a deeper level than Aglantha.

[93] For locality records of Aglantha for the years 1913 to 1916, see Bigelow, 1915, p. 316; 1917, pp. 303 and 304; 1922, pp. 134 and 136. During the spring of 1920 it was taken at stations 20044, 20046, 20049, 20055, 20056, 20058, 20064, 20067, 20068, 20071, 20072, 20073, 20074, 20075, 20076, 20077, 20079, 20081, 20087, 20096, 20105, 20107, 20111, 20115, 20116, 20118, 20122, 20128, and 20129, and at stations 10490, 10491 and 10499 during December–January, 1920–1921.

Although Aglantha abounds on or near the surface in Arctic Seas its usual habitat in the Gulf of Maine is at some deeper level, with only six of our sixty-odd locality records for it from surface hauls;[94] but, although it so seldom rises quite to the top of

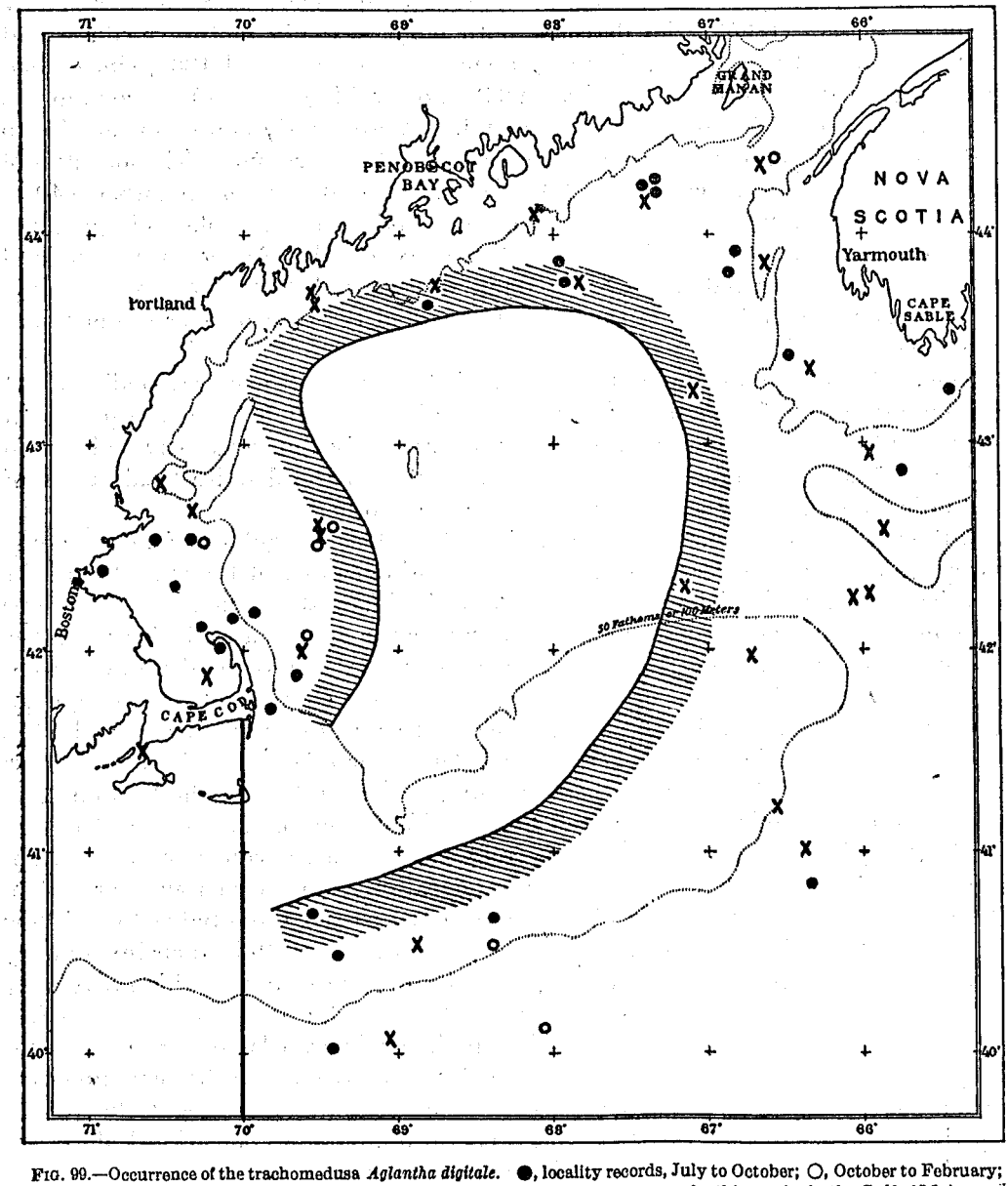


FIG. 99.—Occurrence of the trachomedusa *Aglantha digitale*. ●, locality records, July to October; ○, October to February; X, February to July. The hatched curve incloses the chief zone of occurrence for this species in the Gulf of Maine

the water in the gulf, we have occasionally taken it at not over 15 meters depth, often in tows from 50 or 60 meters, and usually within 150 meters of the surface.

[94] Aglantha has also been found on the surface at Woods Hole by Hargitt (1905), and at Nahant in Massachusetts Bay by A. Agassiz (1865).

Only eight hauls (whether with the open or closing nets) from deeper than 160 meters have yielded Aglantha. Evidently, then, this medusa lives chiefly in the upper strata of water in the Gulf of Maine, just as it does in the North Sea region (Kramp, 1913) and for that matter over the North Atlantic as a whole, though not on the surface. The frequency of captures in hauls made between 50 and 150 meters (a depth range which included about 40 per cent of all Gulf of Maine records for Aglantha) points to this stratum as its chief center of abundance. The greatest depth from which I can definitely establish the presence of Aglantha within the gulf is 180 to 140 meters (closing net, off Mount Desert Rock, March 3, 1920, station 20055). The only specimen we have taken in a tow from deeper than 200 meters (240–0 meters, station 20049, western basin, February 23, 1920) may have been picked up by the open net on its journey down or up; nor is it any more certain that the few Aglanthas which we have collected along the continental slope ostensibly from 400–0 and 500–0 meters (e. g., station 20077, March 19, 1920), but in open nets, actually came from so great a depth.

Aglantha is seldom abundant in the Gulf of Maine; in fact, most of the records obtained by the *Grampus*, *Albatross*, and *Halcyon* (now amounting to the respectable total just mentioned) are for single or occasional specimens. Only five times have we taken it in large numbers—that is, near Lurcher Shoal, May 10, 1915; near Gloucester, July 19, 1916 (station 10340); in Provincetown Harbor the next day (station 10243); off Gloucester, October 31 of that same year (station 10399); and on the southeast part of Georges Bank, March 12, 1920 (station 20069).

Aglantha is present in the gulf throughout the year, taken there during every month except October, when we have done little towing; nor is there anything in our records to suggest that it is notably more abundant at one season than another, for the rich hauls just mentioned were made in spring (March and May), summer (July), and autumn (October). It is probable, however, that a more intensive study of the local occurrence of this medusa in the gulf would show that its numbers there do wax and wane with the succession of the seasons. At Woods Hole it occurs most often in spring (March to May, according to Hargitt, 1905).

Although the distribution of Aglantha in the Gulf of Maine is more consistent with an extralimital source of supply than with widespread local production such as maintains the stocks of Calanus, *Thysanoessa inermis*, *Sagitta elegans*, or even Euchæta in the gulf, the fact that very young specimens as well as adults have repeatedly been taken there not only during our recent cruises but half a century ago (A. Agassiz, 1865) is evidence enough that it reproduces itself to some extent. Occasionally a local wave of production must take place to produce such an abundance of the young medusæ as we found off Cape Ann on October 31, 1916 (Bigelow, 1922, p. 136; station 10399).

Aglantha, large or small, is usually so scarce anywhere in the gulf that such events must be unusual. Additional information on this point would be very welcome, for it is not possible to appraise the faunal significance of the occasional swarmings of Aglantha as indices to influxes of northern water into the Gulf of Maine without knowing how regularly the stock of this species existing there is replenished by local breeding.

The dimensions of the specimens of Aglantha from the Gulf of Maine, compared with their states of sexual maturity, corroborate all previous studies of the genus to the effect that there is a wide range of variation with respect to the size attained by this medusa at maturity. At the one extreme is a large race in which the gonads do not reach full size until the bell is 20 millimeters high or even higher, and there seems to be every gradation from this down to specimens in which the sex organs are already well developed and the eggs plainly visible when the bell is only 6 to 10 millimeters high. The Aglanthas from Massachusetts Bay, described by Alexander Agassiz (1865) as upwards of 25 millimeters high when adult and with the gonads just appearing in specimens of 5 to 8 millimeters, were among the largest known representatives of the species. Most of the Aglanthas collected by the *Albatross* from February to May, 1920, were likewise large, as appears from the following table:

| Station | Height of bell in millimeters | State of sexual development | Station | Height of bell in millimeters | State of sexual development |
|---|---|---|---|---|---|
| 20067 | 9 | No gonads. | 20096 | 18 | Gonads 6 to 7 millimeters long. |
| 20129 | 10 | Do. | 20129 | 18 | Gonads 4 millimeters long. |
| 20129 | 12 | Small gonads. | 20069 | 21 | Gonads 5 millimeters long. |
| 20129 | 13 | Do. | 20088 | 23 | Gonads 7 to 8 millimeters long. |
| 20081 | 19 | Gonads 2 to 3 millimeters long. | 20116 | 26 | Gonads mature, up to 6 to 7 millimeters long. |

A large variety was also represented among the Aglanthas taken in May, 1915, and part (just what proportion is yet to be determined) of the swarm of young just mentioned as encountered off Gloucester on October 31, 1916, were also destined to grow large, for the series taken included many specimens up to 10 millimeters high but without visible trace of gonads. But that same swarm yielded many Aglanthas with gonads of good size and (in the case of the females) eggs already visible, although the bells were only 6 to 7 millimeters high. Our largest catches of the "small" Aglantha were in Massachusetts Bay and especially at Provincetown on July 19 and 20, 1916 (stations 10340 to 10343), when specimens sexually mature, though only 6 to 10 millimeters high, were abundant and no large ones were taken. Examples of this small variety have also been recorded by Hargitt [95] (1902 and 1905) from off Chatham, August 19, 1902.

These data suggest that the large race usually predominates in the gulf during the cold season, giving place to smaller specimens during the warm; and the occurrence of large and small specimens side by side in Massachusetts Bay in October, which I have just mentioned, may mark the transition from the season when most of the Aglanthas are small to that during which they average large. The presence of occasional large specimens in midsummer—for instance, off Grand Manan on August 13, 1913, and in Massachusetts Bay in summer and autumn—shows that there is no hard and fast rule.

To settle the true relationship of the two races to each other, to the physical state of the water, and to their origin in the gulf, whether local or immigrant, calls for a study more intensive than has yet been devoted to the genus. For the present the

[95] Described by him as a new species, "*A. conica.*"

most reasonable hypothesis is that the small form is evidence of conditions less favorable, the larger specimens of an environment more favorable, for growth, though both may mature their sexual products.

## SCYPHOMEDUSÆ

### Cyanea capillata var. arctica, Péron et Lesuéur

The distribution of the genus Cyanea, the largest of all the medusæ, is very wide along the coasts of both sides of the North Atlantic and Pacific Oceans and in the Arctic Ocean. The genus is likewise represented in south Temperate and Antarctic Seas, but not in the Tropics. Numerous supposedly distinct "species" of Cyanea have been described, separated for the most part by color, size, and minor anatomical differences, but these have been found to intergrade in so many cases that, as I have remarked elsewhere (Bigelow, 1913, p. 92), it seems impossible to distinguish more than one species of this genus in northern seas, where all its varieties are connected by intermediates. Several of the latter, however, deserve recognition in nomenclature, being not only well marked but occupying rather definite geographic ranges.

The Cyaneas which occur in the Arctic-boreal waters of the western side of the North Atlantic province, from West Greenland to the region of Cape Cod and Nantucket Shoals, are the largest of their race and usually of a rich brown and yellow color. They form the basis of the "species" *C. arctica* of Péron et Lesuéur and of most recent authors. Following the coast west and south from Cape Cod we find this northern form giving place to smaller, more yellowish Cyaneas (the var. *fulva*) along southern New England and the Middle Atlantic States to the Carolinas, and this form in turn to a still smaller and pinker race christened "*versicolor*" by L. Agassiz, which is very plentiful locally from Cape Hatteras to the southern boundary for the genus off Florida (Mayer, 1910, p. 600).

Cyanea, like Aurelia (p. 362), is neritic and its life cycle is similar. The egg [96] develops to the planula stage among the folds of the mouth parts of its parent, and when it is shaken free it attaches itself to the bottom, to develop there into the tentaculate scyphostoma from which the young medusæ (ephyræ) are produced serially by annular constrictions of the oral end.

The distribution of this common red jellyfish in the Gulf of Maine is interesting because its presence is a sure sign of coast or of banks water, and because it offers a refuge to the fry of the haddock [97]. Locality records for it in the gulf are now very numerous. In the neighborhood of Woods Hole (and probably this applies all along the southern shores of New England) the young medusæ of Cyanea appear in March; by the end of the month "the calm surface of the water in Great Harbor was literally spangled with the slightly protruding discs" (Bumpus, 1898, p. 487); by mid-April some have grown to a diameter of 7 inches (Mead, 1898); many are sexually mature at Woods Hole by May, though the youngest medusæ (ephyra stage) are still to be found there as late as the end of that month; and the mature

[96] On the development of Cyanea see L. Agassiz, 1862; Hyde, 1894; McMurrich, 1891; Hargitt, 1902.
[97] For an account of its movements in Norwegian waters see Damas (1909).

medusæ in the act of releasing their ova are taken in abundance from the early part of June (McMurrich, 1891) until September (Sumner, Osburne, and Cole, 1913a, p. 575).

North of Cape Cod it seems that the ephyræ of Cyanea are liberated later in the season, corresponding to the more tardy vernal warming of the water. I have no direct data as to the precise season when the ephyræ are set free in the Gulf of Maine,[98] for we have never seen a young Cyanea in the inner parts of the gulf during the spring months, but the few we have taken there during the last half of June have been only 2 to 3 inches broad (e. g., north of Georges Bank, June 25, 1915, station 10298). It is not until the first part of July that we have seen Cyanea as large as 6 to 10 inches in diameter in the Massachusetts Bay region, pointing to April and May as the season when their liberation commences. At that time the smallest medusæ of Cyanea must be extremely plentiful along the shores of the gulf. Alexander Agassiz (1865, p. 45) saw great numbers of them measuring ¼ to 3 inches in diameter on the surface in Provincetown Harbor in the early morning, all, however, sinking as the sun rose, and we have found them in abundance on Nantucket Shoals in April (p. 359). Our failure to take them in our tow nets elsewhere in the gulf during those months, in spite of the considerable number of hauls, recalls Louis Agassiz's remark (1862, p. 109) that "there must be something peculiar in the habits of the young Cyanea to render them apparently so rare, when in the adult state they are so common" along the coasts of Massachusetts Bay. His suggestion that they keep near the bottom during their early stages has been corroborated by Mayer's (1910, p. 600) observation that young Cyaneas rarely come to the surface in the aquarium but spend most of their time clinging to the bottom or side of the tank with their widespread oral fringes. The tendency of the small Cyaneas to seek the surface so much more regularly about Woods Hole than in the Gulf of Maine is an interesting local difference in habits still awaiting explanation.

It seems that Massachusetts Bay and the Gulf of Maine generally offer an especially favorable environment for the Cyaneas, which grow so rapidly there that many of them attain a diameter of 2 to 4 feet by the close of the summer. This is about the average size at the end of their lives, though Alexander Agassiz (1865, p. 44) records one monster from Massachusetts Bay that measured 7½ feet across the disk, with tentacles upward of 120 feet in length.

It is certain that the breeding season for Cyanea endures from June until mid-autumn in the Gulf of Maine, for on the one hand Hyde (1894) obtained developing eggs near Cape Ann early in summer, while on the other we have frequently found the medusæ, with mature eggs and carrying great numbers of the planulæ, cast up on the beach in September and early October. Probably Cyanea becomes sexually mature as soon as a certain size is attained, regardless of the precise season when this takes place, and continues to produce eggs or sperm throughout the remainder of its life, with the autumnal storms, which either cast the medusæ on the shore or batter them to pieces at sea, setting the natural period to their existence. We find no record of Cyanea in the Gulf of Maine after October.

[98] One ephyra was taken near Mount Desert on June 14, 1915, but it was probably among the latest produced there.

It is not easy to reconstruct the life histories of planulæ set free at the beginning of the breeding season, which may be in May at Woods Hole or early in June north of Cape Cod. It is possible that some of these pass through the scyphostoma stage, that these produce ephyræ, and that the latter grow to sexual maturity—but probably not to a large size—that same autumn; for Hargitt (1902) found that in high temperatures (19 to 20°, and upwards) the development of Cyanea may go forward so rapidly that the whole cycle, from planula to young medusæ, is sometimes compressed into a period of 18 days. McMurrich's (1891) experience, however, that planulæ of Cyanea produced in May, which he kept under observation in the aquarium at Woods Hole and apparently under favorable conditions, were still in the scyphostoma stage at the end of August is sufficient evidence that the rate of larval development is usually much slower than this even at summer temperatures. Nor is it likely that if any great number of Cyaneas passed through two generations a year at Woods Hole—that is, produced sexually mature medusæ in spring and again in autumn—the fact would so long have escaped detection there, with marine collecting carried on so intensively and continuously. It is also probable that in the Gulf of Maine, with its cooler water, few of the larval Cyanea that are produced in late spring and early summer (none of the late summer and early autumn crop) attain the stage at which the young medusæ are set free ("strobila stage") before autumnal cooling checks their further development.

What few precocious medusæ may be produced in the gulf during some unusually warm autumn or in some locality abnormally warm for its latitude probably perish at the onset of winter without leaving issue. In short, the evidence is strong that there is only one annual generation of Cyanea in the Gulf of Maine. Cyanea passes the winter in the attached ("scyphostoma") stage until stimulated to renewed development by the rising temperatures of spring.

Because of its life history, Cyanea is strictly neritic in its faunistic status. It has generally been taken for granted that the American Cyanea, like Aurelia, passes through the attached phase of its life history close to tide mark only, this being the case in European waters where the larvæ are described as attaching themselves to stones, seaweeds, etc., along the strands where their parents are cast up by wind and wave in the storms of autumn (Damas, 1909). So far as I can learn the scyphostoma stage of the American form of Cyanea has not been found at liberty in its natural surroundings, but the fact that the newly liberated medusæ have often been found in partially inclosed waters—e. g., Woods Hole Harbor—and the facility with which the young can be reared from egg to medusa in the aquarium are sufficient evidence that at least a large part of the stock of Cyanea inhabiting the Gulf of Maine is produced in very shoal water. On the other hand, the presence of the young medusæ on Nantucket Shoals, where we saw many very small ones only one-half to 1 inch in diameter floating by the *Halcyon* while tagging codfish on April 23, 1923, and over the western, northern, and eastern parts of Georges Bank, where specimens 2 to 4 inches in diameter were plentiful on July 23, 1916 (stations 10347 and 10348), and August 13–20, 1926, proves that this medusa is equally able to pass through its scyphostoma stage in depths of from 30 to 70 meters.

We have never taken Cyanea smaller than 2 inches in diameter out in the open gulf, except as I have just noted; but by the time they have passed that size and have scattered farther from their birth places in shoal water, we have either captured them or seen them floating on the surface on many occasions and at many localitites in the gulf. Not only is Cyanea a familiar object to fishermen, for it often swarms in the more open bays from Cape Sable to Cape Cod, though never in our experience in the river mouths and other estuarine and slightly brackish situations where Aurelia so abounds (p. 362), but it is dreaded by swimmers with good cause because of its venomous tentacles. On July 29, 1921, for example, hundreds of persons suffered more or less irritation of the skin from touching red jellyfish while bathing at Nantasket Beach near the mouth of Boston Harbor,[99] and the tentacles retain their irritating power for some time after the medusæ strand on the beach.

Most of our locality records for Cyanea (fig. 100) have been from within or at most only a few miles without the 100-meter contour, which corresponds to its neritic nature. It is universal all around the coastal belt of the gulf, the absence of definite records along western Nova Scotia mirroring the fact that we have made no summer hauls there and not a scarcity of Cyanea. No doubt its range also covers the whole of Georges Bank, though the western part of the latter seems more prolific in Cyanea than the eastern. The *Grampus* found rather small specimens (2 to 4 inches in diameter) so plentiful on July 23, 1916 (station 10348), that one half hour's haul with the 1-meter net at 30 meters depth yielded 3 gallons of them. It is probable that Cyanea also occurs on Browns Bank, though we did not chance to find it there on our June and July visits.[100]

Cyanea shows little tendency to drift out into deep water in the northern and northeastern parts of the gulf east of Cape Elizabeth, but we have taken (or seen) it at several stations well out in the basin off Massachusetts Bay and thence southward toward Georges Bank, its distribution agreeing in this with that of other neritic animals as well as with the general distribution of salinity. The presence of a considerable number of rather small (2 to 3 inches) Cyanea floating over the deep basin in longitude 67° 30′ W., some 15 miles north of Georges Shoals on June 25, 1915, is likewise worth noting, though it is not clear whether they came from the neighboring bank or from Cashes Ledge to the north, which is likewise shallow enough to serve as a nursery for this jellyfish. There is nothing in our records to suggest that Cyanea disperses any more widely over the central portion of the gulf in autumn than in summer, and although it is so widespread in the peripheral zone of the gulf and so plentiful at times near shore, we have never found it in any abundance more than a few miles outside the outer headlands except on the offshore banks as just noted.

Cyanea hugs the coast of the Gulf of Maine much more closely than it does the Norwegian coast, where it may drift as much as 250 miles out to sea with the current by September (Damas, 1909). We found Cyanea similarly restricted to the coastal zone within the 100-meter contour from New York southward to Chesapeake Bay during our summer cruises of 1913 (a warm year) and 1916 (a cold year) (Bigelow, 1915, p. 318; 1922, p. 159).

[99] This event was widely reported in the daily press.

[100] For the offshore records for Cyanea see Bigelow, 1914, p. 124; 1915, p. 316; and 1917, p. 303.

It has long been known that Cyanea, like other large medusæ, often acts as a nurse to young fish, especially to gadoids, which live beneath the bells and follow them in their wanderings. In north European waters, where Cyanea often swarms

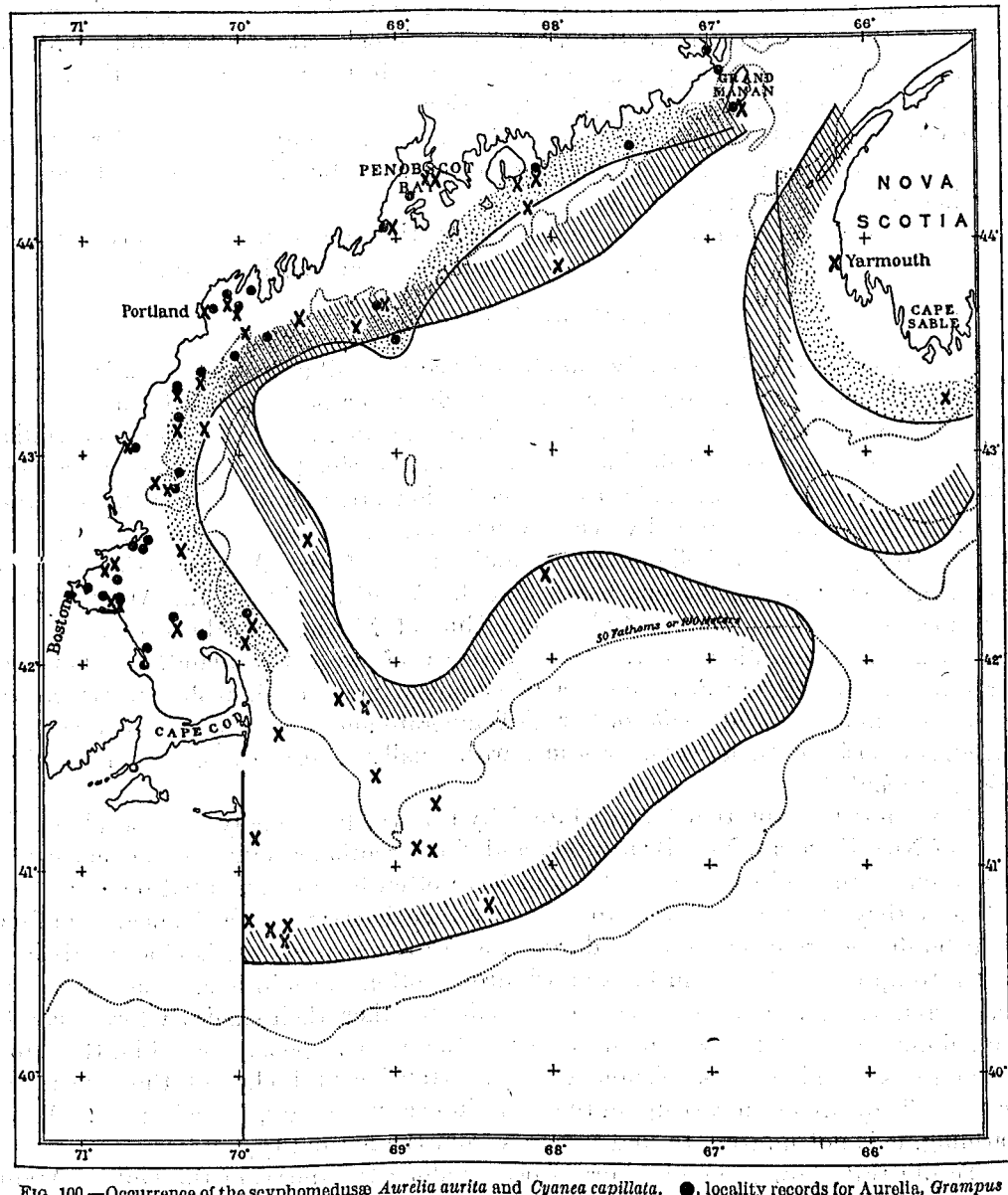


FIG. 100.—Occurrence of the scyphomedusæ *Aurelia aurita* and *Cyanea capillata*. ●, locality records for Aurelia, *Grampus* and *Halcyon* cruises since 1912; X, locality records for Cyanea, *Grampus* and *Halcyon* cruises since 1912. The stippled curve marks the approximate offshore boundary for Aurelia in the Gulf of Maine; the hatched curve the probable offshore boundary for Cyanea

well out at sea, this seems to be the chief means of dispersal for the young of the whiting (*Gadus merlangus;* Damas, 1909a). A large proportion of the European records for the pelagic young of the haddock have also been of specimens taken in

company with these medusæ, and young cod have also been found associating with them. We have found young haddock in company with Cyanea on Georges Bank on one occasion (July 23, 1916, stations 10347 and 10348), as has Huntsman (1922, p. 20) in the St. Andrews region in the Bay of Fundy, but Cyanea is so closely restricted to the neighborhood of the coast and to shoal water in the Gulf of Maine that it can hardly play as important a rôle there as in the northeastern Atlantic and North Sea region, unless it be over Georges Bank.

Young butterfish (*Poronotus triacanthus*) also commonly shelter under Cyanea off the coasts of southern New England (Goode, 1884), but they have not been seen following this habit north of Cape Cod.

The large Cyanea must be extremely destructive to copepods and other planktonic animals, which may usually be found entangled among its curtainlike lips.

### Aurelia aurita (Linné)

The genus Aurelia is probably more nearly cosmopolitan in the coastal waters of all the great oceans than any other neritic medusa, for it is known from Arctic to Tropic latitudes, both in the Atlantic and in the Pacific, as well as from the Indian Ocean. Several supposedly distinct "species" of Aurelia have been described, but it becomes increasingly probable, as one collection after another is examined, that most of these names have actually been given to variants of one wide-ranging Aurelia—the *A. aurita*. This, I believe, is certainly true of the Aurelias that inhabit north European seas, on the one hand, and the American side of the Atlantic from Labrador to the West Indies, Cuba, and Gulf of Mexico, on the other. It still remains an open question whether the Aurelias of west Greenland, the northern shores of Alaska, Bering Sea, the Sea of Okhotsk, and northern Japan, which are separable from the typical *aurita* of boreal-Temperate and Tropic seas by a very complex anastomosis of their canal systems, are actually a distinct species or merely a variety of *aurita*.[1]

The multitudes of this large white jellyfish which annually appear along the coasts of New England, New Brunswick, and Nova Scotia are familiar to every fisherman, yachtsman, and summer visitor and have often been commented on.[2] Indeed, it is lucky they are not venomous to man, like their larger relative Cyanea, or bathers would be driven from our beaches during the Aurelia season. It is characteristic of Aurelia to appear suddenly in lines or windrows, often miles in length, as where two tidal currents meet. On such occasions, in calm weather, their shadowy forms can be seen shimmering as far down in the water as the eye can penetrate, while the white genital rings stand out conspicuously on the translucent bodies of those near the surface. They are often cast up on the shore in heavy weather, to lie in piles. When swarming, it is not unusual to find variants from the normal type.[3]

To illustrate how generally Aurelia occurs along the shores of the Gulf of Maine (fig. 100), I may note that we have encountered it in multitudes in Yarmouth Harbor

[1] The interrelationships of the various Aurelias have been discussed recently by Mayer (1910), Kramp (1913b), and by the author (1913, p. 98).

[2] L. Agassiz (1862, pp. 75 to 78) has given a graphic account of the habits of Aurelia in Massachusetts waters.

[3] I find in my notes that on the evening of July 23, 1912, we "saw one with seven, one with six, and two with five genital rings," the normal number being four, while watching them float by the *Grampus* lying at anchor at Kittery, Me.

(Nova Scotia), about Eastport, in Passamaquoddy Bay, at Grand Manan, about Mount Desert Island, in Penobscot Bay, in Boothbay Harbor, at the mouth of the Kennebec River, in Casco Bay, near Cape Porpoise, in Kittery Harbor, about the Isles of Shoals, in Gloucester Harbor, at many localities and on many occasions in Massachusetts Bay, and off Cape Cod, while I have no doubt that Aurelia may be found in season in every bay, harbor, or river mouth and all along the coast line from Cape Cod to Cape Sable. The localities marked on the accompanying chart fail to do justice to the universal distribution of Aurelia in the coastwise waters of the Gulf because most of our cruises and towings have been carried on outside the outer islands and headlands, whereas Aurelia is most plentiful and appears most regularly in more or less inclosed estuarine waters and bays.

Although Aurelia is so universally plentiful along the coast line of the gulf, it seldom strays more than a few miles offshore. We have only two records of it more than 15 miles from the nearest land, and only one more than a mile or two outside the 100-meter contour (fig. 100).[4] Thus its distribution is more strictly coastwise than that of the red jellyfish (Cyanea, p. 357).

The lack of locality records off western Nova Scotia is not due to any local scarcity of Aurelia (for I have seen it in abundance in Yarmouth Harbor in August) but merely reflects the fact that we have occupied no towing stations close in to this part of the coast during its annual season of plenty.

To emphasize more strongly how closely Aurelia is bound to the coast in the Gulf of Maine, I need only add that whereas it was frequently seen floating on the surface or taken in our tow nets during July and August of 1912, when we did much of our cruising close in along the shore, we saw very few in the open gulf (all of them near land) in July or August, 1913, when we worked mostly outside the 100-meter contour. We had only one specimen during our summer cruise of 1914, when the stations were located well out in the gulf, though Aurelia was plentiful enough during both these summers in bays and harbors. We have not found it on Georges Bank or on Browns Bank, nor has it been recorded from either, though the former is an important center of production for Cyanea (p. 359). Neither is there any record of Aurelia over Nantucket Shoals, although the proximity of Nantucket Island suggests that it will be found there.

The facts of distribution just outlined make it certain that in the Gulf of Maine the attached stage of Aurelia is invariably passed in very shallow water, probably never deeper than 20 meters or so. In fact, many of its planulæ are set free along the tide mark where their parents are cast ashore by the autumn gales. For this reason as well as because of its large size this medusa is perhaps the most trustworthy indicator of coast water in the Gulf of Maine.

Thanks to the definite seasonal periodicity of its occurrence and to the ease with which its early stages may be raised in aquaria, the life history of Aurelia is well known; in fact time has added little but corroboration to Louis Agassiz's (1860 and 1862) account, apart from the details of egg cleavage, histology, etc., which need not concern us here. The course of its life is, briefly, as follows:[5]

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[4] For the offshore records, see Bigelow, 1914, p. 124; 1915, p. 316; 1917, p. 303.

[5] Mayer (1910, p. 626) gives an excellent account of the development of Aurelia and of the different ways in which the formation of the gastrula has been described.

After fertilization the developing eggs remain in small pouches along the free margins of the mouth arms, where, by total and unequal segmentation, they form first a blastula, then a gastrula, and finally a ciliated pear-shaped planula. These planulæ, which swim actively, are shaken loose from the mouth arms of the parent, often accidentally by the stranding of the latter on the beach, and settle to bottom, where they become attached by the wide (anterior) end, to develop into the "scyphostoma," which finally grows to a height of about 4 millimeters with 24 tentacles. The "scyphostoma" then produces as many as 12 disklike "ephyræ," as the young medusæ are called, cutting them off by a series of annular constrictions.

In the northern part of its range one generation of Aurelia is produced each year, the winter being passed in the scyphostoma stage, and the young medusæ appearing later and later in the season from south to north, corresponding to the difference in temperature of the water with the latitude. Thus Bumpus (1898 and 1898a), Hargitt (1905 and 1905a), and Fish (1925) have found both the ephyræ and the slightly older medusæ near Woods Hole from March to May. Many have grown to a diameter of 1 to 2 inches there by April (Mead, 1898) and to 4 to 5 inches by mid May,[6] but few if any Aurelia appear in Massachusetts Bay before May (we found none there during that month in 1915 or in 1920), and it is not until July that they attain their full size of 6 to 10 inches north of Cape Cod.

According to Louis Agassiz (1862, p. 76), the Aurelia off Massachusetts become sexually mature late in July and through August, which I can corroborate, having found the mouth arms of all large adults examined at that season laden with developing eggs and planulæ. No doubt they continue producing young from that time onward, through September and October, until they are destroyed by the autumn gales, which seems to be their normal fate. According to Mayer (1910), Aurelia does not mature until September in the Eastport region, but I have never seen nor heard of one in the Gulf of Maine after October.

It is probable that the breeding season of Aurelia and the seasonal succession of its generations are not so definite in the warmer parts of its range, for I have seen large specimens in April in Santiago Bay, Cuba (according to Mayer (1910) Aurelia matures in May at the Tortugas, Fla.), others collected in Barataria Bay, La., during the last week in September, and half-grown individuals taken in the Indian River, Fla., as late as the second week of December.

### Other Scyphomedusæ

Only one other scyphomedusa (*Phacellophora ornata*) has yet been reported from the inner parts of the Gulf of Maine, and it has been reported so seldom that nothing can yet be said of its distribution, either seasonal or geographic, except that it must be very rare there because it grows to so large a size (up to 18 inches in diameter) that it would be a very conspicuous object if abundant. It has a very wide distribution in latitude, for Browne (1908) has reported a Phacellophora, indistinguishable from the Gulf of Maine species, from the South Atlantic off Montevideo. The recorded captures in the gulf are Eastport, three specimens, 1868 (Verrill, 1869);

[6] An occasional ephyra of Aurelia has been found at Woods Hole as late in the season as mid June. Fish (1925) has also reported its ephyræ there in late summer and early autumn, but it is doubtful whether this second brood survives the winter.

Eastport, one specimen, summer of 1885 (Fewkes, 1888, p. 235); and Western Basin, March 24, 1920, 200–0 meters, *Albatross* station 20087.

*Dactylometra quinquecirrha*, a southern species, is fairly common as far east and north as the Woods Hole region, but has never been taken past Cape Cod.

The bathypelagic *Periphylla hyacinthina* has been credited to Georges Bank.[7] Actually, however, the specimens in question were taken off the southeast slope of the latter well out beyond the 500-meter contour (Smith and Harger, 1874, p. 52, as "*Charybdea hyacinthina*"). *Pelagia cyanella* and the large tropical rhizostome *Stomolophus meleagris* have been reported just outside the 100-meter contour south of Marthas Vineyard (Fewkes, 1886, and Hargitt, 1905a), and the cruises of the *Albatross* from 1883 to 1885 yielded a considerable list of tropical and bathypelagic scyphomedusæ (including Periphylla) outside the edge of the continent abreast of the Gulf of Maine (Smith and Harger, 1874; Verrill, 1885; Fewkes, 1886). However, except as just noted, none of these have ever been taken inside the 500-meter contour off the offshore banks of the gulf or within the latter.[8]

## Ctenophores

### Pleurobrachia pileus (Fabricius)

From the economic standpoint the ctenophore *Pleurobrachia pileus*[9] is the most important pelagic cœlenterate inhabiting the Gulf of Maine, for not only is it extremely voracious and locally abundant beyond all computation, but it is present there throughout the year, not for only a brief season annually, as are Aurelia (p. 362) and Cyanea (p. 357).

The abundance in which Pleurobrachia appears in Massachusetts Bay and elsewhere along the New England coasts in summer and early autumn has often been referred to in literature, but practically nothing was known of its occurrence in the gulf at any other season until the recent systematic exploration was undertaken. During March and April (which is a natural starting point in the seasonal history of any planktonic animal, being the time when vernal warming makes itself felt) we have found Pleurobrachia occurring very generally all around the periphery of the gulf from Cape Cod to Cape Sable (fig. 101), but so closely confined to shoal water that we took it only twice outside the 100-meter contour in the inner parts of the gulf in 1920 and not at all in the basin of the gulf except for the extreme northeastern corner. Nor did we find it on Georges Bank at any of our February, March, or April stations, though it was plentiful on Browns Bank on March 13 (station 20072) and again on April 16 (station 20106).

Our experience in 1915 suggested that Pleurobrachia remains confined to the shoal periphery of the gulf until well into May, if not later, as I have previously noted (Bigelow, 1917, p. 304), but we found it in abundance on the southwestern part of Georges Bank and less plentifully off the seaward slope of the latter on the 17th of that month in 1920 (stations 20128 and 20129), where there had been none

[7] I fell into this error myself (Bigelow, 1914b, p. 27).

[8] See also page 67 for a list of bathypelagic medusæ from our outermost station off Shelbourne, Nova Scotia, Mar. 19, 1920 (station 20077), and page 54 for tropical cœlenterates at the outer station off Georges Bank, July 21, 1914 (station 10218).

[9] For a description, with beautiful figures of the adult, see L. Agassiz, 1849. Mayer (1912) gives a more recent account.

in February. It extends its range offshore in the gulf during the following months until in midsummer and early autumn it is to be expected anywhere north of a line Cape Cod–Cape Sable, both near land and over the deep basin, and with no

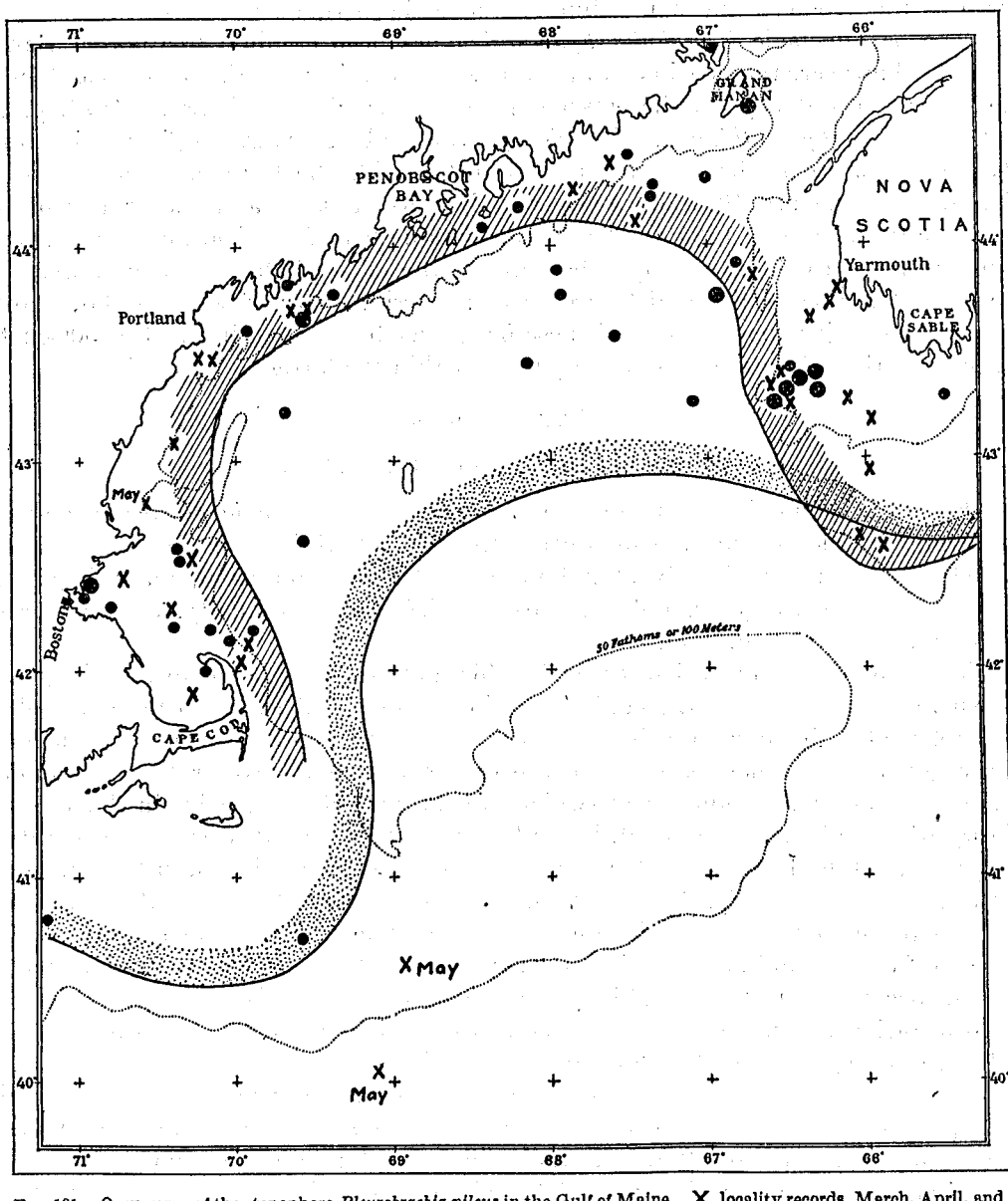


FIG. 101.—Occurrence of the ctenophore *Pleurobrachia pileus* in the Gulf of Maine. X, locality records, March, April, and May; ●, June through September. The hatched curve marks the approximate offshore boundary for this ctenophore in the Gulf in early spring; the stippled curve in summer

decided preponderance of the locality records in one side of the gulf or the other. We have found no Pleurobrachia in the southern deeps of the gulf, in the eastern channel, or over the eastern half of Georges Bank at any season, and the May sta-

tion (20129) just mentioned is our only record for it as far out at sea as the continental slope.

A. Agassiz (1865) describes Pleurobrachia as abundant within Massachusetts Bay in September. In October we have taken it off Cape Cod, off Penobscot Bay, near Mount Desert Island, and off Machias, Me. (Bigelow, 1917, p. 304, stations 10323, 10327, 10328, and 10329), and in Massachusetts Bay and over the western basin abreast of Cape Ann in November (Bigelow, 1914a, p. 403, and station 10401, November 1, 1916). During the last days of December and first week in January of the winter of 1920–21 (*Halcyon* stations 10488, 10491, 10492, 10497, and 10501) it occurred at the mouth of Massachusetts Bay, off Cape Cod, in Ipswich Bay, near Mount Desert, and close to Yarmouth, Nova Scotia, our failure to find it at any of our offshore stations on this last cruise suggesting that its area of distribution in the gulf contracts to the coastal zone as winter advances.

Thus, although Pleurobrachia does not depend on the bottom at any stage in its development, it is more neritic than oceanic in the Gulf of Maine, just as it is over the continental shelf south and west of Cape Cod (Bigelow, 1915, p. 320). This is equally true of it in other seas as well, for although it ranges from the Antarctic Ocean on the south to Spitzbergen on the north (it is not a regular inhabitant of true polar water) and occurs in waters varying as widely in salinity as the Mediterranean, on the one hand, and the inner parts of the Baltic, on the other (Kramp, 1913), it is chiefly confined to the general neighborhood of the land or of the coastal banks and has seldom been taken on the high seas far from the coast (Mortensen, 1912, p. 73).

The region of German Bank and the shoals west of Nova Scotia out to the 100-meter contour generally are the chief and the only constant center of abundance for Pleurobrachia within the limits of the Gulf of Maine. Whether in March, April, May, June, August, September, or in January, we have invariably found these ctenophores, either large or small, swarming there, except that on August 14, 1912, when it abounded at one station (10030), only a few were taken at another close at hand (10029).

We have also seen it in great abundance about Grand Manan in August and have found it numerous off Seguin Island both in August, 1912 (station 10040), and in March (March 4, 1920, station 20058). Rich catches have also been made in Massachusetts Bay in summer and autumn; likewise on April 20, 1920, when Pleurobrachia monopolized the water to the exclusion of almost everything else at a station (20118) in Cape Cod Bay, but when the swarm of these ctenophores was limited to an area so narrow that few of them were taken that same day at a station 30 miles to the northward (station 20119), where they were replaced by a comparatively plentiful Calanus community. The waters over Browns Bank likewise supported an abundance of Pleurobrachia in the spring of 1920, but we have not found it there on our visits in June and July.

Our records do not suggest that any definite ebb and flow takes place in the numbers of Pleurobrachia existant in the Gulf from season to season. There may be a general impoverishment in autumn and winter, but if this actually occurs the

local stock is fully reestablished by the first weeks of spring when (judging from the year 1920) Pleurobrachia may be fully as abundant locally as it is in summer. Its appearances and disappearances are so sporadic, not only in the Gulf of Maine but also in European waters, where it is an equally familiar member of the plankton (Kramp, 1913), that a long-continued series of records of its occurrence will be required before its seasonal fluctuations can be outlined more definitely.

We have no satisfactory data on the absolute numbers in which Pleurobrachia occurs in the Gulf of Maine, but obviously with so large an animal it requires only a fraction as many individuals for the tow-net catches to be measurable by quarts as for creatures as small as copepods to yield very moderate catches. Furthermore, quantitative hauls often fail to afford a true estimate of the local abundance of these ctenophores even when they are plentiful, for they are usually so streaky in their occurrence that the vertical net may catch only a few (or even miss them altogether) at a locality where the horizontal net with its longer journey through the water takes them in multitudes. For example, the quantitative haul yielded Pleurobrachia at the rate of only 220 per square meter of sea surface (less than 10 individuals per cubic meter) off Yarmouth on April 13, 1920 (station 20102), although half an hour's haul of the meter net at 25 meters brought back upwards of 4 liters of them, and a net of 20 centimeters diameter captured 1 liter at the surface. Again, in Massachusetts Bay on March 4, 1920 (station 20058), the vertical net did not yield a single Pleurobrachia (though its catch otherwise showed it to be working properly), whereas many hundreds were taken in the horizontal haul from 30 meters.

*Economic importance.*—Pleurobrachia is an important factor in the economy of waters where it abounds, chiefly as a destroyer of smaller planktonic animals but also in some small degree as food for certain fishes. Wherever these ctenophores swarm they sweep the water so clean and they are so voracious that hardly any smaller creatures can coexist with them. Copepods in particular are locally exterminated in the centers of abundance for Pleurobrachia, though in their own turn they may swarm nearby; and it is common to find these ctenophores packed with copepods or with euphausiid shrimps and larval fishes ingested and partially digested.

There is reason to believe, too, that Pleurobrachia is a serious enemy to the successful reproduction of sundry fishes (e. g., cod and haddock) by feeding on their buoyant eggs (p. 111), few of which can escape destruction in localities where ctenophores are numerous. Indeed, it is doubtful if more than a trifling proportion of the fish eggs of any sort that are spawned on German Bank can survive there, with Pleurobrachia so plentiful in that neighborhood the year round. In short, the local abundance of the latter may well determine the productivity or otherwise of any particular area in the Gulf as a nursery for gadoids or flatfish. Hence, it is fortunate for the inhabitants of New England that the spawning ground for haddock on the eastern part of Georges Bank seems practically free from Pleurobrachia. Neither did we find it in any number on the haddock-spawning grounds off Massachusetts Bay in May, 1920, notwithstanding its local abundance in the southern part of the bay a few weeks earlier (p. 367), nor on the Isles of Shoals–Boon Island grounds in April and May, 1913.

Although Pleurobrachia can hardly be classed as an important food supply for other animals, fish do prey on them more or less. In New England waters this applies especially to the spiny dogfish (p. 105).

Alexander Agassiz, to whom we owe an excellent account of the development of Pleurobrachia, found its eggs in Massachusetts Bay late in July, in August, and in September, when, as he writes (1874, p. 359), "the water round them is filled with eggs floating a few inches below the surface," and when he took the earliest stages after hatching. This, with our own observations, makes it certain that Pleurobrachia is regularly endemic and breeds in large numbers in the Gulf of Maine, of which it is as characteristic an inhabitant as *Calanus finmarchicus* or *Sagitta elegans*. But how many generations are produced there per year is not known. The older view was that there is only one, and that the product of eggs spawned in late summer and autumn live over winter, to mature and spawn in their own turn the following summer. The presence of large Pleurobrachia in winter and spring as well as in midsummer and autumn, together with the various sizes of the individuals which go to make up the different schools in different localities at any given season, makes it more probable that one generation succeeds another irregularly throughout the year.

In spite of conclusive evidence to the contrary, assembled by recent students of ctenophores, Pleurobrachia has often been termed a northern, even an Arctic, form in its occurrence off the New England coast. I must therefore reiterate that this is not the case but that its regular range along the coasts of eastern North America extends southward to Chesapeake Bay; in fact, nearly to Cape Hatteras in the cold season, for I myself have found it plentiful in the waters of Pamlico Sound in winter.

On both coasts of North America Pleurobrachia grows much larger in cool water (10° or colder) than in warm (Bigelow, 1915, p. 322; Esterly, 1914). Judging from the large size (upwards of 30 millimeters long) and local abundance of Pleurobrachia in the Gulf of Maine, the latter is as favorable an environment for it as are the colder waters off Newfoundland and Labrador; and if numbers of individuals present can be trusted as a criterion this applies equally to the coast water off New York and New Jersey, where rather smaller individuals are so abundant in some summers, for instance 1913, that they have been given a vernacular name ("sago") by local fishermen

Pleurobrachia is a creature of the upper strata of water. As Alexander Agassiz (1874, p. 359) remarked long ago, they come to the surface whenever it is smooth, at all times of day; "they are found in the greatest number between the hours of 9 and 11 in the morning, and from 4 to 6 in the afternoon in the summer," which is a common habit of this ctenophore in all parts of the gulf during summer and early autumn. In August, 1912, for example, we made our largest catches of Pleurobrachia at the surface; but they sometimes lie deep throughout the day in midsummer and even in bright calm weather, as was the case on German Bank on August 12, 1913, when we found no Pleurobrachia on the surface at 10 to 11 a. m., although a haul from 40 meters yielded them in abundance. At other times of year this ctenophore occurs more regularly a few meters (say 20 to 30) down than shallower, as exemplified

by the early spring of 1920, which corroborates Alexander Agassiz's suggestion that Pleurobrachia abandons the surface in the cold season.

*Catches of Pleurobrachia in 1920*[1]

| | | | | |
|---|---|---|---|---|
| Off Seguin Island | 20058 | Mar. 4 | Surface | None. |
| | | | 30-0 meters | Many. |
| Off Cape Elizabeth | 20059 | do | Surface | None. |
| | | | 60-0 | Few. |
| Near Isles of Shoals | 20060 | do | Surface | None. |
| | | | 90-0 | Few. |
| Off Boston Harbor | 20062 | Mar. 5 | Surface | Many. |
| | | | 30-0 | Do. |
| Browns Bank | 20072 | Mar. 13 | Surface | None. |
| | | | 75-0 | Many. |
| Off Shelburne, Nova Scotia | 20073 | Mar. 17 | Surface | None. |
| | | | 70-0 | 35. |
| Do | 20074 | Mar. 19 | Surface | None. |
| | | | 125-0 | Few. |
| Do | 20075 | do | Surface | None. |
| | | | 80-0 | Swarm (2 liters) |
| Off Machias, Me | 20080 | Mar. 22 | Surface | None. |
| | | | 40-0 | Many (1 liter). |
| Off Petit Manan | 20081 | Mar. 23 | Surface | None. |
| | | | 140-0 | Occasional. |
| Off Yarmouth, Nova Scotia | 20083 | do | Surface | Do. |
| | | | 30-0 | Many (1 liter) |
| Off Seal Island, Nova Scotia | 20084 | do | Surface | Few. |
| | | | 30-0 | Many. |
| German Bank | 20085 | do | Surface | 100+. |
| | | | 60-0 | Do |
| East side of basin | 20086 | do | Surface | None. |
| | | | 150-0 | Few. |
| Off northern Cape Cod | 20088 | Mar. 24 | Surface | None. |
| | | | 75-0 | Few. |
| Off Cape Ann | 20090 | Apr. 9 | Surface | None. |
| | | | 60 (closing net) | Few. |
| Platts Bank | 20094 | Apr. 10 | Surface | None. |
| | | | 60-0 | Few. |
| Off Cape Elizabeth | 20095 | do | 60-0 | 2. |
| Off Seguin Island | 20096 | do | Surface | Few. |
| | | | 35-0 | Do. |
| Off Mount Desert | 20099 | Apr. 12 | Surface | None. |
| | | | 35-0 | Few. |
| Off Yarmouth, Nova Scotia | 20102 | Apr. 13 | Surface | 12. |
| | | | 30-0 | Many. |
| German Bank | 20103 | Apr. 15 | Surface | None. |
| | | | 60-0 | Swarm. |
| Off Seal Island, Nova Scotia | 20104 | do | Surface | Many. |
| | | | 25-0 | Swarm (4 liters) |
| Browns Bank | 20106 | Apr. 16 | Surface | Few. |
| | | | 40-0 | Many. |
| Off northern Cape Cod | 20117 | Apr. 18 | 40-0 | Few. |
| Cape Cod Bay | 20118 | Apr. 20 | 15-0 | Swarm (6 liters). |
| Massachusetts Bay | 20119 | do | Surface | None. |
| | | | 40-0 | Few. |
| Off Merrimac River | 20122 | May 8 | Surface | None. |
| | | | 65-0 | Few. |
| Southwest part of Georges Bank | 20128 | May 17 | Surface | Many. |
| Continental edge | 20129 | do | Surface | None. |
| | | | 50-0 | Many. |

[1] For records of Pleurobrachia from 1912 to 1916 see Bigelow, 1914, p. 126; 1914a, p. 402; 1915, pp. 318 and 320; 1917, pp. 303 and 304; 1922, p. 158. In the winter of 1920-21 it was taken at stations 10488, 10491, 10492, 10497, and 10501.

In most cases surface hauls alone would not have revealed the existence of the local swarms of Pleurobrachia at these stations, but occasionally they are evenly distributed downward through the upper 30 meters or so of water in the cold season, just as they often are in summer. On the other hand, this ctenophore seldom or never sinks into the deepest strata of the gulf, a statement justified by its absence over the basins as well as by the fact that most of our records and all the richest catches have been from hauls no deeper than 30 to 50 meters.

Since Pleurobrachia is present in the Gulf of Maine throughout the year, it necessarily experiences a wide range of temperature and salinity there. On the one

hand, its habit of rising to the surface on warm summer days brings it into water of 16° and upward, while, on the other, it has been taken in the gulf in water as cold as 2.5°, and there is no reason to doubt that it can survive the minimum to which the temperature of any part of the gulf ever chills. Nor is it surprising to find it in extremes as wide apart as this, for the species is practically eurythermal in its geographic distribution (p. 369). As I have previously pointed out (Bigelow, 1915, p. 323), its optimum salinity in North American waters is from about 32 per mille to about 34 per mille, but since it lives in decidedly more saline water in the North Sea region its absence from the saltest water of the Gulf of Maine does not mean that high salinities are unfavorable to it but is due to its neritic habit and to its preference for the uppermost stratum of water.

It is not unlikely that the vertical movements of Pleurobrachia are influenced by the density of the water in which it lives.[10] Although there does not seem to be any connection between the occurrence of Pleurobrachia and density within a range of 1.022 to 1.026, we have never found it (probably it can not float or swim) in water lighter than 1.022, seldom, indeed, in specific gravity lower than 1.023. On the other hand, the presence of Pleurobrachia has never been established in water heavier than 1.027 in the Gulf of Maine or anywhere off the coast of North America, which may explain its failure to sink into the heavier bottom water of the deep basin of the gulf.

### Mertensia ovum (Fabricius)

This cold-water ctenophore, so abundant in Arctic seas (Mortensen, 1912) and especially along the eastern coasts of Labrador and Newfoundland (Bigelow, 1909a), reaches the Gulf of Maine only as an immigrant from the north and is short ved there. Its faunal status being discussed elsewhere (p. 59), I need only add that recent records of it in the gulf are confined to spring and early summer at the following localities and dates:

Eastern basin, May 6, 1915 (station 10270), in surface, 50–0–meter, and 150–0–meter hauls, a total of about 20 specimens; near Lurcher Shoal, May 10, 1915 (station 10272); off the mouth of Penobscot Bay, June 14, 1915 (station 10287). It is present through a longer season off southern Nova Scotia, for we have taken it along the Shelburne profile both in March, 1920 (stations 20075, 20076, and 20077), and in June, 1915 (stations 10291 and 10294); and off Halifax in August (Bigelow, 1917, p. 249). During some years it appears in the Gulf of Maine in autumn, for Alexander Agassiz (1865, p. 29) records it as "exceedingly common in Eastport Harbor during the month of September," a record indisputable because of his excellent figures and description. Fewkes (1888, p. 212) similarly speaks of it as "the common tentaculated ctenophore" at Eastport and at Grand Manan during the summers of 1885 and 1886, but his failure to mention Pleurobrachia, which is actually so abundant there, suggests the possibility that he confused the two genera.

Large Mertensia are unknown south of Massachusetts Bay, and indeed only one adult has been taken even there (A. Agassiz, 1865), but its young may travel as far west and south as New Jersey during the cold season (Mayer, 1912).

[10] Rose (1913) has experimented on the flotation of this ctenophore in waters of varying densities

### Bolinopsis infundibulum[11] (Müller)

This boreal-Arctic ctenophore is one of the most familiar of pelagic animals along the New England coast, for, as Alexander Agassiz remarked (1865, p. 15), "there is hardly a more common medusa than the *Bolina alata* on our coast." It is equally abundant off Newfoundland and Labrador, in Arctic seas generally, and southward to Norway and Scotland in the eastern Atlantic.

Unfortunately, Bolinopsis is so fragile that the specimens captured by the tow net are usually reduced to a mass of unrecognizable slime among the other plankton, hence our hauls throw no light on its occurrence in the Gulf of Maine. However, we have observed it often enough from the deck of the vessel (for it is a conspicuous and beautiful object at the surface of the water on the calm days so common in July and August) to show that it is to be expected anywhere in the coastal waters of the gulf. It occurs over the deep basin as well (fig. 95), though there we have observed it but rarely (on Georges Bank not at all).[12]

Our earliest spring record for Bolinopsis is May 6 (station 10270), but L. Agassiz (1849) records its presence in Massachusetts Bay in March and April. It is most abundant during the three months July to September, when, like previous observers, I have seen it in numbers in various bays and harbors from Cape Cod to the Bay of Fundy. It apparently disappears after September, for we have no late autumn or winter records of it anywhere in the gulf.

Bolinopsis, like Pleurobrachia, reproduces regularly and abundantly in the gulf. A. Agassiz[13] (1874) found it spawning in late summer and early autumn. This being the only season when large specimens are to be found in the gulf, probably but one generation is produced there annually.

### Beroë cucumis Fabricius[14]

*Beroë cucumis* is as typically oceanic as Aurelia and Cyanea are neritic, and correspondingly it occurs over the basin of the gulf generally as well as in its coastal zone (fig. 102), instead of being chiefly restricted to the latter like the various medusæ that pass part of their lives attached to the bottom. Beroë seems first to have been reported in the Gulf of Maine in 1849, when L. Agassiz noted the occurrence of the genus (as "Idya") at Nahant and on the shores of Massachusetts Bay (L. Agassiz, 1849, p. 365). In 1852 he saw it in numbers in Provincetown Harbor in August, and he writes (1860, p. 272) that in 1858 "it appeared in such quantities upon our coast during the whole summer that at times it would tinge extensive patches of the surface of the sea with its delicate rosy hue during the warmest part of the day."

By 1860 he had established the presence of Beroë from Cape Cod to the Bay of Fundy, and more recent students have found it common all along the New England coast in summer. Being practically cosmopolitan in all oceans—Tropic, Temperate,

[11] Beautifully pictured by L. Agassiz (1849).

[12] For offshore records from 1912 to 1914 see Bigelow, 1914, p. 126; 1915, p. 316; and 1917, p. 303.

[13] A. Agassiz (1865 and 1874) describes and figures stages in its development.

[14] Probably this is the only species of Beroë which occurs in the gulf; at any rate all Gulf of Maine specimens examined so far, which have been in condition good enough to show critical characters, have proved to belong to it. For general accounts of the genus, of the interrelationships and general distribution of its several members, and of its development see A. Agassiz (1874), Mayer (1912), and Mortensen (1912).

as well as Arctic—indifferently on the high seas and in such inland waters as the Baltic (Mortensen, 1912; Kramp, 1913), *Beroë cucumis* was to be expected in the central parts of the Gulf of Maine as well as in its coastal belt; but it was only with

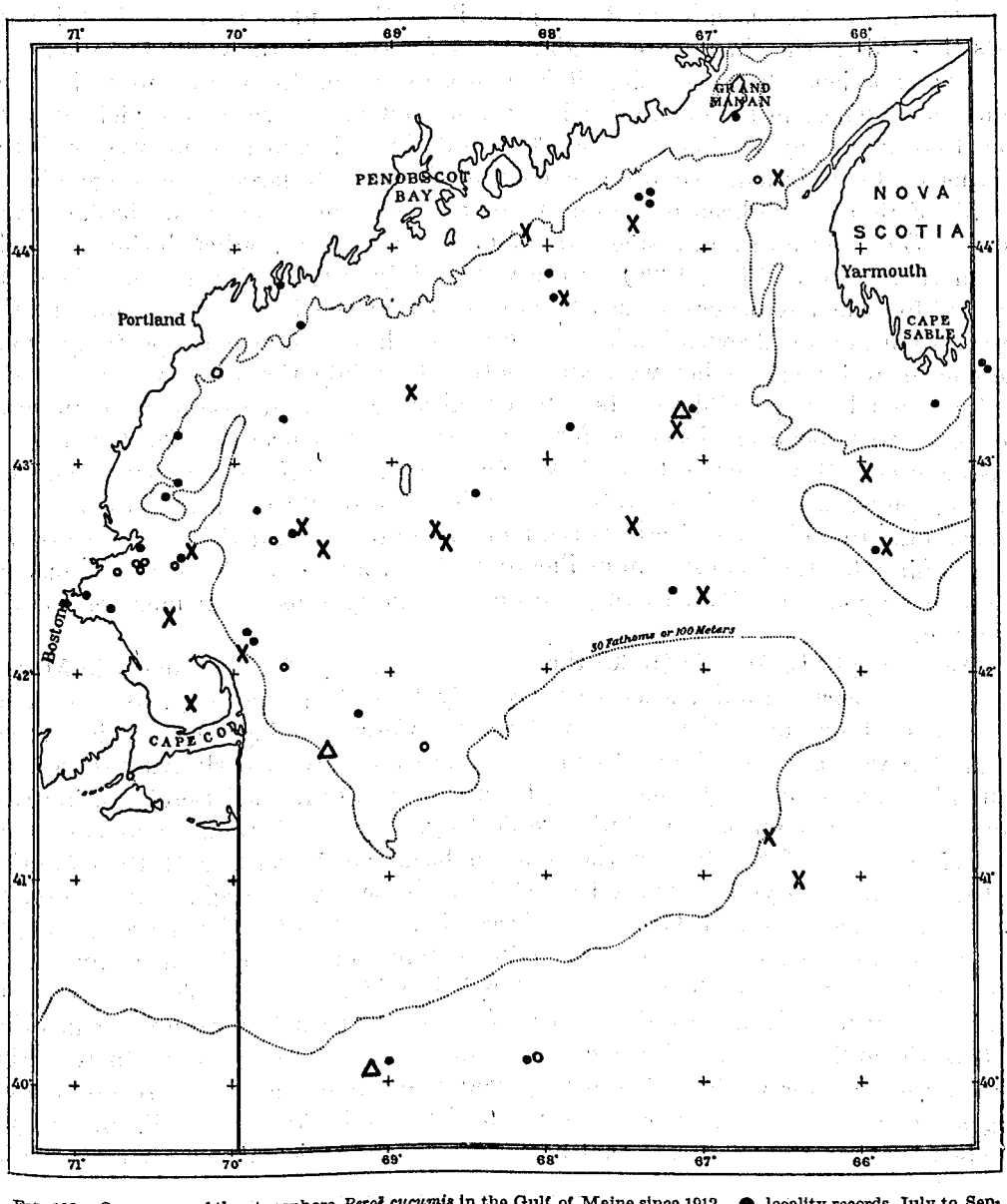


FIG. 102.—Occurrence of the ctenophore *Beroë cucumis* in the Gulf of Maine since 1912. ●, locality records, July to September 15; O, November through February; X, March and April; △, May and June

the inception of the present explorations that definite information of its presence and distribution there was obtained.

Our locality records for Beroë (fig. 102) show that it is universal in the gulf north of Georges Bank, with the actual captures distributed indifferently over the deep

basin and the shoaler coastwise zone, except that we have not found it over the coastal banks along western Nova Scotia—that is, German Bank and near Lurcher Shoal. It is probable, however, that we have simply missed it there. The concentration of records in the Massachusetts Bay region, if anything more than accidental, suggests that this is the chief center of abundance for Beroë in the Gulf of Maine.[15]

Our experience has been that it is a rare event for Beroë to appear in large numbers anywhere in the open gulf; in fact, our tow nets have seldom yielded more than 15 or 20 at any station—a population quite insignificant as compared with the swarms of Pleurobrachia so often encountered—while a large percentage of our records of Beroë have been based on one or two specimens each or on broken fragments. Our failure to find a single Beroë on Georges Bank, either during the cold season (February to May, 1920) or the warm (July, 1914 and 1916) is difficult to account for when it occurs so nearly universally in the basin a few miles to the north, is not rare on Browns Bank to the east, and has been taken repeatedly along the continental shelf farther west and south. Certainly the shoal water over the bank can not be responsible for its apparent absence there, for Beroë is common at still shallower localities inshore—for instance, at Provincetown Harbor and in Massachusetts Bay—nor is there anything in temperature or salinity to suggest that the physical state of the water on the bank is locally unsuitable for it. Nor is our failure to find it over German Bank on any of our several visits to that locality less puzzling, for the local swarm of Pleurobrachia would serve Beroë as food instead of preying upon the latter, as they do on the sundry crustacean members of the plankton.

According to L. Agassiz (1860) the earliest specimens of Beroë appear in Massachusetts Bay early in July, when they are only 1 to 1½ inches long, to grow there to three or four times that size by August. Corresponding to this time-table, Alexander Agassiz (1874) found them spawning from July or early August to early September, and took the young stages, from egg to fully formed Beroë, during that same season. Not all of the adults are destroyed by the September storms, as L. Agassiz supposed, for a tow in the western basin on November 1, 1916 (station 10401, 80–0 meters) yielded many fragments of Beroë with turgid sexual organs, and the 75–0 meter tow off Gloucester, December 29, 1920 (station 10489), brought back parts of one which must have been 40 to 50 millimeters high when alive—that is, it was large enough to be mature. Thus it is evident that Beroë breeds more or less regularly until well into December off Massachusetts Bay (probably in other parts of the gulf as well), and it is certain that a few mature and breed there during the later winter, for we have taken very young specimens less than 10 millimeters long at several stations in various parts of the gulf in March, April, and May.[16] The fact that most of the Beroë that have been taken in the gulf between November

[15] For locality records for 1913 and 1914 see Bigelow, 1915, p. 316, and 1917, p. 303. It was also taken (or seen floating) at stations 10002, 10006, 10007, 10009, 10011, 10012b, 10019, 10023, 10036, 10040, 10043, and 10047 in 1912; at stations 20044, 20050, 20052, 20053, 20055, 20056, 20067, 20068, 20071, 20079, 20081, 20086, 20087, 20088, 20097, 20105, 20112, 20114, 20115, 20118, 20119, 20126, and 20129 in the spring of 1920; and at stations 10488, 10489, 10491, and 10494 during December, 1920, and January, 1921.

[16] Center of gulf, Mar. 3, station 20053; off Mount Desert Rock, Mar. 3, station 20055; between Mount Desert Rock and Mount Desert Island, Mar. 3, station 20056; southeast slope of Georges Bank, Mar. 12, station 20067; Browns Bank, Mar. 13, station 20072; Fundy Deep, Mar. 22, station 20079; northern channel between Browns Bank and Cape Sable, Apr. 15, station 20105; southeast of Cape Cod, May 17, station 20126; and on the southwest slope of Georges Bank, May 17, station 20129; all in 1920.

and May have been small (15 to 20 mm. long) and immature—that is, were the product of the spawnings of the preceding summer and autumn—is evidence that no considerable production of this ctenophore takes place in the Gulf of Maine during the cold half of the year, and it is probable that the coming of spring sees the stock of this ctenophore at its lowest ebb for the year in all parts of the gulf.

Beroës 30 millimeters long and upwards, such as we have taken in mid-April in Massachusetts Bay (station 20119), may be expected to grow so rapidly under the favorable conditions of food supply and temperature prevailing in May as to attain spawning size in June or early in July at latest. It is probable that the few that spawn in winter are the offspring of these early summer spawners, the development of those produced in late summer and autumn being arrested by the low temperature of winter, so that they do not mature until the following summer. Thus, particular groups of Beroë may produce either one or two broods per year, according to the rapidity with which they grow and the season at which they mature; and while the chief production takes place from July to September, probably some spawn at all seasons except perhaps in early spring.

It is worth emphasis here that A. Agassiz's studies on the development of this ctenophore, corroborated by our own captures of its young in almost every month and at localities widely scattered, prove that Beroë is regularly endemic in the gulf, hence that the maintenance of the local stock depends chiefly on local production though it may be recruited more or less by immigration.

Recent captures of Beroë support the suggestion made by Louis and Alexander Agassiz that it passes the winter at some little depth, for only 4 of our records for the cold half of the year (November to April) out of a total of 30 (and these for occasional specimens only) were from the surface, with one other from a 15-meter haul (Cape Cod Bay, station 20118, April 20, 1920). All our other winter–early spring captures of Beroë have been from depths of 40 meters and more. It may sink to a considerable depth in the Gulf during the cold season, for we took it with the closing net at 140–160 meters, and at 125–190 meters in the central part of the basin, March 2 and 3, 1920 (stations 20052 and 20053).

In summer Beroë frequently comes to the surface, most often during the midday hours, to sink again toward the end of the afternoon. This habit, long ago described by Louis Agassiz (1860) as well as by more recent authors, has repeatedly come under our own observation on the *Grampus*, notably during July and August of 1912, when we frequently saw large specimens of this ctenophore floating alongside the ship, usually in calm weather. On stormy days Beroë lies deeper, probably sinking below the limit of destructive wave action, and it is frequently taken at depths of 40 to 100 meters, summer as well as winter. We have no evidence that this ctenophore ever descends into the deepest strata of the Gulf of Maine at any season (a single Beroë taken in a haul from 240 meters in the southeast part of the basin, July 23, 1914, station 10225, may have been picked up by the net on its journey down or up).

The voracity of Beroë being commented on elsewhere (p. 108), I need only remark here that it has been described as preying greedily on other ctenophores in the Gulf of Maine, devouring Pleurobrachia and Bolinopsis whole if they are not too large for its widely distensible mouth to engulf, with digestive process so rapid that

a large Bolinopsis is completely absorbed by a Beroë in four or five hours' time (L. Agassiz, 1860, p. 274). Copepods, also, are often found in its digestive cavity.

Beroë, like all the other pelagic animals that inhabit the gulf throughout the year and are widely distributed there vertically as well as horizontally, necessarily experiences nearly the whole gamut of temperatures and salinities that prevail there at one season or another; and although its habit of sinking in winter results (whether voluntarily or not) in its avoiding the very coldest water, with 2 to 3° the lower limit to its regular occurrence in the gulf, it has been found living actually among the ice in the Arctic Ocean (Mortensen, 1912), apparently thriving, to judge from the large size of the specimens in question. Nor does heat act as a barrier to its vertical migrations within the extremes normal to the gulf—witness how often it comes to the surface on calm days in summer and how abundantly it spawns at that level at the season when the gulf as a whole is at its warmest. Beroë is equally catholic with respect to salinity, except that it has not been found in the very freshest water of the gulf at the time of the spring freshets—that is, in salinities lower than about 31 per mille.

### Other ctenophores

No other ctenophores have actually been recorded of recent years within the geographic confines of the Gulf of Maine as here limited. Another lobate species, *Lesueuria hyboptera*, was described by A. Agassiz (1865) from Massachusetts Bay, but has never been seen since. Mayer (1912, p. 20) has suggested that it was actually Bolinopsis with the oral lobes torn off and the edges healed over to produce a rounded contour, he having seen many in that condition in Halifax harbor after a storm. Its status remains problematical.

*Mnemiopsis leidyi*, a southern neritic form very abundant along the coasts of the middle Atlantic States, is common as far north as the Woods Hole region during some summers, but it has never been known to round Cape Cod.

The Venus' girdle (*Cestum veneris*) was taken off the southeastern slope of Georges Bank in 1872, among an assemblage of other tropical plankton (Smith and Harger, 1874).

## Siphonophores

Although the siphonophores are well represented in the warm oceanic waters off the continental slope abreast of the Gulf of Maine, only one member of this group of oceanic cœlenterates—*Stephanomia cara*—is anything but a rare stray within the latter. It is probable that the low salinity of the gulf, as much as its comparatively low temperature, makes it inhospitable to siphonophores, for, as I have previously pointed out (Bigelow, 1911a, p. 381), they "are almost a negligible factor in the plankton in waters with a salinity less than 35 per mille" and "are entirely absent when the salinity is below about 30 per mille," a generalization that applies as well to the North Sea region on the eastern side of the North Atlantic as to North American coastal waters on the western.

**Stephanomia cara (A. Agassiz)**

Although this siphonophore is widely distributed in the gulf both in time and in space, we know little more of its natural history or of its status in the economy of the plankton than when Alexander Agassiz (1865) first recorded and beautifully pictured young specimens of it from Massachusetts Bay; and although Fewkes (1888) has since given a description and figures of the adult, it is still doubtful whether the "*S. cara*" of northern seas is identical with or distinct from the "*S. bijuga*" of warmer latitudes. Unfortunately our Gulf of Maine collections can not settle this question, because these very delicate animals are usually battered almost past recognition in the tow nets; but the presence of a spherical red or yellow oil globule at the base of each palpon (a conspicuous character first described by Fewkes and visible in the least damaged of the Gulf of Maine series) is apparently peculiar to the northern *cara*, and since *cara* grows much larger than its warm-water relative, besides differing from it in minor anatomical details, it probably deserves recognition as a distinct species. The relative ranges of the two—*cara* and *bijuga*—are consistent with this, for while *S. cara* is common in the Gulf of Maine [17] we did not find it along the coast south or west of Cape Cod during the summers of 1913 or 1916, the autumn of 1916, the winter of 1914 (Bigelow, 1918), or in February of 1920. On the other hand, the southern *bijuga* is not known to occur north of Key West in the western Atlantic, which leaves a gap of something like a thousand miles between the southern limit of the one and the northern limit of the other, as now known. Similarly, there is a long gap between the most southerly known record of the northern and most northerly record of the southern race or species in the eastern Atlantic.

Just what relationship the *S. cara* of North American waters bears to the Arctic-boreal Stephanomia of the northeastern Atlantic is also uncertain, no detailed account having appeared of the specimens most recently recorded thence (Sloan, 1891; Browne, 1900); but probably the two are identical; in fact, it would run counter to all our experience of the northern pelagic fauna as a whole to find them otherwise.

During our recent cruises we encountered Stephanomia in the months of January, March, July, August, September, and December, and at the various localities indicated on the chart (fig. 103), but it is not safe to base a definite statement of its status in the gulf on these records, both because it is decidedly erratic in its occurrence and because its bells are so fragile that they are apt to be battered past recognition by the other plankton taken with them in the tow nets.

Stephanomia may usually be found in one part of the gulf or another during the summer months, but it can not be very generally distributed at that season, for we have never taken it at more than a small percentage of our stations during any one summer's cruise. In 1913, for example, it was detected at three stations only, once, however, in abundance (p. 19; station 10058). There are only four records of it in the July and August towings of 1914; none for 1916. If the years 1920 and 1921 can be taken as representative, it is decidedly more abundant and widespread during the winter, for it occurred at about half our December and Janu-

[17] Some long-stemmed physophore, and probably this species, ranges northward as far as Lady Franklin Bay on the west coast of Greenland (Fewkes, 1888a) and to Robeson Channel (Moss, 1878).

ary stations and again at four stations in early March, 1921; but it was detected at one station only (20048) in February, 1920, and not at all during that March, April,

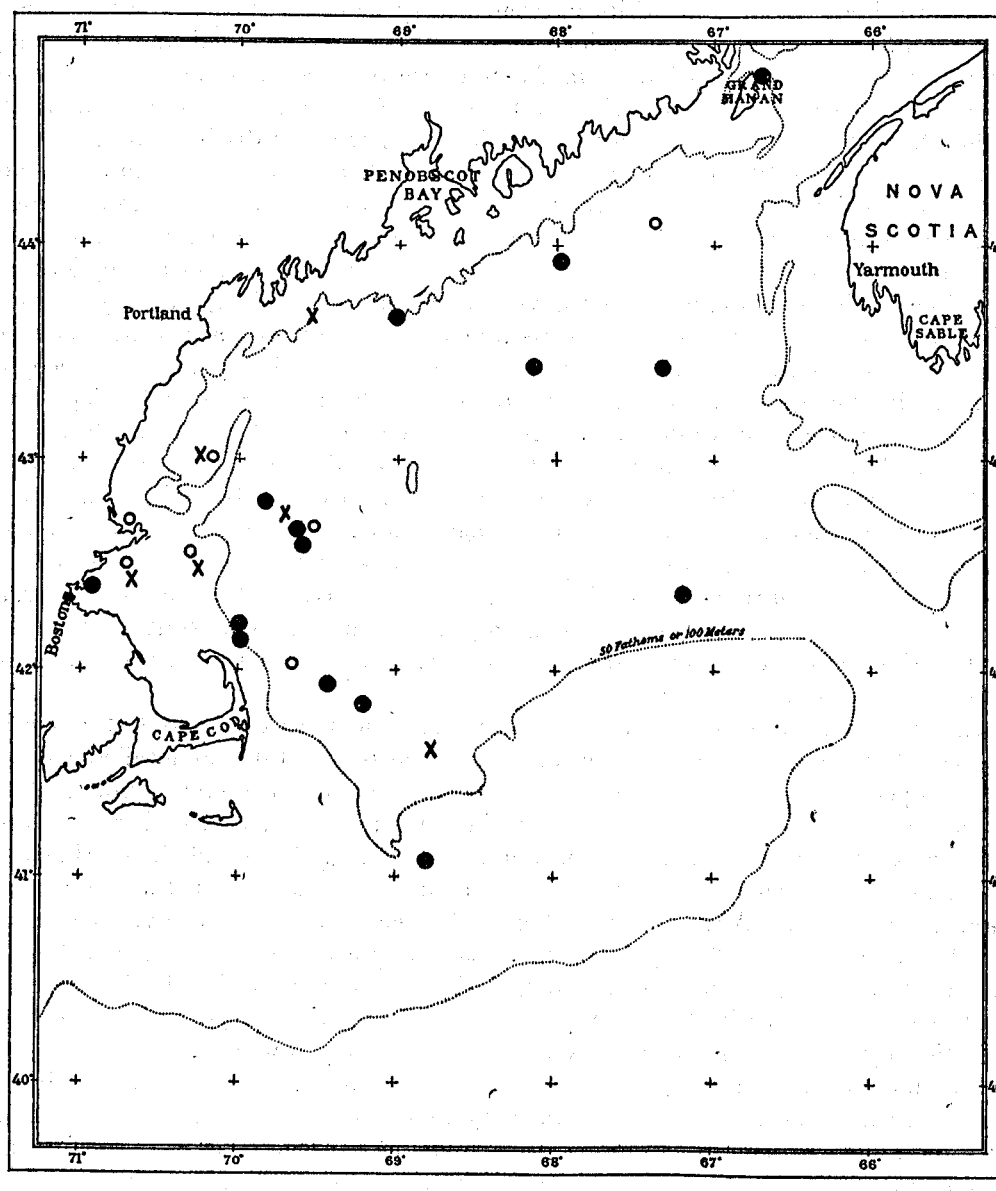


FIG. 103.—Occurrence of the siphonophore *Stephanomia cara* in the Gulf of Maine. ●, locality records, June through November; ○, December, January, and February; X, March through May

or May, in spite of the considerable number of tows, both horizontal and vertical, made during that cruise. Neither did we find it in May or June of 1915.[18]

[18] For records of Stephanomia from 1912 to 1914, see Bigelow, 1914, p. 126 (as "*Agalma elegans*"); 1915, p. 316; and 1917, pp. 303 and 306. Fragments tentatively referred to it were taken at stations 10488, 10489 to 10491, 10493, 10497, 10502, 10508, 10509, 10510, and 10511 during the winter and early spring of 1920–1921

The obvious inference from this is that there is a winter maximum and spring minimum for Stephanomia in the Gulf of Maine. Other years might yield quite different results, however, and it is questionable whether the concentration of Stephanomia in the southwestern part of the gulf, suggested by the chart (fig. 103), and its apparent rarity in the southeastern part and on Georges Bank, are anything more than accidental, especially when we remember that the neighborhood of Grand Manan is the only locality in the gulf where it has ever been found of large size (Fewkes, 1888).

Alexander Agassiz's (1865) discovery of very young stages of this species in Massachusetts Bay in early summer is undeniable evidence that it breeds in the gulf, but how regularly it does so from year to year, what proportion of the local stock results from local reproduction and what from immigration, and what relationship the fluctuations in the local stock of Stephanomia bear to hydrographic conditions are questions for the future.

### Diphyes arctica Chun

The faunal status of this species is discussed in an earlier chapter (p. 64). The Gulf of Maine records are as follows: Southeast slope of Georges Bank, July 22, 1914 (station 10220); outside the continental edge off Shelburne, Nova Scotia, June 24, 1915 (station 10295), and March 19, 1920 (station 20077); near Lurcher Shoal and in the Eastern Channel, April 12 and 16, 1920 (stations 20101 and 20107).

### Other siphonophores

The occurrence of Physophora and Physalia is discussed above (p. 55). To complete the record of the group in the Gulf of Maine I have only to mention a single *Diphyes truncata*[19] from the northeast slope of Georges Bank, July 22, 1914 (station 10220), a few more examples of this species from our deep stations off its southwest face in February and May, 1920 (stations 20044 and 20129), and two taken in the northeastern basin of the gulf off Grand Manan on April 12 of that same year (station 20101). The beautiful *Agalma elegans*, so common in the inner edge of the Gulf Stream and which sometimes even reaches the coast west of Cape Cod (Fewkes, 1881), has never been taken within the Gulf of Maine.[20]

## Pelagic hydroids

In an earlier chapter (p. 33) the floating hydroids that we have encountered over Georges Bank are mentioned. The records on which this observation is based are as follows:

On April 14, 26, and 27, 1913, campanularian hydroids were found floating on the top of the water over the bank (Bigelow, 1914a, p. 414; lat. 41° 37′ N., long. 67° 18′ W., and about lat. 41° 40′ long. 68° 30′), some of the specimens being complete—that is, with all the ends of the stems rounded, closed, and apparently growing, as Dr. S. F. Clarke reported on examining them. On the 9th of the following July

[19] For a discussion of this species see Bigelow, 1913, p. 73; 1918, p. 422; and Moser, 1913, p. 232.

[20] Agalmid fragments taken during the summer cruise of the *Grampus* in 1912 were provisionally referred to this species, but subsequent study leads me to believe that they were in reality the common *Stephanomia cara* (p. 378)

our surface net took great numbers of them over the northwest part of the bank (station 10059). These were submitted to Dr. C. McLean Fraser for study, and the reader is referred to his report (in Bigelow, 1915, pp. 268 and 306) for details. It will suffice to say here that the catch of hydroids was not only considerable in amount but included no less than 13 species, belonging to 4 families. Most of these were represented by broken fragments only, or by colonies attached to bits of eelgrass (Zostera); but the hundreds of colonies of *Clytia cylindrica* (the predominant species) were floating free of any support, and not only in a perfectly healthy state as far as appearances go, but so completely regenerated that there were few or no broken ends visible.

As it can hardly be supposed that these colonies had passed through their whole development, from the planula stage onward, at the surface of the sea, the most reasonable explanation for their presence afloat is that they had been torn from their attachments on the bottom by the strong tidal currents and kept suspended in the water by this agency. Finding a rich food supply in their pelagic surroundings, with nothing fatal in such an environment, they regenerate, grow, and even propagate their kind, as appears from their development of gonophores. After all, there is nothing surprising in such a phenomenon, for it is "not unusual to find fragments of hydroid colonies torn from their support or from the rest of the colonies, living for a considerable time as they float on the surface" (Fraser, 1915, p. 307). Similar congregations of floating hydroids have been encountered thrice since 1913, always on Georges Bank—viz., July 23, 1914 (station 10224), July 23, 1916 (stations 10347 and 10348), and February 23, 1920 (station 20047). Judging from the geographical grouping of these stations (fig. 98) their place of origin is probably on the shallows known as "Georges" and the "Cultivator" Shoals.

## SECTION 2.—GENERAL SURVEY OF THE PLANKTONIC PLANTS (PHYTOPLANKTON) AND UNICELLULAR ANIMALS

Unicellular pelagic plants, or, to use the more convenient term, "phytoplankton," play as large a rôle in the natural economy of the Gulf of Maine as in other boreal seas. Strangely enough, however, systematic collection and examination of them in this particular region date back only to 1912 (Bigelow, 1914). Since then many hauls of phytoplankton have been made in the offshore parts of the Gulf of Maine, but time and the assistance available have so far allowed only a preliminary examination of these. Besides these records for the open sea in the gulf, McMurrich (1917), Bailey (1910, 1915, and 1917), Bailey and Mackay (1921), and Fritz (1921) have published valuable surveys of the phytoplankton (particularly the diatoms) from the estuarine waters near the Canadian biological station at St. Andrews in the Bay of Fundy, and in addition Doctor McMurrich has very kindly allowed the use of his unpublished notes, to which frequent reference will be found in the following pages.

Gran (1912) has recently given such an excellent and readable account of the phytoplankton of the high seas as a whole and of the rôle it plays in the economy of nature that no general survey is called for here. Suffice it to say that these unicellular algæ are the chief marine producers (organisms, that is, capable of elaborating organic compounds from inorganic substances in sunlight) and the only producers over the high seas outside the narrow coastal zone within which seaweeds flourish. I do not know who first paraphrased the expression "all flesh is grass" with the words "all fish is diatoms," but if not taken too literally it expresses the fundamental truth that the whole system of animal life in the sea (as on land) depends on plants in the last analysis and chiefly on the tiny unicellular algæ, which we often capture in millions in our tow nets.

The groups that play the major rôles in the phytoplankton of the Gulf of Maine, as well as in other northern seas, are the diatoms and the peridinians, which alternate in more or less regular seasonal succession, to be described below; and since the value of the following account depends chiefly on the correct identification of the several species, a word on this subject will be germane here. The diatoms are proverbially a "difficult" group because fresh and brackish waters support a multitude of species, which are separable one from another only by most painstaking study with the microscope. Fortunately, however, although the planktonic diatoms are probably the most numerous of all marine organisms in number of individuals, the species occurring regularly in the plankton of northern seas are comparatively few,[21] while those that dominate the northern planktonic communities at one time or another (and these are, of course, the most important from both the geographic and the

[21] Gran (1908) lists about 170 species as typically pelagic in boreal-Arctic waters.

ecologic standpoints) are fewer still. Until comparatively recently the identification of even these few could hardly be attempted by anyone not a specialist in the group, but thanks to Gran's (1908) excellent synopsis, to Meunier's (1910) beautiful figures, and to the fact that most of the important species are distinguished by rather precise characters, they are now no more difficult to name than are other planktonic groups; far less so, for instance, than the smaller copepods. A certain number of species, of course, are hardly to be determined except under most favorable circumstances. For example, certain members of the genus Chætoceras are separable only when carrying their resting spores, but these are in the minority. It chances that most of the diatoms that are prominent numerically in the phytoplankton of our gulf at one time or another—for example, the members of the genera Thalassiosira and Rhizosolenia and most of the predominant members of the genus Chætoceras—are characterized by such well-marked structural features that no one trained in systematics in general and in the study of marine plankton in particular should experience any unusual difficulty in referring them to their respective species by Gran's (1908) tabular keys. What is required for this is close observation of small characters, often under high powers of the microscope; but the technique is simple, amounting usually to nothing more than examination in water or in formalin—at most to the drying process employed by Gran (1908, p. 6) or to one of the modes of mounting described by Mann (1922). The complicated methods of cleaning, so valuable in the study of estuarine and bottom-living diatoms as a whole, are not essential when the object in view is merely the identification of the comparatively large and already well-known species of marine planktonic diatoms preserved in formalin as taken from the tow net.

Since no attempt is made in the present paper to contribute to the systematics of marine diatoms, the nomenclature follows Gran (1908) strictly, except as noted below. The identification of the representative lists (p. 423) having been verified by Dr. Albert Mann, a leading student of the group, they are offered with some confidence, although the catches still await final examination.

The peridinian element in the plankton of the gulf is represented chiefly by members of two genera—Ceratium and Peridinium—genera so unlike in appearance as to be separable at a glance; and while a good deal of discussion has centered about the relationships, specific, varietal, or genetic, of the numerous representatives of Ceratium (which is usually the dominant peridinian in the Gulf of Maine), it is not difficult to refer the specimens in question to the proper subgroup—call it species or what you will—by the use of Paulsen's (1908) recent synopsis. The following identifications follow him strictly. Fortunately the naked peridinians,[22] which are not only far more difficult to discriminate among but apt to be mashed past recognition in the nets, have never been prominent in our tows; in fact, never detected except for a brief period in the spring (p. 417).

[22] For descriptions and beautiful figures of these the reader is referred to Kofoid and Swezy's (1921) monograph.

## PHYTOPLANKTONIC COMMUNITIES

Although our studies in the Gulf of Maine are in their infancy, as compared with the intensive surveys that have been made in north European waters, they have progressed sufficiently to give a general idea of the groups of microscopic plants primarily concerned, and of their seasonal alterations; and although periodic or sporadic fluctuations are to be expected in the composition of the pelagic communities, the seasonal cycle here outlined and the accompanying charts, based on our tow-net hauls, are offered with some confidence as representing what may be called the basic status of the phytoplankton of the Gulf of Maine.

It is necessary to select some arbitrary starting point in describing the general seasonal succession of diatoms, peridinians, and other groups, though necessarily this is an artificial one because the planktonic cycle is uninterrupted from year's end to year's end. Perhaps the most convenient is the status late in February or during the first days of March, when the phytoplanktonic community falls to its lowest ebb over the Gulf of Maine as a whole, just prior to the vernal awakening that takes place in the sea as well as on the land. Unfortunately our data for the open gulf at this season are not all that could be desired, for although the *Albatross* made a general planktonic survey of the gulf between the 22d of February and the 24th of March in 1920, this, as it proved, did not altogether forestall the earliest flowerings of diatoms. But from this cruise, added to winter tow nettings made in 1912 and 1913 (Bigelow, 1914a), and during December to January, 1920–1921, and from the counts of diatoms tabulated by Fritz (1921), it is safe to assert that when the temperature of the gulf is at its minimum for the year, just prior to the first trace of spring warming, its offshore waters as a whole and the estuarine tributaries of the Bay of Fundy [23] support only a very scanty phytoplankton, in which peridinians (p. 407) and oceanic diatoms mingle (fig. 104), except that vernal flowerings of diatoms are already under way locally along its northwestern shore and over the western part of Georges Bank. In 1920 this description applied to the entire basin of the gulf as well as to the eastern part of Georges Bank, at least up until the middle of March. But flowerings of diatoms, resulting in local swarms so dense as to be the most spectacular event in the yearly planktonic cycle, were already under way along a narrow coastal zone between Cape Ann and Cape Elizabeth by the first week of that month (stations 20059 and 20060), and their future expansion was foreshadowed even thus early in the season by the fact that diatoms in small numbers had replaced the peridinians as far east along the coast as Mount Desert Island, on the one hand (stations 20056 and 20058), and bulked about as large as the peridinians in a very sparse phytoplankton off Gloucester on March 1, on the other (station 20050; genera Coscinodiscus and Thalassiosira). On March 4, 1913, diatoms dominated near this last locality, and on March 5, 1920 (station 20061), we found a pure diatom plankton with only an occasional peridinian; but on both these occasions the total catch of phytoplankton was still very scanty. As April 3 (Bigelow, 1914a, p. 405) is the earliest date when we have found diatoms in great abundance at the mouth of Mas-

[23] No planktonic data are yet available for other inclosed waters or harbors around the gulf at this season.

sachusetts Bay, it is not likely that the vernal flowerings become active there until after the middle of March—that is, at least three weeks later than in the waters between Cape Ann and Cape Elizabeth, or in Cape Cod Bay (p. 396).

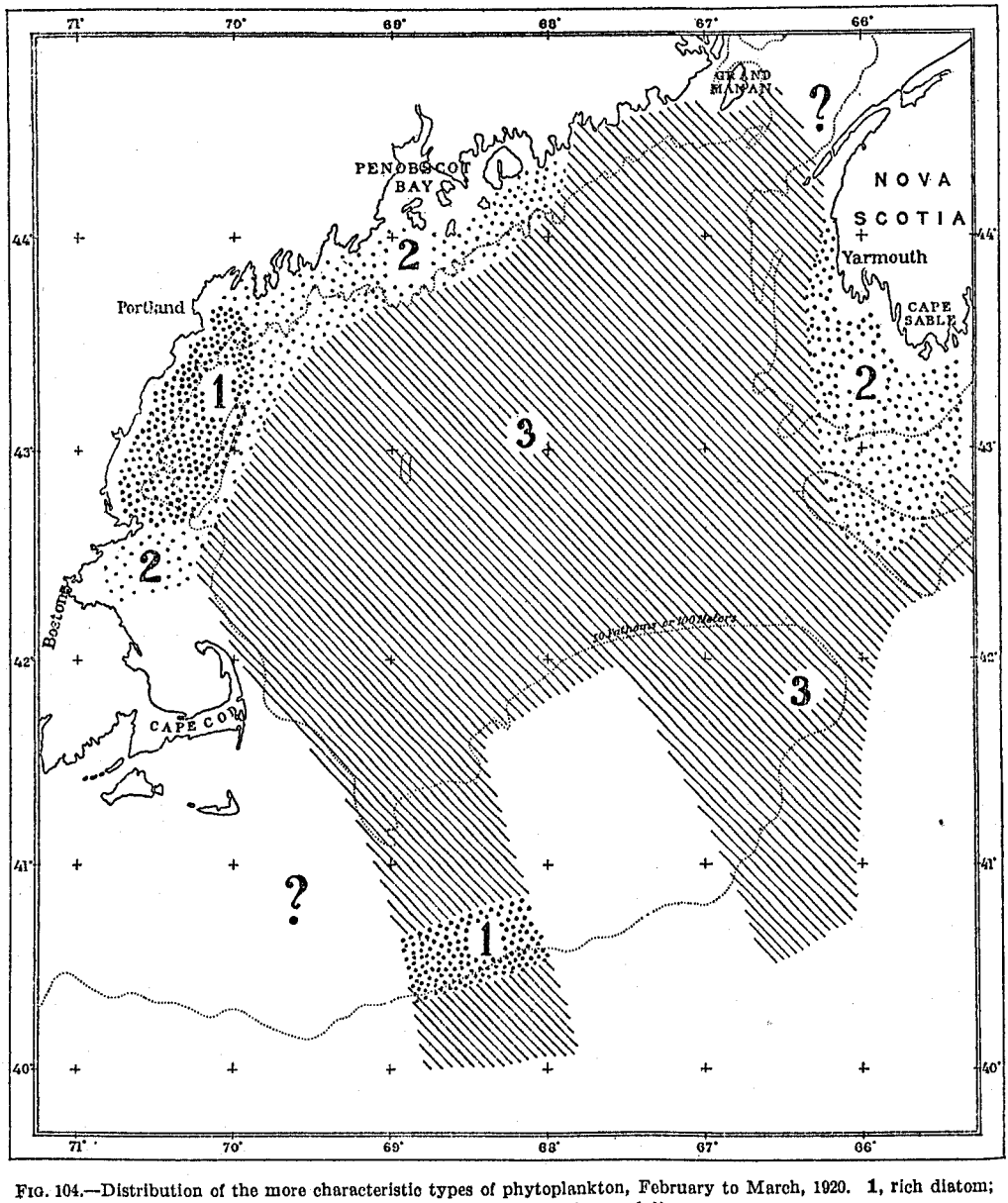


FIG. 104.—Distribution of the more characteristic types of phytoplankton, February to March, 1920. 1, rich diatom; 2, sparse diatom; 3, sparse Ceratium and diatom

The shallow waters off western and southern Nova Scotia, out to and including German and Browns Banks, are the site of a second center of propagation for diatoms late in March, for though the phytoplankton was still very scanty there on

the 23d of that month in 1920 (stations 20078 and 20082 to 20085), it consisted chiefly of diatoms with few peridinians; and by April 15 (stations 20101 and 20103 to 20106) the waters in this part of the gulf were cloudy with neritic diatoms of the species listed below (p. 427). A rich diatom community was also discovered by the *Albatross* on the southwestern part of Georges Bank even earlier in the year (February 22, station 20046).

The diatom flowerings of the western side of the gulf expand in all directions and at the same time multiply so rapidly during the last half of March that their numbers are soon countless. By the 3d of April we have found them so abundant in Massachusetts Bay as to cloud the water and clog our nets (Bigelow, 1914a, p. 405), a state again observed from the 6th to the 9th of April in 1920 (stations 20089 and 20090); and by that season diatoms swarm from Cape Cod on the south to Cape Elizabeth and Casco Bay on the north, as far out from land as the 200-meter contour at the inner edge of the western basin (fig. 105). Fritz also found diatoms augmenting suddenly and to an extraordinary abundance at St. Andrews between the end of March and the end of April. Meantime the eastern diatom community vastly augments in numbers over the whole coastal bank off southwestern Nova Scotia and out across Browns Bank to the eastern channel (stations 20103 to 20107), where we found them swarming on April 12 to 16 in 1920.

A rich gathering of diatoms off the southeast slope of Georges Bank on that date (station 20109) is especially interesting because there were comparatively few (and these of more oceanic species) in the waters over the neighboring parts of the bank (stations 20108, 20110 to 20111). The presence of the abundant flowering in question at just that place therefore points to a drift from Browns and the other shallows to the eastward, as did a shoal of Calanus at that same locality the month previous (p. 189). However, Georges Bank is itself the site of extremely productive flowerings in April, though we did not chance to encounter them there in that month in 1920, for Douthart's tows yielded a great abundance of several species on its northern part during the last half of the month in 1913 (Bigelow, 1914a, p. 415).

Hand in hand with this vernal multiplication of diatoms, peridinians diminish almost to the vanishing point. As the impoverishment of this group apparently takes place nearly simultaneously over all but the southeast corner of the gulf, and so early in the season that the rich diatom flowerings are still restricted to the coastal waters within the gulf, to the shallows of Browns and of Georges Banks, and to the intervening channel and the continental slope, there is a very sharp contrast during the last half of April between these swarms of diatoms and a very scanty diatom plankton in the central and northeastern deep of the gulf, which is reminiscent of the mixed peridinian and diatom community existing there in March.

During late April the flowerings of diatoms that have originated in the northwest part of the gulf two months earlier (fig. 104) spread eastward beyond Mount Desert Island, while at about this same time a great increase takes place in the numbers of diatoms (though of other species) present in the waters of the Western Basin [24] and thence throughout the center of the gulf generally, where we found

[24] In 1915 diatoms were extremely abundant in the Western Basin and near Cashes Ledge on May 4 (stations 10267 and 10268, fig. 121).

diatoms swarming and peridinians practically nonexistent during the first half of May in 1915 (Bigelow, 1917, p. 324), the result being that the vernal flowerings of diatoms reach their widest expansion at this season.

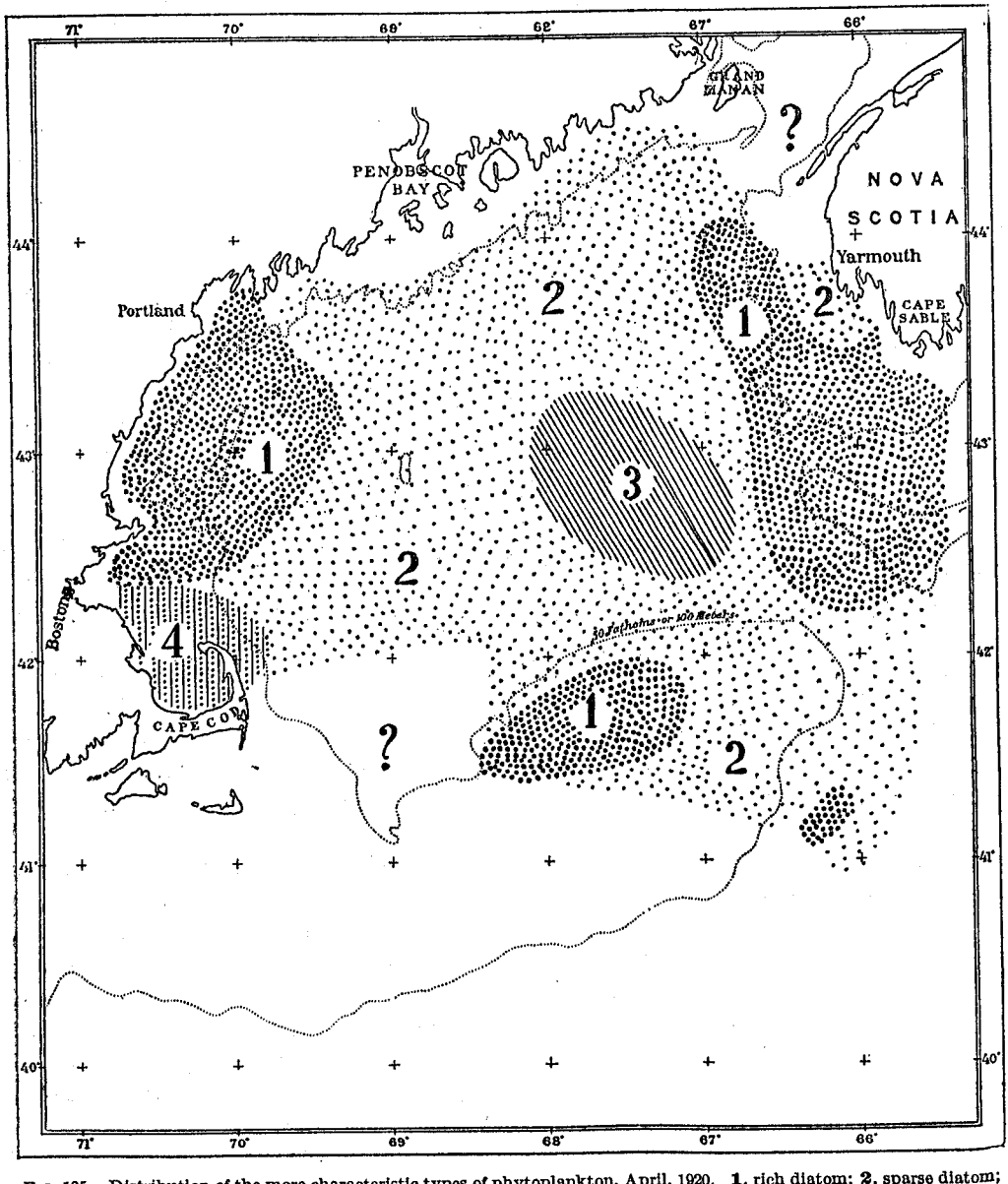


FIG. 105.—Distribution of the more characteristic types of phytoplankton, April, 1920. 1, rich diatom; 2, sparse diatom; 3, sparse Ceratium and diatom; 4, rich Phæocystis and diatom

The unicellular alga Phæocystis may also swarm, even to the extent of monopolizing the surface waters locally, for a brief period during the month of April, but shortly disappear once more, as occurred in the southern part of Massachusetts

Bay and off Cape Cod during the last half of the month in 1920 (p. 458). Although this is the only occasion on which we have actually observed this event, it is to be expected equally in other parts of the gulf, where the peak of abundance for Phæocystis may have chanced to fall between the dates of our successive cruises.

These diatom flowerings of the Massachusetts Bay region are so short-lived and dwindle so suddenly after they have attained their plurimum that we found them reduced to an occasional Coscinodiscus only among a scanty community of Ceratium, Peridinium, and Halosphæra on May 4 to 16 in 1915 [25] and again in 1920, although diatoms continue swarming in the central parts of the gulf and along its northern shore line generally until considerably later. Diatoms vanish equally from the waters along Cape Cod by the middle of May, where only an occasional diatom was to be found among the small catches of Ceratium and Peridinium at three stations on a line run by the *Albatross* from Cape Cod out to the north slope of Georges Bank in 1920 (stations 10225 to 10227, May 16), though the water over the southwestern part of the bank still supported much the same diatom community as the last week of February (p. 383). This late flowering was strictly limited, however, to the shallows of the bank because our tow nettings over the continental slope a few miles to the south yielded little except a sparse gathering of peridinians (station 20128).

In the western side of the gulf the shrinkage of the diatom communities, following their season of abundance, which, as we shall see, foreshadows their eventual disappearance from the plankton, proceeds progressively from south to north during May. Thus tow-net catches made about the Isles of Shoals, where we were able to follow the rise, culmination, and eclipse of the diatom flowerings at close intervals during the spring of 1913, were still exceedingly abundant (almost purely diatom) and very clean up until the first week in May in 1913, whereas there were very few diatoms on the other side of Cape Ann as late as this. From that time forward, however, the plankton of the Isles of Shoals area began to contain noticeable amounts of diatom débris, and as the season advanced the relative amount of dead specimens and variously fragmented remnants grew progressively greater until the 25th of the month, when there were very few living diatoms (Bigelow, 1914a, p. 406), though the nets still yielded large amounts of their débris.

Peridinians, on the other hand, and especially the genus Ceratium, multiplied as the diatoms dwindled (perhaps more relatively than absolutely), changing the general composition of the phytoplanktonic community so rapidly, from rich diatom at the beginning of May to peridinian with but few diatoms at the end of the month in the area bounded on the south by Cape Ann, on the north by Cape Porpoise, and offshore by Jeffrey's Ledge, that it is represented as "mixed diatom and peridinian" on the accompanying chart for May (fig. 106).

The duration of the spring flowerings of diatoms in the shoal waters off southwestern Nova Scotia is likewise brief, for though they filled our tow nets there on April 15, 1920 (stations 20103 and 20105), we found a sparse Ceratium plankton in that general region from May 7 to 10, 1915 (stations 10271 and 10272), with but few diatoms.

[25] Station 10266, May 4, 1915; station 10220, May 1 and 16, 1920.

In the deep offshore waters of the gulf, diatoms do not attain their maximum abundance for the year until some time during the last half of May or first week in June, after which they diminish so rapidly in number that in 1915 (the only year

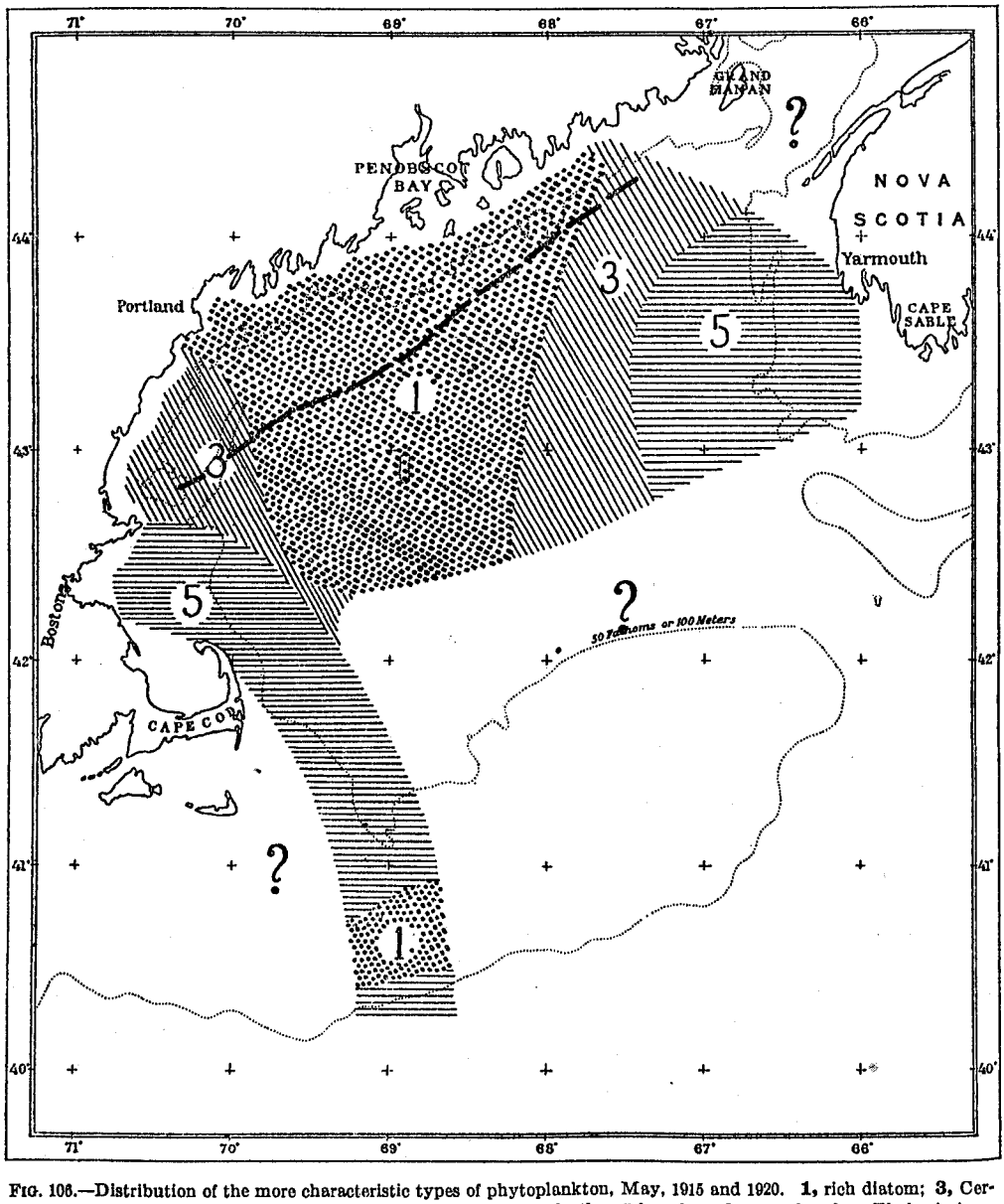


FIG. 106.—Distribution of the more characteristic types of phytoplankton, May, 1915 and 1920. **1**, rich diatom; **3**, Ceratium and diatom; **5**, Ceratium. The heavy broken curve marks the offshore boundary to abundant Thalassiosira

of record) we found that diatoms had practically vanished by mid-June from the tow nettings made in the basin of the gulf south of the line Cape Ann–Cape Sable, having been replaced there by a scanty peridinian plankton. Diatoms had also

fallen to a low ebb everywhere in the offshore waters of the northern half of the gulf by June 10 to 19, when they mingled with a scanty community of peridinians. Diatoms, however, were still flowering abundantly in the coastal zone east of Penobscot Bay at that time, for we found them in swarms off Petit Passage on the southern side of the Bay of Fundy on June 10 and again near Mount Desert Island (stations 10285 to 10287) on June 14 in 1915. Fritz (1921) also records diatoms in comparatively large numbers at St. Andrews in June, though not as abundantly as in May, on the one hand, or in July, on the other. It is probable that in June these three localities are local centers of production and not parts of a continuous coastwise belt of rich diatom plankton for two reasons—first, because Fritz found very few diatoms in the open Bay of Fundy on June 15, 1917, and, second, because they were but sparsely represented in our tow in the Grand Manan Channel on June 4, 1915 (station 10281).

Thus, a general and very pronounced diminution in the number of diatoms takes place over the offshore waters of the gulf as a whole and all along its western shore during May and June; but in the year 1915 diatoms reappeared, though not in great numbers, and mingled with peridinians, over the shoal coastal bank off western Nova Scotia during the last half of June (station 10290, June 19). The scarcity of diatoms in that region in May of that year may be assumed to have followed rich April flowerings and coincides with the greatest expansion of the Nova Scotian current in that region. Unfortunately we have made no hauls close in to this part of the Nova Scotian coast during June and have no data on the phytoplankton of the eastern half of Georges Bank, of the southeastern part of the basin of the gulf, or of Browns Bank for May.

As I have pointed out in an earlier report (Bigelow 1917, p. 326)—indeed, the facts outlined above would suggest it—the seasonal history of peridinians in the Gulf of Maine is just the reverse of that of the diatoms. In late February and during March they join with the latter to characterize the sparse plankton of the whole basin of the gulf, this "mixed" zone extending into its northeastern corner, on the one hand, and over most of Georges Bank, on the other, likewise over the shelf abreast of Shelburne, Nova Scotia. But even this early in the season they are entirely dominated in the several centers where diatoms have commenced flowering actively, and by April they are so wholly overshadowed in the regions where the diatom flora is at its climax that only an odd ceratium or peridinian is to be found among the masses of diatoms that clog the nets. Over most of the central and southern parts of the gulf, where diatoms are not yet very plentiful, they are sufficiently so to make the few peridinians a minor element in the tows (though these never wholly disappear from any part of the gulf at any season), leaving only a small area in the southeastern part of the gulf where there are so few diatoms that the few Ceratium still color the plankton of April.

As the flowering of diatoms reaches its climax and then diminishes in its regular seasonal progression, the peridinians (chiefly Ceratium) take their place in constantly augmenting abundance. This happens earliest in the season in the Massachusetts Bay region in the western side of the gulf and off southwestern Nova Scotia in the

eastern, where Ceratium dominated the plankton as early as the first week of May in 1915, leaving diatoms still overwhelmingly dominant in the central deeps of the gulf and along its northern coastline. Comparison of the chart for May (fig. 106) with that for April (fig. 105) illustrates the encroachment of these two peridinian centers—western and eastern—on the areas previously characterized by abundant diatoms, the former replacing the latter over the coastal zone from Cape Cod northward across Massachusetts Bay and past Cape Ann, on the one side of the gulf, southward, too, as far as Georges Bank, and offshore over the eastern side of the basin on the other, by the last half of May.

Probably peridinians would also have been found to dominate the phytoplanktonic community right across the southern part of the deep basin of the gulf at that

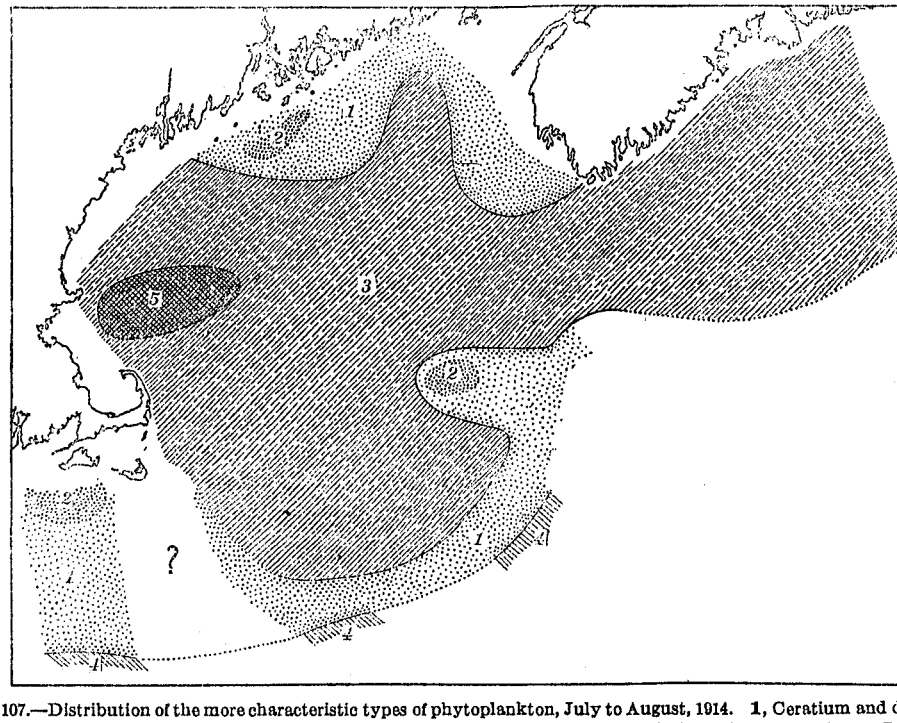


FIG. 107.—Distribution of the more characteristic types of phytoplankton, July to August, 1914. 1, Ceratium and diatom; 2, diatom; 3, Ceratium; 4, tropical, characterized by Trichodesmium; 5, Radiolarion. (Reproduced from Bigelow, 1917, fig. 97)

time. This is certainly the case by mid-June, when we have found them in considerable abundance at all our stations near the coast as well as offshore (and this covers the whole northern half of the gulf), except in the rich but circumscribed diatom areas just described for that month, where peridinians were still extremely rare.

No doubt variations from this planktonic cycle are to be expected from year to year, but it is sufficiently established that the vernal flowerings of the pelagic diatoms, followed by their eclipse, with the coincident disappearance and reappearance of peridinians, are as characteristic of the spring season in the offshore waters of the Gulf of Maine as are the spring freshets from the rivers that discharge along its coast, in which, as in so many other ways, the gulf closely parallels other northern seas.

In midsummer (fig. 107) we have usually found the entire basin of the gulf occupied by a peridinian (Ceratium) plankton, with only occasional diatoms, and we have never found diatoms in abundance anywhere in the gulf in July or August except close along the coast, on the one hand, and on Georges Bank, on the other.

We found diatoms flowering in abundance on each of our summer visits to the latter locality, but in different regions in different years. Thus they dominated on the western end of the bank on July 9, 1913 (station 10059) and on July 23, 1916 (stations 10347 and 10348), but when we visited that general locality on July 20, 1914, the water contained very few diatoms but, instead, a characteristic peridinian plankton. Three days later, however, we encountered a rich flowering of diatoms near the northeastern edge of the bank (station 10224). Furthermore, the Georges Bank flowerings of July, 1913 and 1914 (stations 10059 and 10224; see list, p. 430), though far apart geographically, were both dominated by Guinardia. In July, 1916, however, we found no Guinardia on a traverse of the western part of the bank but swarms of Thalassiothrix (p. 455) and Rhizosolenia (p. 444) in its stead. With so little data available it is not possible to outline the normal summer status of diatoms for the Georges Bank region. Nevertheless, the fact that we have found them in such abundance on some part of the bank on each visit in summer, with the abundant flowerings encountered there in February and May of 1920 by the *Albatross* (pp. 383, 387), and in April, 1913, by Douthart (p. 385), shows that swarms of diatoms may be expected somewhere on its extent at any time from late winter until midsummer. It is not unlikely that this applies to Nantucket Shoals also, for Dr. W. C. Kendall writes, in his field notes, that on September 2, 1896, the water "was very full of brown slimy stuff" at latitude 40° 47′, longitude 69° 43′, which could only have been diatoms.

It is not yet clear whether any particular region on the banks is more favorable for the multiplication of diatoms than another, except that we have always found these rich flowerings on its shoaler parts and never close enough to the continental slope to be within the influence of the high temperature outside the edge, which, in its own turn, supports various oceanic diatoms in small numbers mingled with peridinians of similarly Tropic origin.

The fertility in diatoms of the waters over Georges Bank is interesting, not only from the standpoint of the phytoplankton *per se*, but because of the great importance of the bank as a spawning ground for haddock. The prevalence of the genus Guinardia on the bank, contrasted with its absence or rarity in the deeper waters of the gulf to the north, is likewise instructive for its bearing on the circulation of the water in this region.

Turning now to the coastwise belt, diatoms continue a more important factor in the phytoplankton of estuarine situations throughout the summer than they are in the open waters of the deeper parts of the gulf at that season. Owing to the fact that most of our towing has been well out at sea, we have few data to offer on this regional differentiation. It was clearly demonstrable in Massachusetts Bay on August 22 to 24, 1922, however, when several stations close in to the land, following around the coast line from Cape Cod Bay to Cape Ann,[26] were dominated by diatoms

[26] Stations 10633, 10634, 10637, 10639, and 10642.

(chiefly Skeletonema and *Rhizosolenia alata;* pp. 448 and 447), whereas hauls at several stations farther out in the bay or off exposed stretches of the coast line[27] were dominated by the peridinian genus Ceratium (p. 407), as the open gulf as a whole usually is in summer.

We also found the water in Casco Bay, near the Harpswell biological laboratory, so cloudy with diatoms and Peridinium with bright red chromatophores on July 27, 1912, that its transparency was only about 4 meters. Two days later, however, a tow at the same location yielded hardly a diatom and very little phytoplankton of any kind, its place being taken by a fair representation of copepods, small medusæ, and many ophiuran larvæ.

Tows for the years 1912, 1914, and 1915 proved diatoms a major element in the phytoplankton in the neighborhood of Mount Desert Island in August; locally swarming (p. 431). Fritz (1921) also found this to be the case in the St. Andrews region. She also records an abundant July plankton of diatoms in the more open waters of the Bay of Fundy. Our few August tows in the Grand Manan Channel have yielded chiefly diatoms, though the phytoplanktonic community as a whole has been extremely sparse there. Diatoms have likewise shared with the peridinians the domination of our summer tows in the northeastern corner of the gulf off the mouth of the Bay of Fundy, and we have found this condition on German Bank and off Lurcher Shoal during each August when we have visited that region, while there were a few diatoms as far offshore as Browns Bank on July 24, 1914, among the more abundant peridinians that characterized the phytoplanktonic community there. Cape Sable, however, seems to mark the eastern boundary for diatoms as an appreciable factor in the plankton during the latter half of the summer.

Diatoms were a much more important factor in the plankton of the gulf in the summer of 1912 than at that season in 1913, 1914, or 1915. During that July and August they occurred in great abundance all along the coast from Seguin Island (situated a few miles east of Casco Bay) as far eastward as the mouth of the Grand Manan Channel, and were plentiful enough over the whole northeastern corner of the gulf, mingled with the peridinians, to give a distinctive aspect to the catches, instead of being limited to the narrow confines just outlined as the usual bounds to their summer flowerings. More interesting than the unusual abundance of diatoms which characterized that summer is the fact that this was mostly due to a species (*Asterionella japonica*) which has not been found in the offshore waters of the gulf since that time (p. 432). The genera Thalassiosira and Chætoceras likewise were more widespread and numerous in the eastern side of the basin then than we have since found them at that season, reflecting an unusually late continuance of their vernal flowerings (Bigelow, 1914, p. 132).

This much stress has been laid on the midsummer status of diatoms in the Gulf of Maine because of the very important rôle which this group of microscopic plants plays in the economy of the sea earlier in the season; but when all is said, diatom plankton occupies only a small part of the area of the open gulf during the warm months, as contrasted with the much more extensive area which then supports a typical peridinian plankton dominated by the genus Ceratium.

[27] Stations 10630, 10631, 10632, 10636, 10638, 10640, and 10641.

The record of towings is now sufficient to show that this peridinian community, with only an occasional diatom, normally dominates and usually monopolizes the phytoplankton of the whole of the central part of the gulf outside the 100-meter contour during the late summer and early autumn, from off Cape Elizabeth and Cape Cod, on the one side of the gulf, to German Bank and Cape Sable, on the other, and from about the 100-meter contour on the north, southward across the whole breadth of the basin to include the Eastern Channel, though with an admixture of diatoms in the northeastern part, as just noted.

A typical Ceratium plankton, or at least a predominance of Ceratium mingled with the diatoms, has likewise characterized all our summer tows on Georges Bank except for the local diatom flowerings just described. But, judging from St. Andrews and from conditions in north European seas, it is not likely that Ceratium, the peridinian genus that is predominant out at sea in the gulf, ever attains abundance in its estuarine waters, for according to McMurrich (1917, p. 3) none of the dinoflagellates were sufficiently numerous to be an important quantitative constituent of the plankton at St. Andrews at any season, "*C. tripos* only on one occasion being in sufficient quantity to be regarded as frequent." Nevertheless, Ceratium follows essentially the same seasonal pulse there as at our stations out at sea, reaching its plurimum in autumn and practically vanishing from the tows in April and May.

It is impossible to prepare a chart of the mutual limits of the chief classes of phytoplankton in the gulf for midsummer, which shall be as true for one year as for another, because of the yearly fluctuations in the abundance of and area occupied by diatom plankton near its northern coast and of the variable midsummer flowerings of diatoms on Georges Bank. On the whole, however, the state obtaining during July and August of 1914 (fig. 107) seems fairly representative of the offshore waters of the gulf in the summer season, bearing in mind the different locations of the diatom swarms on Georges Bank of July, 1913, and July, 1916. A corresponding chart of the northern part of the gulf for 1912, published in an earlier report (Bigelow, 1914, pl. 8), illustrates a summer more productive of diatoms.

The sporadic occurrence of swarms of acantharian radiolarians in the western part of the gulf in some summers, though perhaps not annually, a conspicuous feature of the chart for 1914 (fig. 107), need be mentioned but briefly here, being discussed below (p. 460).

It is in July and August, if ever, that tropical phytoplanktonic communities may be expected to drift northward from the Gulf Stream across Georges Bank and thus to penetrate the inner parts of the Gulf of Maine. But if our hauls are to be trusted as fairly representative, this rarely takes place, the only positive records of this sort which have yet been obtained for the inner parts of the gulf or even for the shoaler parts of Georges Bank itself being a fragment of gulf weed (Sargassum) picked up on German Bank on September 2, 1915 (station 10311; Bigelow, 1917, p. 246), and an occasional *Ceratium macroceras* detected among other boreal species of the genus off the Merrimac River on December 30, 1920 (station 10492).

Planktonic forms of tropic origin, plant as well as animal, are, of course, more important along the slope south of Georges Bank (p. 54), thanks to the close proximity of the tropic water. Thus gulf weed is often seen floating there in some quantity,

as was the case at our outermost stations in the summer of 1914 (stations 10218 and 10220). July and August stations (10218 and 10261) in 1914 over the slope west of longitude 68° W. and south of latitude 42° 10′ N. likewise yielded small amounts of the characteristically tropical alga Trichodesmium, together with *Ceratium macroceras*, which also occurred off the southeast face of Georges Bank in July (station 10220) and in the coastal waters off Martha Vineyard in August (stations 10258 to 10260); but we have never found *C. macroceras* along the continental slope farther east than the Eastern Channel.

Although tropical pelagic plants, both large and miscroscopic, as well as planktonic animals belonging to this same category in their relationship to temperature, may be expected to encroach on the western half of Georges Bank at some time during most summers, just as they do more regularly and abundantly farther west and south, the exact season when this happens varies considerably from year to year, as might be expected from the fluctuations in the location of the inner edge of the Gulf Stream, a fact illustrated by their failure to appear there by the third week of July in 1916. Probably they are hardly to be expected along Georges Bank earlier than the first of that month, even in warm years, and are locally more characteristic of the months of August and September.

Autumnal data on the phytoplankton of the gulf outside the Bay of Fundy are limited to a series of stations covering its northern half for September, 1915, and to occasional October and November hauls between Cape Cod and the Grand Manan Channel during the years 1912, 1915, and 1916. Bailey (1910 and 1917) and Fritz (1921) have also published lists of diatoms from St. Andrews and neighboring parts of the Bay of Fundy, for the autumn as well as for other seasons of the year, and Doctor McMurrich's plankton lists include the status of several genera of diatoms and of peridinians at St. Andrews in autumn. These records, united, show that diatoms practically disappear from the deeper parts of the gulf—not, however, from the Bay of Fundy— after the last days of August, leaving almost its entire area outside the outer headlands occupied by a Ceratium community, with the Mount Desert and Massachusetts Bay regions and the Bay of Fundy alone supporting diatoms in appreciable number. In fact, we have never found abundant diatom plankton anywhere else in the open gulf, either in September or in October, though diatoms were present in some numbers, together with the peridinians, along shore from Penobscot Bay to the Bay of Fundy up until the 9th of October in 1915, and dominated the phytoplankton near Mount Desert Island on that day (station 10328).

Considerable catches of diatoms at the mouth of Massachusetts Bay during the last week of September, 1915, resulted from a rich flowering of Skeletonema. This genus is comparatively rare there in spring (p. 448), but in the summer of 1922 it had commenced flowering in the coastwise belt and among the islands along the northern shore of the bay by August, and the three successive states—spring, August, and September—though for different years, suggest that its normal cycle is to spread offshore as the season advances. Its flowering period was apparently brief in 1915, however, and probably is in most years, having come to an end before October 26 or 27, by which date its place had been taken once more by Ceratium, with only occasional diatoms (Coscinodiscus and *Thalassiothrix longissima*) in the

tows on a line across the mouth of the bay (stations 10337 to 10339), where it had dominated the phytoplankton a month earlier.

Bailey (1917, p. 101) also records an abundance of diatoms (Skeletonema) near Grand Manan Island in the Bay of Fundy in early September, and Dr. McMurrich's lists show a rather pronounced maximum of diatoms (chiefly Thalassiothrix) at St. Andrews in September and October, 1916. But during the season of 1917, when Fritz's (1921) counts located the vernal maximum in late April and early May at St. Andrews, with a period of scarcity for diatoms in June, the second maximum fell in July, followed by a sudden diminution in the number of diatoms in August, with much smaller numbers in September. The wide fluctuations in her counts at the same locality on different dates in July and August is an instructive illustration of the streaky way in which shoals of diatoms often occur. Note especially an increase from 632,000 on July 23 to 7,186,000 on August 2, falling to 14,900 on the 8th. It is more likely that the net chanced to hit a streak of diatoms on the occasion of the rich catch, which a haul made shortly previous or later might have missed, than that an active flowering culminated during the two-weeks interval.

It is dangerous to generalize from a small number of hauls, especially for a tide-swept locality, but it seems that a secondary maximum of diatoms is to be expected sometime during the late summer or early autumn both in Massachusetts Bay and in Passamaquody Bay, and therefore probably all along the coast line in estuarine situations; one, however, which is less abundant than the vernal flowering and likewise less regular in the date of its occurrence.

Little change has been noted in the general composition of the phytoplankton of the Massachusetts Bay region during the period November–January, Ceratium dominating. Hauls off Gloucester on November 20, December 4, and December 23, 1912, yielded a scanty plankton, chiefly Ceratium, with few diatoms (Bigelow, 1914a, p. 404). In 1920 the several species of diatoms that are most abundant from spring to early autumn had practically vanished from the whole coastal belt between Cape Cod and the mouth of the Bay of Fundy by December and January; but by contrast the diatom genus Coscinodiscus apparently has a flowering period in midwinter, for it rivalled Ceratium at all the stations occupied by the *Halcyon* off the western and northern shores of the gulf from December 28, 1920, to January 9, 1921, dominated locally off the Merrimac River (station 10442), and was the most numerous diatom genus (though dominated by the peridianians) in the eastern side of the basin, in the Fundy deep, and off western Nova Scotia at this time (stations 10499 to 10502).

Judging from the midwinter data just outlined and from our experience during the first days of March in 1920 and 1921, peridinians are predominant and diatoms—except for Coscinodiscus—fall to a very low ebb out at sea in the Gulf of Maine during the later winter. Fritz (1921) found only very small numbers at St. Andrews from November until the middle of March, compared with the tremendous flowerings of spring. But diatoms may be a considerable element, quantitatively, in the plankton here and there along the open coast even in midwinter, as was the case off Gloucester on January 16 and in Ipswich Bay, a few miles north of Cape Ann, on January 30 in 1913, on which occasions our towings yielded about as great a bulk

of the diatom genus Chætoceras as of the peridinian genus Ceratium (Bigelow 1914a, p. 405).

In 1925 Cape Cod Bay was likewise the site of a rich flowering of *Rhizosolenia alata* (p. 447) from the middle of December (appearing between the 10th and 15th) through January. But while the Ipswich Bay diatoms may have been the precursors of the vernal flowerings for the coastal belt Cape Ann–Cape Cod, marking the site of their inception, this flowering of Rhizosolenia can hardly be so classed for Massachusetts Bay, both because the waters in the western and central parts of the latter contained almost no diatoms in January when Rhizosolenia was at its maximum in Cape Cod Bay, and because when flowerings suddenly appeared off Plymouth to the west and near Stellwagen Bank to the north during the last week in that February, the plankton at the latter locality was dominated by Thalassiosira, with very few Rhizosolenia detected in such of the towings for later dates as have yet been examined. So far we have no other record of *R. alata* flowering richly in the Gulf of Maine in winter; in this respect the shoal waters of Cape Cod Bay agree rather with the Wood Hole region, where Fish (1925) has reported winter maxima of Rhizosolenia for two different years.

In summary, diatoms and peridinians alternate in dominating the phytoplankton of the gulf. The former, scarce in the offshore waters of the gulf during late autumn and winter, flower in tremendous abundance during the spring, the flowerings commencing in the coastal belt. Probably they always appear between Cape Ann and Cape Elizabeth as early as the first week in March, perhaps earlier. In early years the vernal flowerings appear in Massachusetts Bay by the last week of February, perhaps not till the last week of March in late years, preceded (at least in some years) by winter flowerings of Rhizosolenia in Cape Cod Bay. Eastward along the coast from Cape Elizabeth to the Bay of Fundy diatoms swarm from early April on. The diatom flowerings are of but brief duration in Massachusetts Bay, having passed their climax in its southern side by the first week of April of 1925, and by the last week of the month in the northern side of the bay in 1913; but the diatom maxima endure till May to the northward of Cape Ann and to some extent throughout the summer along the northern shore of the gulf. At St. Andrews the vernal flowerings continue through May, followed by a period of scarcity in June. On the Nova Scotia side diatoms swarm in April, but only for a brief period, reappearing in some numbers in June (p. 389). Over the central deeps of the gulf the spring flowering reaches its climax in May; and shortly after mid-June diatoms practically vanish from the western basin, though in some summers diatoms are an element in the plankton of the eastern part of the basin all summer. During some years, if not annually, a secondary brief flowering of diatoms takes place in Massachusetts Bay in late August or September, and at some time in late summer or early autumn (the precise date varies from year to year) in the St. Andrews region and likewise in the open Bay of Fundy. Diatoms probably play a more important rôle in estuarine situations generally and close in to the shore than they do out at sea, but I can offer little on this point, most of our towing having been done well out from the land.

Diatoms may also be expected to flower on one part of Georges Bank or another at any season from late winter to midsummer, but nothing is known of their status there in autumn or early winter.

Fish (1925) has pointed out that the waters just west of the barrier of Cape Cod show quite a different seasonal cycle—namely, rich diatom plankton throughout the winter, usually with a brief summer maximum, but with few diatoms in spring—this seasonal distribution corresponding to the Mediterranean, as that of Massachusetts Bay and of the Gulf of Maine generally does to the diatom cycle of the North Sea, Irish Sea, and Skager-Rak. Thus, as Fish (1925, p. 111) emphasizes, the same relationship between the seasonal succession of diatom maxima and the latitude and temperature obtains in the western side of the North Atlantic as in the eastern.

Peridinians dominate the phytoplankton of the open gulf throughout the summer and autumn, but they become very scarce, actually as well as by contrast, during the flowering period of the diatoms. The latter are much the more important group of the two in estuarine situations, where they occur in greater or less abundance throughout the year instead of dwindling almost to the vanishing point between their flowering periods. Peridinians, on the other hand, are seldom more than a very minor constituent of the plankton in estuarine situations.

Finally, before turning to the quantitative records, I may point out that the Gulf of Maine diatoms are chiefly of local origin—that is, that they are produced in the gulf itself and are not immigrants thither from elsewhere. For the western center of dispersal this may be taken as proved; and while the chain of evidence favoring the endemic origin of the diatom plankton of the Nova Scotian side of the gulf is not so complete, there is nothing in our records to suggest that it receives any important accessions from the east around Cape Sable. On the contrary, none of the hauls made east of the cape during March, 1920, June, 1915, or July and August, 1914, have yielded diatoms in any abundance; nor are the diatoms of the eastern side of the gulf more Arctic in their affinities than those of the western, as might be expected if the Nova Scotian current were responsible for their presence there, but rather the reverse.

## QUANTITATIVE DISTRIBUTION OF THE PHYTOPLANKTON

When the study is undertaken of the plankton of an ocean area previously virgin ground in this respect, a general qualitative and seasonal survey is the first task. Until we know what groups of organisms are the chief constituents of the pelagic community, at what seasons they reach their maximum abundance, and have outlined their temporal and geographic fluctuations in general, it is difficult to plan counts of the actual numbers in which they occur, to yield results commensurate with the vast amount of labor entailed. For this reason our hauls in the Gulf of Maine have so far been made with the ordinary horizontal nets of appropriate mesh, but I believe that with the information now at hand the time is ripe for more intensive quantitative studies of the phytoplankton of the offshore waters of the gulf, such as Fritz (1921) has undertaken for the St. Andrews region.

In north European waters this stage has long been passed, and since the time when Henson (1887) first focused scientific attention on the productivity of the high seas, quantitative determinations innumerable of marine and fresh-water

plankton have been made by methods the reliability of which has steadily increased through the medium of successive trial and criticism. Inasmuch as our Gulf of Maine studies touch only the edge of this field, I may simply refer the reader to Hensen himself, to Lohmann (1903 and 1911), to Steuer (1910), and especially to the summaries by Johnstone (1908) and by Gran (1915),[28] for general accounts of such undertakings. Much of the earlier work of this sort was robbed of part of its value by the impossibility of determining how much of the vertical column of water fished through by the net was actually filtered by it. But thanks to Lohmann's (1911) demonstration that satisfactory counts of many of the most important pelagic plants could be obtained by centrifuging a water sample obtained with an ordinary water bottle, and to Gran's (1912a; 1915) discovery of a satisfactory preservative (Flemming's fluid) for such samples, a simple but exact method for quantitative plankton work is now available, which it is to be hoped American biologists will soon adopt.

While this method gives far more reliable results for the smaller planktonic plants, "many of the larger species," as Lebour (1917, p. 135) points out, "do not get into the water samples in anything like a representative number," and as a rule this method is quite worthless for the larger animal plankton. In fact, no one collecting apparatus can be expected to be equally satisfactory for all the members of the plankton, large as well as small.[29]

Horizontal hauls with ordinary tow nets yield useful information as to the relative abundance of phytoplankton, but only if hedged about by the same precautions as are necessary for the zooplankton (p. 79), the need of which is now universally recognized. For example, we face the impossibility of insuring that all the tows shall fish through an equal column of water, because it is practically impossible to keep even a steamer moving at a uniform rate at the low speed that towing requires. The uncertainty introduced by imperfect filtration is much more serious for phytoplankton than for zooplankton, for the much finer-meshed nets that must be employed become clogged much sooner and to a greater degree. This is especially the case when Phæocystis and certain diatoms swarm (that is, just when information on their abundance is most to be desired), for they often clog the silk so thoroughly that the nets become quite impervious to water after a few minutes, so that the catch becomes the product of the first part of the tow only.

There is also the problem of a method of estimating the amount of phytoplankton caught, on the one hand sufficiently accurate for the results to be instructive and on the other rapid enough to deal in a practical manner with the large amounts which horizontal tows at the surface often yield. The total volume—simplest and easiest measure—is estimated by the same method as for the zooplankton, described above (p. 81), and entails the same sources of error, the worst being the uncertainty as to what proportion of the measured volume represents the actual plankton and how much of its bulk is due to the spaces between its members.

[28] W. E. Allen (1921) has recently formulated a formidable list of sources of error inherent in all collections of plankton taken with tow nets.

[29] Lebour's (1917) tables give instructive examples of the discrepancy between net hauls and collections made with the water bottle off Plymouth, England.

This depends somewhat on the shapes of the plant cells, smooth ones naturally fitting together much more closely than setose or irregular cells or chains (Michael, 1921, p. 564). Unfortunately, measurements of volume have little value as a measure of the phytoplankton for tow nettings containing appreciable proportions of larger organisms (e. g., copepods), unless these be painstakingly picked out. Nevertheless, even the most critical supporter of more rigorous methods must allow a certain value to estimates of the volume of plankton, at least for comparative purposes, especially when diatoms are flowering, for as a rule there is then very little else in the water. At their worst horizontal hauls tell whether the plankton is comparatively rich or scanty, as between stations where similar hauls are made; and when prosecuted over a period of years, as has been done near the Isle of Man under the leadership of Professor Herdman,[30] very instructive results may be expected. Because of their inherent inaccuracy, however, they can not be used as a measure of the absolute amount of plankton present in the water, nor even as a basis of comparison between different areas, unless the requirements of hauls of uniform duration, at uniform speed, and with nets of uniform type be rigorously adhered to.

In midwinter the production of phytoplankton in the inner parts of the gulf is so low that the volumes recorded in December, 1920, and January, 1921, ranged only from 0.5 to 6.5 cubic centimeters;[31] but toward the end of February or early in March of 1920 the vernal flowerings of diatoms on the southwestern part of Georges Bank, on the one hand, and in the immediate vicinity of Cape Elizabeth, on the other, were responsible for catches of phytoplankton 40 to 200 times as great as in the center of the gulf or along its northern and eastern coast, where the catches made during the March cruise of the *Albatross* in 1920 were often too small to measure (fig. 108). During April of that year, the month when the diatom flowerings attain their maximum abundance in the two sides of the gulf, the amount of vegetable matter present in the surface waters of the Cape Elizabeth region in the west and from the shallows off Cape Sable out to Browns Bank on the east is so much larger still, without any corresponding augmentation in the central or northern part of the gulf, that, allowing for the clogging of the nets, which I have repeatedly emphasized, it is not out of bounds to claim plankton volumes a thousandfold greater in the most productive regions than in the more barren localities (fig. 109). Two successive stations located 25 miles west of Cape Sable, where the volume of plankton increased from less than 1 cubic centimeter to at least 380 cubic centimeters (actually, no doubt, much more) during the three-weeks interval between March 23 and April 15 of that spring, is a notable illustration of the rapidity with which the pelagic flora augments in quantity when diatoms are flowering actively. The plankton

[30] See especially Herdman, Scott, and Dakin, 1910.

[31] The volumes here listed are the total yields of surface hauls of one-half hour's duration with a No. 18 bolting-silk net 14 centimeters in diameter, not the amounts in any given volume of water or below any given areas of sea surface. They, therefore, are not absolute measures, though comparable one with another. Since the unavoidable errors preclude accuracy, measurements have been only to the nearest cubic centimeter, and all the larger volumes should be regarded as too small because of the clogging of the net already alluded to. Probably none of the volumes of 200 cubic centimeters or more represent much more than half the amount of plankton that was actually present in the horizontal column of water through which the net was dragged, but through a part of which it failed to fish after its meshes were clogged.

augmented similarly in volume at the mouth of Massachusetts Bay from less than 5 cubic centimeters on March 1 (station 20050) to at least 200 cubic centimeters on April 9 (station 20090), while Fritz (1921) records the numbers of diatoms per haul

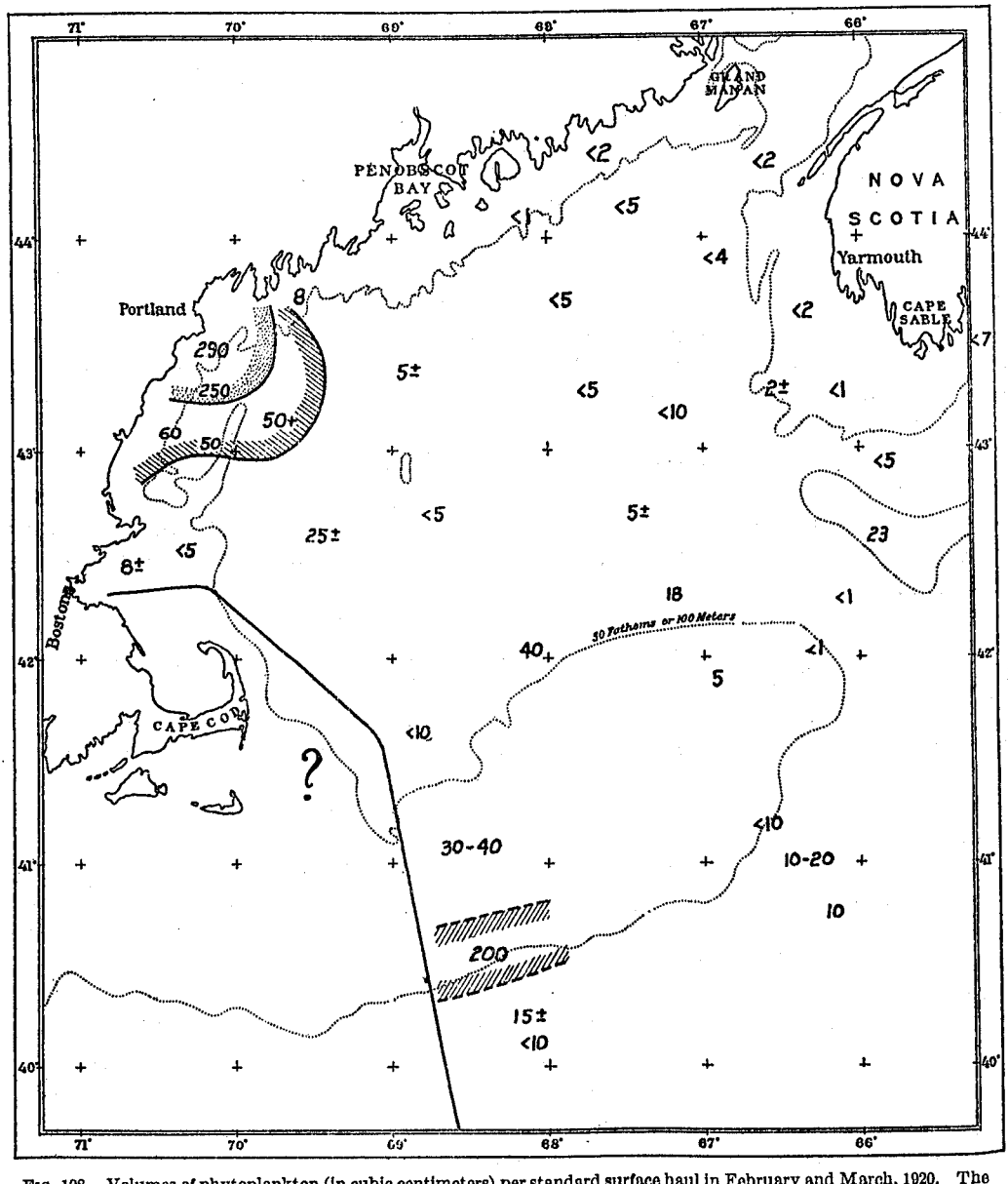


FIG. 108.—Volumes of phytoplankton (in cubic centimeters) per standard surface haul in February and March, 1920. The hatched curve incloses areas with more than 50 cubic centimeters; the stippled curve with more than 250 cubic centimeters

as increasing from about 28,000 on March 15 to upwards of 9,000,000 on May 1 at St. Andrews.[32] When the water is cloudy with diatoms, as is the usual state when

[32] Fritz's counts are for the catches of horizontal hauls that fished through an unmeasured volume of water.

these microscopic plants are flowering most intensively, volumes even as large as those noted (fig. 109) are but a pale reflection of the mass of vegetable matter actually present in the water.

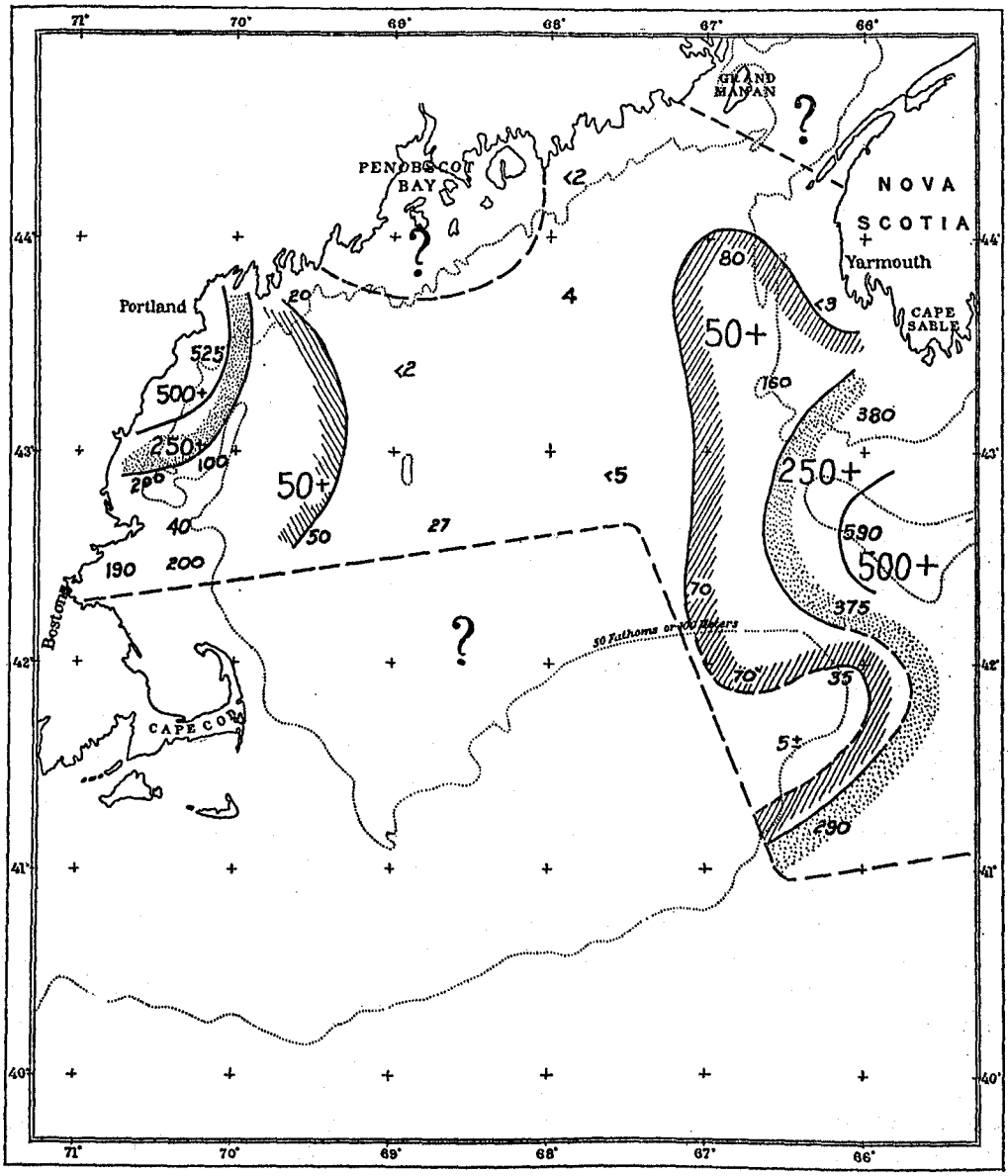


FIG. 109.—Volumes of phytoplankton (in cubic centimeters) per standard surface haul, April, 1920. The hatched curve incloses areas with more than 50 cubic centimeters; the stippled curve with more than 250 cubic centimeters

The accompanying chart (fig. 109) for the last half of April is necessarily imperfect, because records for the several stations ought to be taken simultaneously (which has not been practicable). But the variations that appear there in the local

density of the eastern diatom center, reflected by the volumes of plankton, and more especially the rather large volumes along the 100-meter curve west of Nova Scotia contrasted with the barren water both over the basin to the west and close in to the neighboring coast on the east, point directly to a tonguelike drift of diatoms northward toward the Bay of Fundy from the rich center of production off Cape Sable.

The rich catches in the Eastern Channel (375 cubic centimeters at station 20107) and off the southeast face of Georges Bank (290 cubic centimeters at station 20109) similarly suggest another line of dispersal for the Cape Sable–Browns Bank diatoms toward the southwest, a thesis supported by the qualitative uniformity of the April catches in that region, illustrated by the following table:

| Diatoms | Browns Bank, station 20106; volume, 590 cubic centimeters | Eastern Channel, station 20107; volume, 375 cubic centimeters | Southeast slope of Georges Bank, station 20109; volume, 290 cubic centimeters |
|---|---|---|---|
| Chætoceras laciniosum | × | × | × |
| Chætoceras debile | × | × | × |
| Chætoceras atlanticum | × | | × |
| Chætoceras decipiens | × | × | × |
| Chætoceras diadema | × | × | × |
| Chætoceras didymum | × | × | × |
| Chætoceras convolutum | | × | × |
| Chætoceras criophillum | | × | × |
| Thalassiosira gravida | × | × | × |
| Thalassiosira nordenskioldi | | × | × |
| Thalassiothrix nitschioides | × | × | × |
| Coscinodiscus | | | × |
| Rhizosolenia semispina | × | × | × |
| Lauderia glacialis | × | × | × |
| Fragillaria sp | | × | × |
| Coscinosira | | × | × |

If such a drift of diatoms from the Nova Scotian center was actually taking place at the time of our April cruise in 1920 it must have been strictly confined to the outer edge of Georges Bank, because the shallows to the northward (stations 20108, 20110, and 20111) supported a phytoplanktonic community not only much less abundant (15 to 120 cubic centimeters per haul), but one of rather a different type, in which the oceanic diatoms *Chætoceras decipiens*, *C. criophillum*, *C. atlanticum*, *C. densum*, and Coscinodiscus were dominant, with the several species of Ceratium continuing as an important factor in April just as they had been in March.

As long as the diatom flowerings continue at their peak, volumes of plankton as large as or larger than those noted on the chart (fig. 109) are to be expected all along the coast north and east of Cape Ann, on the one side of the gulf and over the banks west and southwest of Nova Scotia on the other (Browns Bank yielded one of our largest spring catches, as appears on the chart), locally, too, on Georges Bank (p. 385); and while the central part of the gulf is hardly less barren in April than in March, the spring flowering may be no less intensive there, once it is under full headway, than in the coastal zone. For example, diatoms were so plentiful in the western basin on

May 4, 1915 (station 10267) that every interstice of the fine net was clogged and its silken bag transformed into a cone of slime almost impervious to water after a few minutes submergence at a locality where a net of the same specifications took only 5 cubic centimeters of phytoplankton on March 24, 1920, and 50 cubic centimeters on April 18 of that year. Even a coarse (No. 5 silk) net, 24 centimeters in diameter, yielded over 2,000 cubic centimeters, mostly diatoms of one species, after 20 minutes' towing, though a large part of the phytoplankton must have escaped through it.

Perhaps I should remark in passing that while very rich catches are the rule throughout the areas occupied by the flowerings of diatoms during these periods of abundance, considerable local variations in the volumes of plankton present in the water are to be expected from place to place, for instead of being uniformly and evenly distributed, the congregations of diatoms are often so streaky that one can actually see the net pass through alternate bands of brownish diatoms and of clear water (Bigelow, 1914a, pp. 405 and 407).[33] Conceivably it might miss the productive spots altogether, and very likely this happened off Cape Ann on April 9, 1920 (station 20091), when the catch of phytoplankton was very small though diatoms were then extremely abundant (200 + cubic centimeters) both south and north of the cape a few miles away. In the deeper waters offshore, however, the phytoplankton is much more evenly distributed, and it may even approach perfect uniformity over large areas in the open sea.

The duration of the flowering season of the diatoms determines the period during which large volumes of phytoplankton (say upwards of 50 cubic centimeters per haul) are to be expected anywhere in the Gulf of Maine. After the diatoms pass the peak of their abundance the amount of phytoplankton rapidly diminishes, and from that time forward, as copepods, Sagittæ, and other animals form an increasing proportion of the catch, measurements of its volume become less and less instructive.

In Massachusetts Bay the phytoplankton attains its maximum abundance (as measured by volume) by the last half of April, diminishing again so suddenly that the amount taken among the copepods during the first week in May, 1920 (after the brief swarming of Phæocystis had come to an end), was hardly measurable. And while large volumes may be expected in the western basin until well into May (p. 338), the volume of phytoplankton taken there in the standard haul on June 26, 1915, after diatoms had practically disappeared, was less than 3 cubic centimeters (station 10299).

Near land, east of Penobscot Bay, where diatoms persist more or less throughout the summer (p. 396), we have occasionally made large catches in August, notably in 1912, when Asterionella (p. 431) occurred in such abundance that although the net came back aboard filled to the brim with several liters of slimy brown diatom soup (Bigelow, 1914, p. 133), its yield was only a part of what was actually present in the water through which it was drawn. In fact, this has been the richest haul of phytoplankton ever recorded for the Gulf of Maine.

In most parts of the gulf where the spring diatom flowering is a short-lived phenomenon, its dissipation leaves but little vegetable plankton in the water; nor does the augmentation of peridinians, characteristic of late spring and early summer,

[33] This has often been remarked by previous students.

produce a flora at all comparable in abundance to the diatoms which it succeeds. As a rule, indeed, the Ceratium plankton of midsummer has seldom yielded volumes much larger than 25 cubic centimeters, rarely as much as 40 cubic centimeters except when fortified by diatoms, or by Acanthurian radiolarians, as was the case off Cape Ann in August, 1914 (p. 460; Bigelow, 1917, p. 324). Occasionally, however, Ceratium occurs in greater abundance—for example, on August 13, 1912 (Bigelow, 1914, p. 131), when "we were struck by the slick, oily appearance of the water some 35 miles off Cape Elizabeth, and consequently stopped the vessel for a surface tow (station 10026b). The net, when brought aboard, was distinctly reddish, and its meshes clogged with what proved to be a mass of Ceratium, * * * and this phenomenon continued for several miles." It is not unlikely that a swarming of Ceratium was reponsible for a streak of white water 65 to 75 miles long and 30 to 40 miles wide reported off Monhegan Island in 1882 (Collins, 1883, p. 282). But such events as these are quite exceptional for the Gulf of Maine, our subsequent cruises having shown that 1912 was, generally speaking, a very "rich" summer for Ceratium as well as for diatoms. With our standard net and time of towing, 50 cubic centimeters would be a very rich catch of Ceratium for the gulf, whereas 10 times as much as this is nothing remarkable for diatoms during the period of their greatest abundance. Neither do the local swarms of Acanthometron, which are sometimes met with in the western part of the gulf in midsummer (p. 460), produce any such abundance of organic matter as do the diatoms; at the greatest, they have raised the volume of the catch to 70 or 80 cubic centimeters, as was the case off Cape Ann on August 12, 1914 (station 10253).

In summer, as a general rule, the greatest volumes of phytoplankton are to be expected in the coastal zone east of Penobscot Bay, especially over the small area near Mount Desert Island, where diatoms usually persist in numbers right through the season into autumn. But this productive area does not extend westward past Penobscot Bay, on the one hand, nor more than a few miles eastward past Mount Desert Island, on the other. July and August hauls near the coast off the mouth of the Grand Manan Channel and in the latter itself have been decidedly barren. Local swarms of diatoms may also produce an extremely abundant phytoplankton in July on Georges Bank (p. 391). In other parts of the gulf, where the abundance of the summer phytoplankton, or the reverse, depends on the numbers of Ceratium locally present, no division into "rich" and "barren" areas is yet possible, for our large hauls of peridinians have been at widely separated localities in different summers. Thus in 1912 our richest hauls of Ceratium (the largest we have ever made) were off Cape Elizabeth, as just noted; off Cape Cod in July, 1913, and July, 1916 (stations 10057 and 10058, Bigelow, 1915, p. 334; station 10345); and near Lurcher Shoal in August, 1914 (station 10245). On the whole, the deep offshore waters of the gulf have always proved decidedly barren of phytoplankton in midsummer, contrasted either with these Ceratium centers or, more markedly, with the diatom flowerings of the coastal waters.

In the Massachusetts Bay region the September flowering of Skeletonema is reflected in the amount of phytoplankton taken in the nets, as might be expected, raising the volume to some 25 to 30 cubic centimeters on September 29, 1915 (station 10320), when this diatom formed the bulk of the catch, contrasted with a volume of

only 2 to 3 cubic centimeters at a neighboring locality on August 31 (station 10306). Though the eclipse of Skeletonema left the phytoplankton hardly richer at the mouth of the bay in that October (volume about 4 cubic centimeters on the 26th, in 1915, station 10338) than it had been at the end of August, it is probable that a general increase over its midsummer state takes place in the volumes of phytoplankton of Massachusetts Bay in late autumn, because peridinians, chiefly *Ceratium tripos*, were abundant enough there in November, 1916, to yield volumes of 18 to 20 cubic centimeters on the 8th (stations 10403 and 10404).

With the falling temperatures of winter the volume of phytoplankton as a whole shrinks to its annual minimum in all parts of the gulf which we have visited at that season; so much so that the greatest measured volume for the winter cruise of 1920–1921 (stations 10489 to 10502) was only 6.5 cubic centimeters (station 10488), and ranged down to less than 1 cubic centimeter per haul at the other stations, as follows:

| Station | Approximate volume in cubic centimeters | Station | Approximate volume in cubic centimeters |
|---|---|---|---|
| 10488 | 6.5 | 10495 | 3.5 |
| 10489 | 5 | 10496 | 3 |
| 10490 | 4.5 | 10498 | 2.5 |
| 10491 | 3.5 | 10499 | 2 |
| 10492 | .5 | 10500 | .5 |
| 10493 | 2 | 10502 | 4.5 |

Having made no vertical hauls for the phytoplankton in the Gulf of Maine, counting of diatoms or of peridinians has not seemed worth while. Fritz's (1921) counts of diatoms in the Bay of Fundy are likewise based on horizontal hauls, and hence do not represent the number present in any known volume of water; but Peck (1896) made a quantitative study of the diatoms of Woods Hole and Buzzards Bay based on the filtration of large samples (5 liters each) of sea water through a sand filter.[34]

Unfortunately, Peck's tables do not give the actual counts per sample, but are based on combinations of the several samples for a given level—surface, intermediate, and bottom—at all four stations and for all these levels combined for each station. On averaging them, however, it appears that the largest catches of diatoms were at least 420,000 per liter—that is, 420,000,000 per cubic meter of sea water.

To give the reader a more concrete idea of the numerical strength to which marine diatoms may attain when flowering actively, some of the oft-quoted counts for European waters will not be out of place here. One of the richest catches ever recorded, Johnstone (1908, p. 210) tells us, is Brandt's (1902, p. 71) of 3,173,000,000 diatoms, besides 500,000 peridinians and a few thousand copepods, in a net 1 square meter in mouth diameter, hauled up vertically from 30 meters, which, says Brandt, indicates an actual diatom flora of at least 6,000,000,000 per cubic meter of sea water after allowing for imperfect filtration by the net. To make these collossal numbers

[34] Essentially the Sedgewick-Rafter method, for an account of which see Whipple (1905, p. 15).

even more impressive, Johnstone (1908, p. 163) has calculated that on the basis of this haul "every drop of sea water from this part of Kiel Bay contained some 200 diatoms;" and though by Hensen's (1887) calculations less than one-tenth as many diatoms as this are present on the average in the West Baltic, their numbers are sufficiently appalling when extended to any considerable sea area.[35]

During the years that have passed since Hensen's pioneer studies in this field many similar counts have been made in the Baltic and in various parts of the North Sea, with the details of which it is unnecessary to delay here.[36] Lohmann, for instance (1908, Table B), has recorded some very large counts by the centrifuge method, including 7,800,000,000 Skeletonema per cubic meter in June, 1906, with another individual catch of about 2,000,000,000 diatoms in Kiel Bay on April 11, 1906. As still another example of the results of this modern method, the accuracy of which leaves little to be desired, though, as Gran (1915) himself points out, it is not of universal application, I may quote his own average of about 228,000,000 diatoms per cubic meter in the surface waters of the Skager-Rak for February, 1912.

The centrifuge, however, is not the "last word" in quantitative determination of the phytoplankton, for E. J. Allen (1919) has recently essayed the following totally novel procedure: To a small sample of sea water (0.5 cubic centimeters) he added a large amount (1,500 cubic centimeters) of a nutrient solution that had previously been found suited for the cultivation of marine diatoms (Allen and Nelson, 1910; E. J. Allen 1914). The culture was then examined after a period of incubation, whereupon he found a total of 232 different kinds of organisms. A second experiment yielded similar results. Since now it is obvious, to use his own words (E. J. Allen, 1919, p. 4), that each of these organisms "must have been represented by at least one individual or unit, either cell or spore, in the original ½ cubic centimeter of sea water from which the experiment was started," the latter must have contained at least 464 organisms (mostly diatoms) per cubic centimeter—that is, 464,000 per liter—and probably, as he calculates, as much as 1,000,000 per liter for the part of the English Channel whence his sea-water sample was taken. How much more effective this method is than centrifuging, even for such comparatively large organisms as diatoms (for which the culture method is particularly well adapted, as indicated by their great predominance in the final product), is illustrated by the fact that whereas the two culture experiments call, respectively, for 378,000 and 290,000 diatoms as the absolute minimum per liter, centrifuging a similar sea-water sample at the beginning of the experiment revealed only about one-thirtieth as many. Nor can even the method of the culture medium be relied on to give a total census of the phytoplankton, because it is by no means certain that the nutritive fluid employed was as suitable for the growth and reproduction of peridinians, infusorians, coccolithophorids, etc., as it was for diatoms. In short, as Herdman says (1920, p. 819), "every new method devised seems to multiply many times the probable total population of the sea."

[35] There has been much discussion as to the reliability of numerical results yielded by nets of the "Hensen" type, owing to uncertainty as to their coefficient of filtration. In the present connection it is enough to point out that in any case the ostensible results are always smaller, never larger, than they should be.

[36] For details of such I may refer the reader to Hensen (1887) himself, Driver (1908), Lohmann (1903 and 1908), and Gran (1915).

How closely the foregoing data, obtained in European waters, would apply to the Gulf of Maine is yet to be determined, but judging from Peck's results and from the large volumes of phytoplankton which we have ourselves obtained, there is no reason to suppose that its fecundity is lower than that of the North Sea or even than the still more prolific waters of the West Baltic. When such numbers as I have listed as examples are expanded from the trifling bulk of a cubic meter of water to cover the 36,000 square-mile area of the Gulf of Maine north of its offshore banks, and to a stratum at least 20 meters thick, they become too vast for the human mind to envisage. Peridinians never approach the diatoms in actual numbers so far as is known. For example, the largest count recorded by Gran (1915) in the North Sea (May 9, 1912) was 3,740 per liter for *Ceratium longipes*, a species with an April to June maximum, and hence to be expected in relatively large numbers at that particular season.

## PERIDINIANS

The peridinian communities of the Gulf of Maine, like those of the North Sea, consist chiefly of one or other of two species (*longipes* and *tripos*) of the genus Ceratium,[37] with smaller numbers of *C. fusus* and at times *C. arctica*. The two predominant species alternate in dominance with the season of the year.

### Ceratium

Judging from winter data for Massachusetts Bay (Bigelow, 1914a) and from our December and January stations of 1920–1921, *C. tripos* predominates everywhere in the gulf throughout the winter, though *C. longipes* likewise occurs in small numbers in most of the winter catches. *Tripos* was still the predominant member of the pair at every station in the western, central, and northern parts of the gulf and on Georges Bank as a whole during early March, 1920, except in the flowering centers for diatoms (p. 383; fig. 104), where so few Ceratium occurred that the relative numbers of the two species are not significant. *C. longipes* or intermediates between it and *C. arctica*, such as are reported by Paulsen (1908), occurred side by side with *C. tripos* at most of the March stations. Off the southeastern slope of Georges Bank *longipes* was at least as numerous as *tripos*, outnumbered it in the Eastern Channel, on Browns Bank, and over the slope farther east, and was the only member of the pair detected in tows made in the Northern Channel and over the shelf abreast of southern Nova Scotia, from March 17 to 20 (stations 20073 to 20076 and 20078).

*Ceratium arctica*, interesting because its occurrence is associated with low temperatures (Jørgensen, 1911), was likewise very generally distributed over the gulf in March, 1920, occurring only in very small numbers in the western half, but relatively more abundant in the Eastern Basin (though subordinate to *tripos* there); predominant, or at least as numerous as either *C. longipes* or *C. tripos*, at our several stations from Browns Bank to Cape Sable and off Shelburne; and more abundant, absolutely as well as relatively, in the eastern side of the gulf than in the western. The distribution of *C. arctica* at this season suggests an intrusion on its

[37] Identifications of peridinians follow Paulsen (1908) strictly. Being concerned here only with questions of distribution and relative abundance, not with systematics or genetic relationships, Paulsen's view that *C. longipes* and *C. arctica* are distinct (not varieties of one species as Meunier (1910) maintains) is accepted without comment.

part around the cape from the eastward. But if *C. arctica* occurs in the gulf chiefly as an immigrant from the north, as seems probable at present, its quantitative distribution within the gulf in early spring does not parallel the distribution of temperature, for at the time of the winter minimum the water is coldest next the western side of the gulf while *arctica* is most abundant in the eastern side.

The actual proportions in which the several species of Ceratium occurred during the early spring of 1920 appears from the following list of actual counts of samples at representative localities:

*Relative numbers of species of Ceratium in samples, "Albatross" cruise, March 1 to 19, 1920*

| Locality | C. tripos | C. longipes | Intermediates between longipes and arctica | C. arctica | C. fusus |
|---|---|---|---|---|---|
| Massachusetts Bay, station 20050 | 22 | 1 | 0 | 1 | 0 |
| Western Basin, station 20049 | 25 | 0 | 1 | 1 | 0 |
| South center, station 20063 | 49 | 0 | 6 | 2 | 2 |
| Eastern Basin, station 20054 | 12 | 0 | 1 | 4 | 1 |
| Off Mount Desert, station 20056 | 9 | 3 | 0 | 2 | 0 |
| Southeast Basin, station 20064 | 8 | 2 | 8 | 3 | 1 |
| Georges Bank: | | | | | |
| Northwest, station 20047 | 20 | 0 | 0 | 0 | 0 |
| Southwest, station 20045 | 22 | 5 | 5 | 4 | 1 |
| East, station 20065 | 11 | 1 | 8 | 2 | 1 |
| Southeast, station 20068 | 7 | 9 | 2 | 2 | 1 |
| Southeastern slope, station 20069 | 5 | 7 | X | 3 | 0 |
| Eastern Channel, station 20071 | 5 | 8 | 2 | 5 | 2 |
| Browns Bank, station 20072 | 1 | 6 | 6 | 9 | 1 |
| Off southern Nova Scotia: | | | | | |
| Station 20074 | 1 | 6 | 10 | 7 | 1 |
| Station 20077 | 1 | 2 | 4 | 15 | 3 |

With the advance of the season and hand in hand with the augmentation of diatoms, peridinians of all species so diminish in numbers that in 1920 they had practically disappeared from the two productive centers for diatoms in the two sides of the gulf by mid-April and were so scarce elsewhere that counts of the relative numbers of the several species of Ceratium are no longer significant. But when they reappear in the Massachusetts Bay region late in April or early in May in the western side of the gulf, and in the Nova Scotian waters in the eastern, following the eclipse of the diatom flowerings, a complete reversal has taken place in the relative importance of the two leading species, for we have found *longipes* far more numerous than *tripos* during the first week in May at every station where the genus as a whole was sufficiently abundant for counts to be of value, only excepting the southwestern edge of Georges Bank, where the two species were about equally numerous (station 20129, May 18, 1920). In fact, *C. tripos* is then practically nonexistent within the gulf, or at best represented by occasional examples only. A slight recrudescence of *C. arctica* (or perhaps a fresh wave of immigration) apparently takes place during the first half of May, when occasional examples have been detected at most of our stations (except among the diatom swarms); and on the seventh of that month in 1915 *C. arctica* proved to be as abundant on German Bank (station 10271) as *C. longipes*, its area of abundance coinciding with the location of the cold

water from the Nova Scotian current (then near its maximum flow for the year), which corresponds to a northern extralimital origin.

*Relative abundance of species of Ceratium in samples, "Grampus" cruise, May 4 to 14, 1915, and "Albatross" cruise, May 1 to 17, 1920*[1]

| Locality | C. tripos | C. longipes | C. arctica | C. fusus |
|---|---|---|---|---|
| Off Cape Ann, 1920, station 20124 | 1 | 30 | 0 | 0 |
| Off Cape Ann, 1915, staton 10266 | 1 | 39 | 8 | 4 |
| Off Cape Cod, 1920, station 20125 | 2 | 12 | 1 | 1 |
| Eastern Basin, 1915: | | | | |
| Station 10269 | 0 | 30 | 5 | 1 |
| Station 10270 | 0 | 20 | 1 | 1 |
| German Bank, 1915, station 10271 | 0 | 100+ | 100+ | 0 |
| Off Lurcher Shoal, 1915, station 10272 | 1 | 18 | 6 | 0 |
| North of Cape Ann, 1915, station 10278 | 0 | 12 | 1 | 0 |
| Southwestern Basin, 1920, station 20127 | 1 | 10 | 0 | 0 |
| Western part of Georges Bank, 1920, station 20128 | 25± | 25± | 0 | 1 |
| Southern edge of Georges Banks, 1920, Station 20129 | 0 | 25± | 0 | 0 |

[1] In this table no account is taken of the intermediates between *C. arctica* and *C. longipes*, although occasional examples of this sort were noted at most stations, because it was usually possible to refer the specimens to one species or to the other.

*C. longipes* continues the dominant species in the Gulf during the last half of May and throughout the month of June, when peridinians play an increasingly important rôle in the phytoplankton, as illustrated by the following counts of samples for the year 1915:

| Locality | C. tripos | C. longipes [1] | C. arctica | C. fusus |
|---|---|---|---|---|
| Off Cape Cod, May 26, station 10279 | 3 | 100+ | 0 | 1 |
| Off Mount Desert, June 11, station 10284 | 0 | 9 | 0 | 0 |
| Southeast Deep, June 25, station 10298 | (2) | (3) | 0 | 0 |
| Western Basin, June 26, station 10299 | 4 | 19 | 0 | 0 |

[1] Including occasional intermediates between it and *arctica*.
[2] Occasional.
[3] Swarm.

During this period *C. arctica* practically vanishes from the gulf, where our only June record of it is in the extreme northeast corner (Bigelow, 1917, p. 328, stations 10283, 10284, and 10286), and off Petit Passage in the southern side of the Bay of Fundy (June 10, 1915). *C. arctica* has been detected only twice in the gulf in the later summer or in autumn—that is, off Mount Desert, August 13, 1914 (Bigelow, 1917, p. 323, station 10248), and off Cape Ann, August 31, 1915 (station 10306)—though it persists in some numbers along the southern coast of Nova Scotia at least as late in the season as August (Bigelow, 1917, p. 323).

*C. tripos* reappears in numbers in the Gulf of Maine tow nettings in July. During the first half of that month, when the surface temperature of the gulf is approaching its seasonal maximum and Ceratium its annual plurimum of abundance, *C. longipes* has still predominated over *C. tripos* (usually markedly so) at almost all the stations, both in the western half of the gulf generally,[38] over Georges Bank as a whole, and across the whole breadth of the shelf abreast of southern Nova Scotia (Bigelow, 1917, p. 323). Late in July, 1914, we found *C. tripos* dominating off the

[38] At one station (10301) off the mouth of the Grand Manan Channel, July 15, 1915, there were 16 *longipes* to 3 *tripos*.

southeast slope of Georges Bank (station 10220), where *longipes* slightly outnumbers it in March and April (p. 407), and local phenomena of the same sort noted on the western part of the bank and in the southwest corner of the basin of the gulf in July, 1913 and 1914 (station 10058, July 8, 1913; station 10215, July 20, 1914), fore-

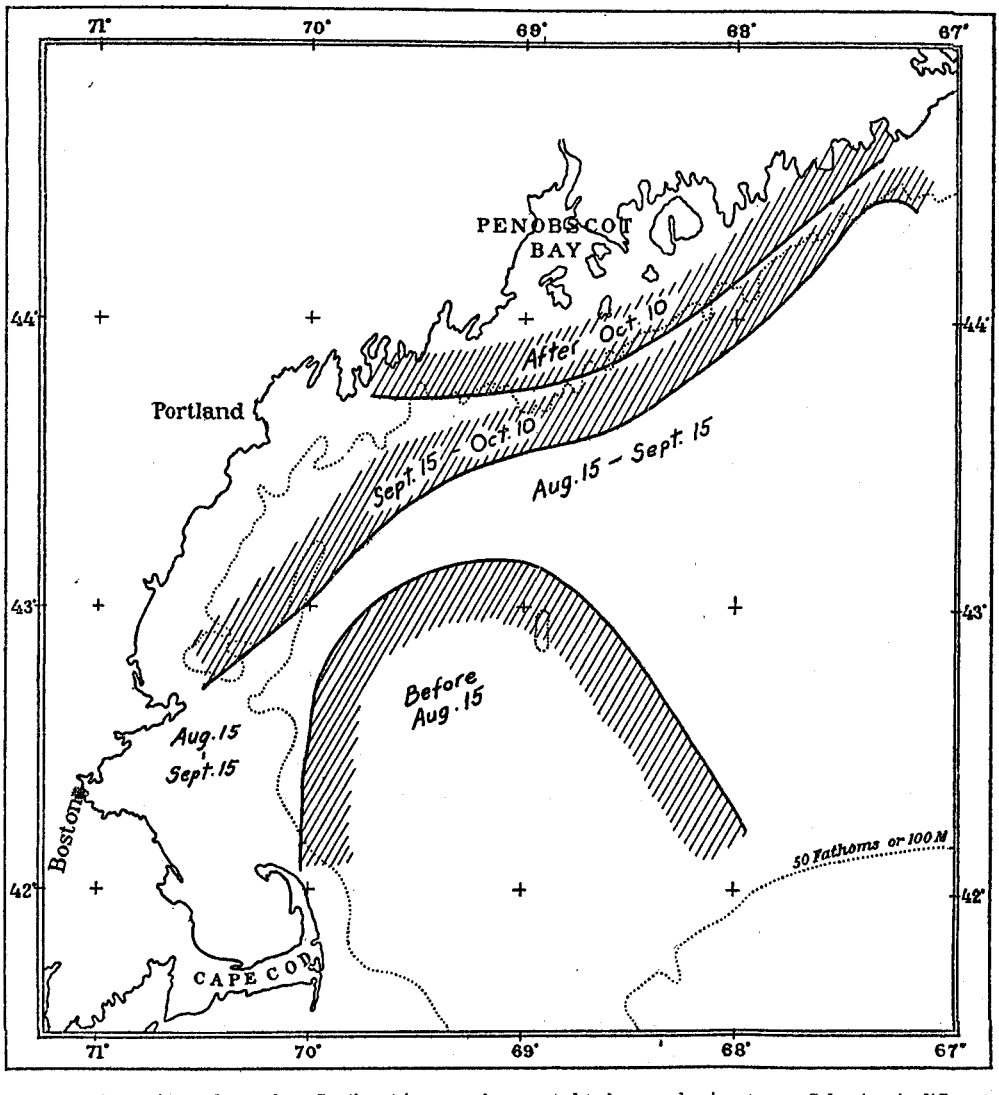


FIG. 110.—Approximate dates when *Ceratium tripos* may be expected to become dominant over *C. longipes* in different parts of the Gulf of Maine

shadow a second alteration in the mutual relationship of the two species during the latter part of the summer, which once more makes *C. tripos* the dominant member of the pair.

A detailed account of the augmentation of *C. tripos* in the gulf with the advance of the summer can not be given as yet, but the approximate dates when it may be

expected to dominate the plankton in different regions, by our experience, are laid down on the chart (fig. 110). Our records show that it outnumbers or replaces *C. longipes* first in the offshore parts of the gulf, and that it may be expected to predominate over the latter in the western and central deeps and in the eastern branch of the basin north to latitude 43° or 43° 30′ N. by mid-August.

The following counts of samples from corresponding pairs of stations illustrate how completely the relative importance of the two species is reversed between June or the first half of July and the first days of August, and how nearly to the vanishing point *C. longipes* sinks in these particular parts of the gulf as *C. tripos* multiplies.

| General locality | Relative numbers in samples | |
|---|---|---|
| | C. longipes | C. tripos |
| 100-meter curve, off Cape Cod: | | |
| July 8, 1913, station 10057 | 43 | 15 |
| Aug. 5, 1913, station 10086 | 5 | 60 |
| 50-meter curve, northeast of Cape Cod: | | |
| July 19, 1914, station 10213 | 50 | 1 |
| Aug. 28, 1914, station 10264 | 1 | 23 |
| Southwest part of deep basin: | | |
| July 19, 1914, station 10214 | 63 | 3 |
| Aug. 23, 1914, station 10256 | 5 | 76 |
| Western Basin, off Cape Ann: | | |
| June 26, 1915, station 10299 | 19 | 4 |
| Aug. 31, 1915, station 10307 | 1 | 50+ |
| Eastern Basin, lat. 43° 17′: | | |
| Aug. 13, 1914, station 10249 | 13 | 47 |
| Eastern Basin, lat. 43° 08′: | | |
| Sept. 1, 1915, station 10309 | 4 | 28 |

A corresponding preponderance of *tripos* (32 to 2 *longipes*) likewise characterized a haul made by Capt. John McFarland off Chatham (Cape Cod) on August 26, 1913.[39]

The multiplication of or intrusion by *C. tripos* is apparently a slower process, and *C. longipes* persists correspondingly longer as an important factor in the plankton over the northeastern part of the basin. Thus in mid-August of 1914, when *tripos* already greatly predominated right across the gulf along a line from Cape Ann to Cape Sable, *C. longipes* still outnumbered it a few miles to the northward, as follows:

| Locality | Number in samples | |
|---|---|---|
| | C. longipes | C. tripos |
| Off Lurcher Shoal Aug. 12, 1914, station 10245 | 105 | 1 |
| Extreme northeast corner of basin, Aug. 12, 1914, station 10246 | 62 | 1 |
| Off Mount Desert Rock, Aug. 13, 1914, station 10248 | 29 | 1 |
| Off Penobscot Bay, Aug. 14, 1914, station 10250 | 32 | 2 |
| Off Cape Elizabeth, Aug. 14, 1914, station 10251 | 115 | 1 |

In 1913 *longipes* still continued about as numerous as *tripos* in the deep hauls in the eastern side of the gulf (latitude about 43° 25′ N., stations 10092 and 10093) on August 11 and 12, by which date *tripos* was already predominant in the western basin (stations 10088 and 10089).

[39] In the report on the cruise of 1912 the two species were listed together as *tripos* (Bigelow, 1914).

Whether the summer augmentation of *C. tripos*, accompanied as it is by a decrease on the part of *C. longipes*, actual as well as relative, originates as the result of local propagation of the few specimens that survive the spring, or from immigration from the south and west, or of both processes, is not yet clear; but in either case the central deeps may be looked upon as its chief area of multiplication in the Gulf of Maine. From this center it gradually expands its area of abundance right in to the immediate vicinity of the land where *C. longipes* decreases in abundance as the numbers of *C. tripos* augment, just as happens offshore.

*Relative abundance of the two predominant species of Ceratium, July and August, 1914*

| Station | C. longipes | C. tripos | Station | C. longipes | C. tripos |
|---|---|---|---|---|---|
| 10213 | 50 | 1 | 10249 | 13 | 47 |
| 10216 | 38 | 14 | 10250 | 32 | 2 |
| 10223 | 21 | 1 | 10251 | 115 | 1 |
| 10225 | 9 | 4 | 10253 | 2 | 10 |
| 10227 | 34 | 1 | 10254 | 4 | 50 |
| 10229 | 21 | 1 | 10255 | 0 | 50 |
| 10230 | 60 | 0 | 10256 | 5 | 76 |
| 10245 | 105 | 2 | 10258 | 1 | 11 |
| 10246 | 62 | 4 | 10264 | 1 | 23 |
| 10248 | 29 | 1 | | | |

*C. tripos* usually predominates near Cape Cod and in the southern part of Massachusetts Bay by the last week in August. For example, we found 23 *tripos* to 1 *longipes* off the east side of Stellwagen Ledge on August 28, 1914 (station 10264), while the relationship between the two species was much the same near Provincetown on the 29th of the month in 1916 (station 10298). In some years, at least, this practical elimination of *C. longipes* from the catches happens equally early in the season near Cape Ann, where we found *C. tripos* much the more abundant of the two as early as August 22 in 1914 (station 10253, five times as many *tripos* as *longipes*), but in other summers *C. longipes* persists in numbers in the northeastern part of Massachusetts Bay long after *tripos* has taken its place off Cape Cod. This was the case in 1915, when the former predominated off Cape Ann on August 31 (station 10306, 17 *longipes* to 2 *tripos*) and about equaled *tripos* there as late as September 29 (station 10320), though the latter abounded, with almost no *longipes*, inside Stellwagen Ledge and near the tip of Cape Cod, only a few miles distant to the south, on the same day (stations 10221 and 10222). In fact, it was not until well into October that *tripos* finally replaced *longipes* at our standard station off Gloucester during that autumn (station 10330, October 18, 100+ *tripos* to 1 *longipes*). Probably the fact that *C. longipes* may persist in abundance in the northern side of Massachusetts Bay long after it has dwindled almost to the vanishing point in the southern, and such variations as I have just recorded in the precise date when *C. tripos* replaces it off Cape Ann from summer to summer, are due to variations in the drift flowing southward past Cape Ann, which may be expected to bring a constant supply of *C. longipes* with it throughout the summer, for the latter continues predominant over *C. tripos*, or at the least is a large factor in the peridinian plankton of the more northerly and easterly parts of the coastal belt of the gulf until well into the autumn as follows:

*Relative numbers of C. tripos and C. longipes in samples*

| General locality and date | C. longipes | C. tripos | General locality and date | C. longipes | C. tripos |
|---|---|---|---|---|---|
| Off Isles of Shoals: | | | Near Mount Desert Island: | | |
| Aug. 5, 1913, station 10105 | (1) | (1) | Aug. 13, 1913, station 10099 | (1) | (1) |
| Nov. 1, 1916, station 10400 | 1 | 3 | Aug. 18, 1915, station 10305 | 20+ | 1 |
| Off Cape Elizabeth: | | | Sept. 15, 1915, station 10317 | 13 | 3 |
| Aug. 14, 1913, station 10103 | 40 | 18 | Oct. 9, 1915, station 10328 | (2) | (4) |
| Aug. 14, 1914, station 10251 | 115 | 1 | Off Machias, Me.: | | |
| Sept. 20, 1915, station 10319 | (2) | (2) | Aug. 13, 1913, station 10098 | 26 | 7 |
| Off Penobscot Bay: | | | Aug. 12, 1914, station 10247 | 42 | 3 |
| Aug. 14, 1914, station 10250 | 32 | 2 | Sept 11, 1915, station 10316 | 9 | 25 |
| Sept. 16, 1915, station 10318 | 13 | 5 | Oct. 9, 1915, station 10327 | (2) | (3) |
| Oct. 9, 1915, station 10329 | 8 | 5 | | | |

[1] Numbers about equal. [2] Predominant. [3] Fewer. [4] Not found.

Just how rapidly *C. tripos* may be expected to spread eastward toward Cape Sable from its offshore center of abundance in the center of the gulf is yet to be learned. It is established, however, that on August 12, 1913 (station 10095), and again on September 2, 1915 (station 10311), the two species were present in roughly equal numbers on German Bank, where *longipes* alone was found in June, 1915 (station 10290). *Tripos* greatly outnumbered *longipes* near Lurcher Shoal (station 10245) and in the neighboring part of the basin (station 10246) as early as August 12 in 1914. It is also probable that *tripos* will usually be found to dominate close in along the west Nova Scotian coast before the middle of September, for it outnumbered *longipes* near land off Shelburne (a few miles east of Cape Sable) on the 6th of that month in 1915 (station 10313, 30 *tripos* to 12 *longipes*), where we had found *longipes* predominant the previous June,[40] as well as during July and August of 1914.[41]

*Ceratium tripos* comes finally and definitely to dominate over *C. longipes* in all parts of the gulf by the middle or end of October, including even the coastal belt east of Penobscot Bay. McMurrich (1917) did not find *longipes* at all at St. Andrews after the 16th of that month, whereas *C. tripos* occurred there regularly from that date until March 2, when Ceratium disappeared with the inception of the vernal flowering of diatoms.

*C. tripos* has greatly outnumbered *C. longipes* in all the parts of the gulf we have visited in midwinter; in fact, the latter, if not wanting, was at least so rare that I failed to find it in several of the samples examined.

*Relative abundance of the several species of Ceratium in winter, from samples*

| Locality | C. longipes | C. tripos | C. fusus | C. arcticum |
|---|---|---|---|---|
| Massachusetts Bay, Dec. 29, 1920, station 10488 | 1 | 19 | 2 | 2 |
| Off Cape Ann, Dec. 29, 1920, station 10489 | 1 | 20 | 1 | 0 |
| Western Basin, Dec. 29, 1920, station 10490 | 0 | 50 | 2 | 0 |
| Off Cape Cod, Dec. 30, 1920, station 10491 | 2 | 30 | 3 | 0 |
| Off Merrimac River, Dec. 30, 1920, station 10492 | 1 | 18 | 1 | 0 |
| Off Isles of Shoals, Dec. 30, 1920, station 10493 | 0 | 15 | 3 | 1 |
| Off Cape Elizabeth, Dec. 30, 1920, station 10494 | 0 | 15 | 3 | 1 |
| Off Penobscot Bay, Jan. 1, 1921, station 10496 | 1 | 40 | 2 | 0 |
| Off Mount Desert Island, Jan. 1, 1921, station 10497 | 2 | 35 | 4 | 3 |
| Off Machias, Me., Jan. 4, 1921, station 10498 | 1 | 15 | 1 | 0 |
| Fundy Deep, Jan. 4, 1921, station 10499 | 1 | 52 | 7 | 0 |
| Eastern Basin, Jan. 4, 1921, station 10500 | 3 | 20 | 13 | 0 |
| Eastern Basin, Jan. 5, 1921, station 10502 | 7 | 43 | 1 | 0 |
| Off Yarmouth, Nova Scotia, Jan. 4, 1921, station 10501 | 1 | 19 | 2 | 0 |

[40] Station 10291, 19 *longipes*, 1 *tripos;* station 10294, many *longipes* and intermediates between it and *arctica*, no *tripos*.

[41] Station 10232, July 28, many *longipes*, no *tripos;* station 10233, July 28, 42 *longipes*, 3 *tripos;* station 10243, August 11, many *longipes*, no *tripos*.

The hauls listed above are further interesting as showing that *C. arcticum*, so widely distributed in spring (p. 407) but not detected in the gulf in late summer or autumn, reappears there in small numbers in midwinter, but curiously enough along its northern and western shores and not in the eastern side.

There is no reason to suppose that any notable alteration takes place in the relative numbers of the several species of Ceratium during the months of January and February; certainly not off Gloucester during the winter of 1913, where *C. tripos*

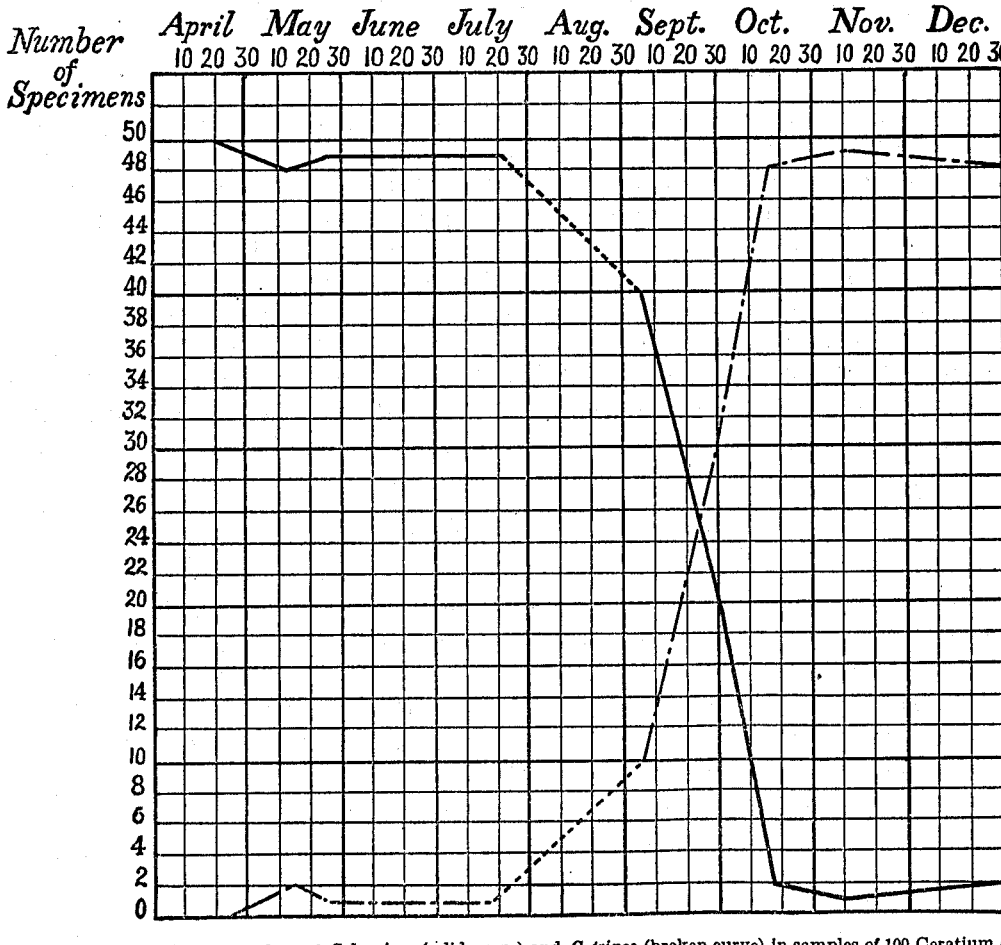


FIG. 111.—Proportionate numbers of *C. longipes* (solid curve) and *C. tripos* (broken curve) in samples of 100 Ceratium of all species in the Massachusetts Bay region at different seasons, 1913 to 1922

continued predominant until the diatom flowerings commenced in March. Doctor McMurrich's plankton lists also show this to have been the case at St. Andrews during 1916.

The mutual fluctuations of *C. tripos* and *C. longipes* in the northern part of Massachusetts Bay are represented in the accompanying diagram (fig. 111) based on the combined data for the years 1912, 1913, 1915, 1916, and 1920, which will serve equally for the offshore parts of the gulf if the reversal of dominance be imagined as

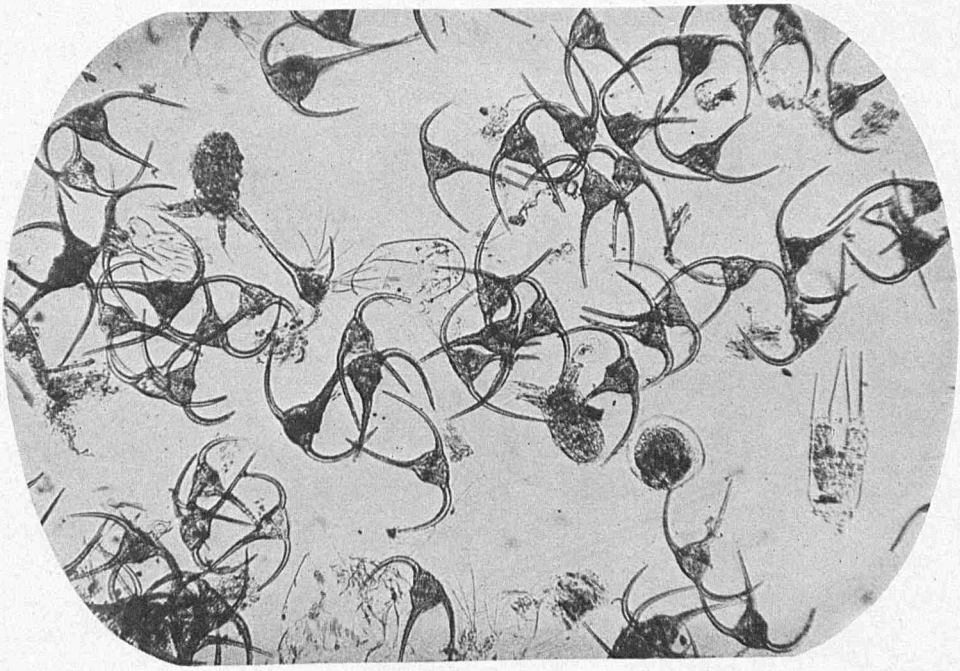

FIG. 112.—Phytoplankton dominated by *Ceratium longipes*, with only an occasional *C. tripos*. The photograph also shows copepod nauplii. Surface haul off Cape Elizabeth, August 14, 1914 (station 10251). × 50

FIG. 113.—Monotonous *Ceratium tripos* plankton, with occasional *C. fusus*, Peridinium, and copepod nauplii. Surface haul off Cape Cod, October 26, 1915 (station 10336). × about 25

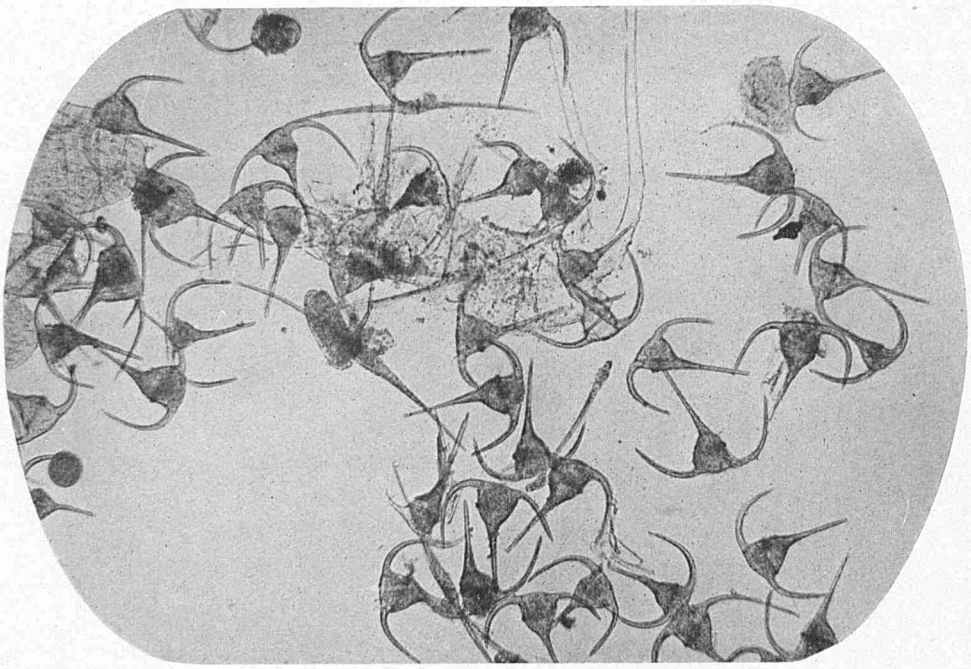

FIG. 114.—Phytoplankton dominated by *Ceratium tripos* with fewer *C. fusus*. Surface haul in Massachusetts Bay, October 26, 1915 (station 10337). × 50

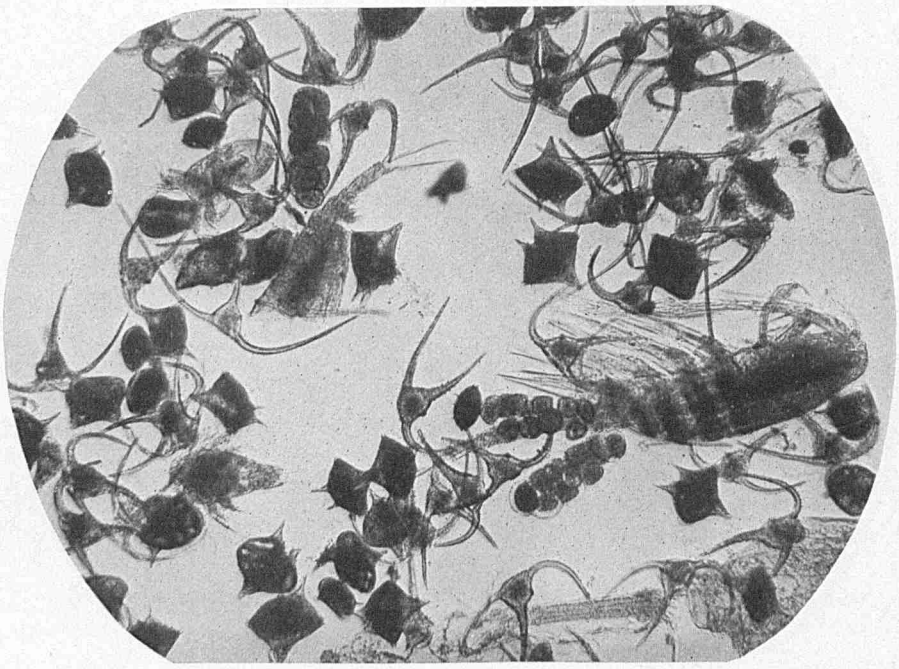

FIG. 115.—Peridinian plankton dominated by Peridinium, with *Ceratium longipes* and *C. arctica*. Surface haul, eastern side of basin of the Gulf of Maine, May 6, 1915 (station 10270). × 40

taking place a month or so earlier in the season. With similar emendation in date in one direction or the other, it would apply to Massachusetts Bay equally in an "early" year, such as 1913, or in a late year.

The mutual fluctuations of *C. tripos* and *C. longipes* may be summarized as follows for the Gulf of Maine as a whole:

Early in spring when the vernal augmentation of diatoms is at its height, Ceratium (and indeed all peridinians) practically vanishes from the gulf, an event taking place first along the northwest coast, where the diatoms flower earliest, and soon afterwards in other parts of the gulf. After the flowerings of diatoms dwindle, *C. longipes* (fig. 112) multiplies until July, when all the gulf, except for a narrow zone along its northeast and east coasts, supports an abundant Ceratium plankton. During July *C. tripos* (figs. 113 and 114) multiplies in the central deeps. As the summer advances the area of abundance of *C. tripos* expands coastwise and the stock of *C. longipes* dwindles until *tripos* becomes predominant along the southwestern, the eastern, and finally along the northwestern and northern coasts of the gulf, with *C. longipes* persisting latest as an important factor in the plankton in the region between Cape Elizabeth and the Grand Manan Channel. *C. tripos* predominates throughout the winter, but even then, when *C. longipes* is at its lowest ebb, the latter has occurred in small numbers at most of our stations; nor does either species vanish wholly from the gulf at any season, though either may be so scarce when the other is at its peak of abundance, as well as during the flowering period of the diatoms, that careful search of considerable amounts of plankton may be required to reveal its presence.

The seasonal changes in the relative abundance of these two peridinians must not, of course, be understood to take place in as orderly a manner as they are represented here, for they are undoubtedly accompanied by temporary interruptions and even reversals, which would alter the smooth curves to a succession of zig-zags, were daily or weekly records available. In fact, such a reversal is known to have taken place in 1915 off Machias, Me., where *longipes* was predominant on July 15 (in the proportion of 16 *longipes* to 3 *tripos* at station 10301), was outnumbered by *tripos* on September 11 (station 10316), was again predominant on October 9 (station 10327), and would doubtless have been found outnumbered by *tripos* a month after that, had we visited that region again later in the season. Sporadic alternations of this sort do not weaken the general thesis that the succession, as here outlined, is a regular and characteristic feature of the planktonic cycle of the gulf, however, though its time table varies from year to year, as do all other seasonal changes in the sea.

In the foregoing account I have purposely refrained from alluding to the status of the two leading species of Ceratium on Georges Bank in late summer or autumn (*longipes* predominates there in spring and early summer (p. 408) as it does elsewhere in the gulf), because no collection of phytoplankton has yet been made on the bank during the half year, August to February.

A fourth species of Ceratium—*C. fusus*—has been taken so often in our tow nets that it deserves brief mention, though it is never predominant in the Gulf of Maine. *C. fusus* has been found at most of the stations where the genus as a whole

occurs in any numbers, and at all seasons,[42] both in the inner parts of the gulf, on Georges Bank, on Browns Bank, and off southern Nova Scotia (Bigelow, 1917, p. 323). It has been lacking, or at least so rare as to be overlooked, whenever diatoms swarm, in which it parallels the more abundant species, *tripos* and *longipes*; occasionally, also, among catches of Ceratium plankton. However, no more definite seasonal fluctuation in abundance has been established for it in the Gulf of Maine, nor any regional concentration. Notwithstanding its nearly universal distribution in the gulf and almost constant occurrence there, it seldom rivals the tricornuate forms of Ceratium in abundance, the only instance of this sort so far recorded being that *C. tripos* and *C. fusus* were about equally numerous in the center of the gulf on August 10, 1913 (Bigelow, 1915, p. 334, station 10090).

The sporadic occurrence of the tropical species, *C. macroceras*, in the inner parts of the gulf has already been alluded to (p. 393). *C. bucephalum* (Paulsen, 1908, p. 77, fig. 100) has also been recognized once in early spring (mouth of the Bay of Fundy, station 20079, March 22, 1920); likewise off the southeast face of Georges Bank on February 22, 1920 (station 20044), and south of Marthas Vineyard, November 11, 1916 (station 10406).

### Other peridinians

Only two other genera of peridinians have so far been definitely recognized in the Gulf of Maine—Peridinium and Dinophysis—though others doubtless occur. The former has been noted in practically every summer sample in which Ceratium occurs (Bigelow, 1915, p. 334); that is, it is practically universal in the gulf except in regions and at times where diatoms flower abundantly, (and even there it may be present but overshadowed by their masses) or when the plankton is so scanty that it may have been overlooked, though actually present, as, for example, at several of our stations in the early spring of 1920. Peridinium is usally a minor element in the phytoplankton; far less numerous than its companion genus Ceratium. In summer and early autumn the only exceptions to this rule have been on the western part of Georges Bank, July 20, 1914 (stations 10215 and 10216); near Mount Desert Island, September 15, 1915 (station 10317); and off Penobscot Bay, October 9 of that same year (station 10329), where the genus as a whole (represented by several species) was nearly as numerous as either species of Ceratium. Peridinium is relatively even less important in early spring, as exemplified by our cruises of March and April, 1920, when it was represented by few or occasional examples only, though it occurred at about half the stations, distributed over the gulf generally [43] except in the rich diatom centers. In May of 1915, however, Peridinium not only occurred at every station where Ceratium was detected, but rivaled the latter in abundance in the eastern side of the gulf (fig. 115, stations 10270, 10272, and 10273).

As it was again an important element in the plankton of the southwestern part of the basin and of the South Channel on May 17, 1920 (stations 20127, 20128, and

[42] For records of its occurrence in the summer hauls of 1913 and 1914 see Bigelow, 1915, p. 333, and 1917, p. 323. During the autumn of 1916 it was recognized at stations 10400 to 10406; during the spring of 1920 at stations 20044 to 20046, 20048, 20049, 20052 to 20055, 20057, 20063 to 20065, 20067, 20068, 20070 to 20074, 20077, 20080, 20086, 20087, 20093, 20096 to 20098, 20101, 20108, 20111, 20112, 20116, 20118, 20125, and 20128; and at all the stations during December, 1920, and January, 1921 (stations 10488 to 10502).

[43] Recorded for stations 20044, 20045, 20046, 20048, 20057, 20060, 20064, 20065, 20068, 20071, 20074, 20075, 20080, 20086, 20088, 20089, 20096, 20111, 20118, and 20119 for these months.

20129), it is probable that a considerable production of Peridinium takes place during that month. Doctor McMurrich likewise notes Peridinium as appearing in May at St. Andrews, and occurring in some numbers from June until September, while Willey (1913) describes it as sometimes abundant there in July and August.

Specific identification of the several members of this genus which occur in our tow nettings must await a specialist, but I may note that *P. depressum* [44] was the species chiefly responsible for the May maximum in the eastern half of the gulf in 1915, whereas most of the specimens so far identified in the rich catches from the other side of the gulf in the same month of 1920, especially station 20127, were *P. crassipes.* Inasmuch as the few Peridinium so far named from the summer and autumn catches likewise belong to *P. crassipes*, it is probable that that species occurs in the gulf throughout the year. *P. pallidum* is also recorded from the center of the gulf (Bigelow, 1915, p. 334, station 10090). The only species so far identified, in the estuarine waters off St. Andrews is *P. divergens*, typically a neritic form (Willey 1913; McMurrich, 1917).

The genus Dinophysis has been noted often enough in a preliminary examination of the catches to show that it may be expected anywhere in the gulf in summer, at which season its presence has been established in the central basin, off Lurcher Shoal, in the northeast corner of the gulf, in the coastal belt between Cape Elizabeth and Penobscot Bay, on the northwest part of Georges Bank, and off Shelburne, Nova Scotia; but only occasional specimens have been noticed among the Ceratium. Until its presence in the hauls has been fully listed, discussion of its seasonal and regional distribution would be idle; but its absence or at least rarity in the spring hauls for the years 1913, 1915, and 1920 suggests that it is at its lowest ebb at that season. Most of our records for Dinophysis are based on *D. norvegica*, a species widely distributed in northern waters (Paulsen, 1908). *D. homunculus*, native to warm seas and a valuable index for warm currents because it is easy to recognize, has not been found within the gulf although a lookout has been kept for it, but was noted south of Marthas Vineyard on October 1, 1915 (station 10332).

No doubt the plankton of the gulf will finally be found to include many if not most of the naked peridinians known from other seas.[45] So far, however, I can only record the presence of considerable numbers of an unidentified gymnodinid among the scanty plankton of the Eastern Basin on March 3, 1920 (station 20055).

## DIATOMS

It is probable that with sufficient search all the diatom species that are pelagic in northern seas would be found in the Gulf of Maine at one season or another, but few species or groups of species, and fewer genera, are ever sufficiently abundant there to dominate the plankton.[46]

The following remarks apply chiefly to the open gulf. Quite different associations of diatoms are to be expected in its estuarine tributaries, especially a rich representation of brackish-water species that have been practically nonexistent at our *Grampus*, *Albatross*, and *Halcyon* stations. No study has yet been made of the plankton of

[44] Identifications follow Paulsen (1908).
[45] For descriptions of these, see Kofoid and Swezy's (1921) monograph and beautiful illustrations.
[46] On the identifications of the diatoms see p 382.

the various river mouths, bays, and harbors between Cape Cod and Grand Manan, but McMurrich (1917), Bailey (1917), and Fritz (1921) have published extensive lists of the diatoms occurring in the neighborhood of St. Andrews as well as at other localities in the Bay of Fundy and its tributaries, and Fish (1925) has done so for Woods Hole diatoms.

The survey of the diatoms, like that for the peridinians (p. 407), may commence at the end of the winter or first days of spring. At this season, as exemplified by the cruises of the *Albatross* during February and March, 1920, the diatom communities of the gulf fall naturally into three groups, according to locality—1, the sparse diatom flora of the whole deep basin and of the eastern half of the gulf from the mouth of the Bay of Fundy and the Nova Scotian coast on the one side to Cape Cod on the other, and from the 100-meter contour on the north to the shallows of Georges Bank on the south (p. 383); 2, the rich area on the western part of Georges Bank (p. 385); and 3, an even more productive zone along the western shore of the gulf (p. 383).

Over all the considerable expanse of the first area, noted on the chart (fig. 104) as "sparse mixed", Coscinodiscus (mingled with peridinians, as I have noted above) is the dominant diatom genus in March (dominant, however, not so much for its own numbers as for the scarcity of anything else), with the easily recognized *C. asteromphalus* (p. 437) its chief though not its only representative at that time. At most of the March stations offshore the three species of Chætoceras—*C. decipiens*, *C. atlanticum*, and *C. criophilum*—were likewise practically universal in the gulf in 1920.[47] These three are all oceanic in nature (Gran, 1908 and 1912; Ostenfeld, 1913); such, likewise, are *Chætoceras densum*, *Rhizosolenia semispina*, and *R. styliformis*, which have been detected at 5, 12, and 2 of the February and March stations in 1920. The offshore hauls likewise yielded an unmistakable if minor component of neritic origin, contributed by the coastal belt or by the offshore banks, including the following species: *Chætoceras debile*, *Ch. didymum*, *Ch. diadema*, *Ch. mitra*, *Ch. sociale*, *Ch. laciniosum*, *Ch. contortum*, *Biddulphia aurita*, *Eucampia zodiacus*, Licnophora, *Lauderia glacialis*,[48] *Thalassiothrix nitschioides*, Skeletonema, and Thalassiosira. *Thalassiothrix longissima*, which is partly oceanic and partly neritic on the other side of the Atlantic (Ostenfeld, 1913), was likewise detected just north of Georges Bank (station 20064) and on its eastern part (station 20066) on March 11.

When the occurrence of these several neritic forms is plotted for March, 1920 (fig. 116), it is evident (as might be expected) that they were most abundant around the periphery of the gulf, and especially in its western side between Massachusetts Bay and Portland, where diatoms were flowering actively at the time (p. 383); very rare, indeed, in the central deeps of the gulf, to whose diatom flora neither the coast line nor the shallow banks were contributing appreciably. It is interesting that this was equally true of the eastern part of Georges Bank in that March, though neritic diatoms swarm there at other seasons (p. 391).

[47] These three species were detected side by side at 21 stations for February and March, 1920 (stations 20044 to 20046; 20048 to 20050, 20053, 20057, 20061 to 20069, 20071, 20082, 20086, 20088); *decipiens* and *criophyllum* at stations 20070, 20078, 20079, 20088; *atlanticum* and *criophyllum* at station 20052; *atlanticum* and *decipiens* at stations 20056 and 20083; *atlanticum* only at station 20054; and *decipiens* only at stations 20058, 20059, 20060, 20072, and 20084.

[48] This species is well described and figured by Gran (1908), but Dr. Albert Mann, in a letter, remarks that several other diatoms are confused under the synonyms there given.

I may add, for the sake of completeness, that much the same list of diatoms occurred over the whole breadth of the continental shelf off Shelburne, Nova Scotia, on March 19, 1920 (stations 20073 to 20076), though here the variety of species per

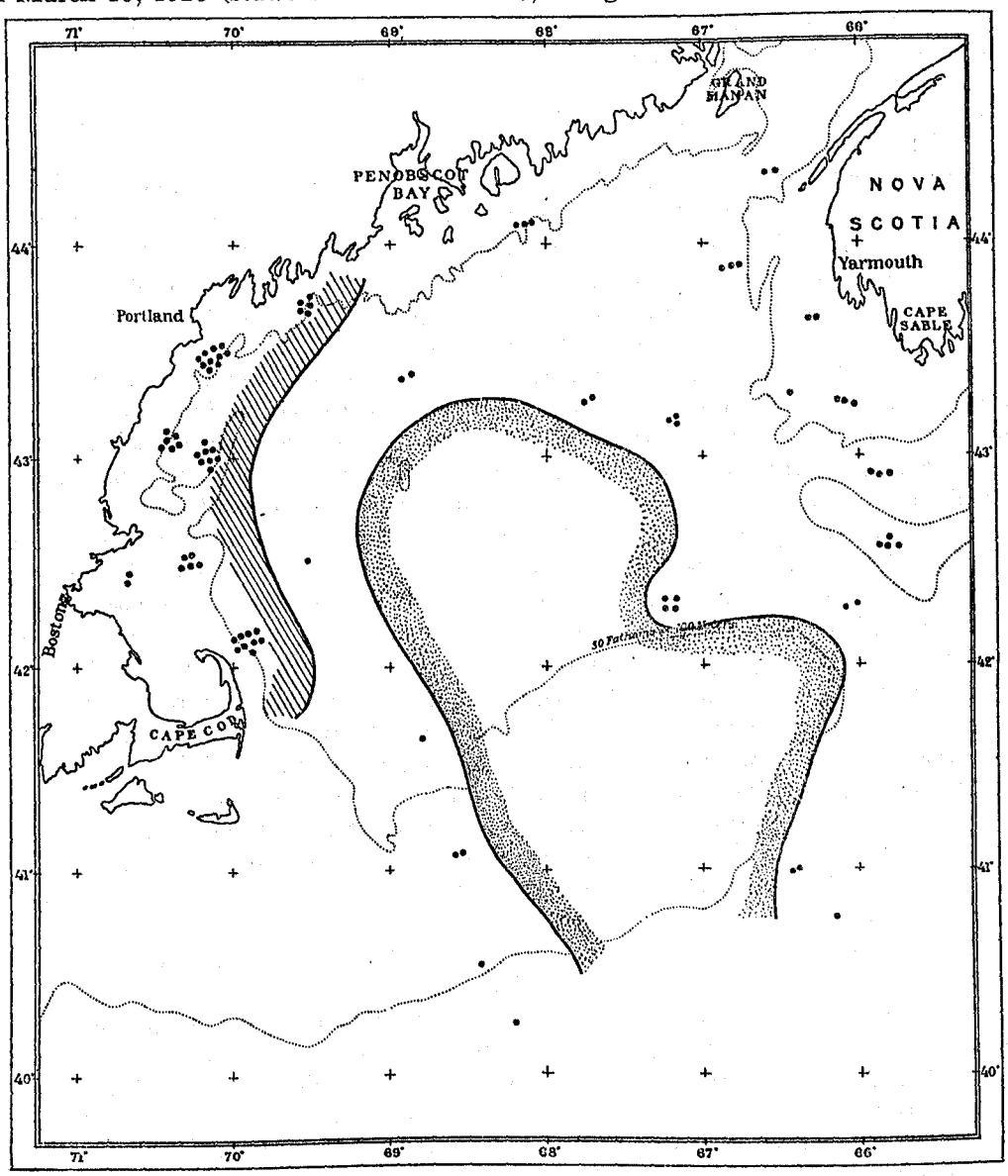


FIG. 116.—Occurrence of certain neritic diatoms in February and March, 1920, a dot for each locality record of the following species: *Biddulphia aurita*, *Chætoceras debile*, *Ch. contortum*, *Ch. diadema*, *Ch. didymum*, *Ch. laciniosum*, *Ch. mitra*, *Ch. sociale*, *Eucampia*, *Lauderia glacialis*, Lienophora, Skeletonema, *Thalassiothrix nitschioides*, and Thalassiosira. The hatched curve incloses the area where most of the stations yielded five or more of these species; the stippled curve where we found none of them

station averaged larger than in the neighboring parts of the Gulf of Maine, as, for example, in Browns Bank, in the Northern Channel, and along western Nova Scotia. The most interesting feature of the diatom communities along this line is

that Coscinodiscus was most numerous over the inner half of the shelf where it, together with the oceanic species *Chætoceras criophilum* and *Ch. decipiens*, composed the bulk of the catch (stations 20073 to 20075), but occurred only sparsely at the outer stations (stations 20076 and 20077); whereas neritic species (notably *Ch. mitra*, *Ch. diadema*, *Ch. laciniosum*, *Ch. debile*, and *Thalassiothrix nitschioides*) were most plentiful over the outer half of the shelf (stations 10275 and 10276), not next the land as one might have expected, and even occurred outside the continental slope as well (station 20077).

Such a concentration of neritic forms at the outer stations off Shelburne instead of at the inner is intelligible when hydrographic conditions are taken into account, because the axis of the cold Nova Scotian current of low salinity, itself essentially neritic in its biologic aspect, occupied precisely the same location at the time.

The abundant diatom community already mentioned (p. 383) as characterizing the western part of Georges Bank on February 23, 1920, consisted chiefly of slimy masses of the tiny neritic species *Chætoceras sociale*, not of Coscinodiscus nor of the oceanic species of Chætoceras, though *Ch. decipiens*, *Ch. criophilum*, and *Ch. atlanticum* all occurred there, as did the neritic forms *Rhizosolenia shrubsolei*, *Eucampia zodiacus*, and Leptocylindrus. This flowering of *Ch. sociale* was very local, as seems usually to be the case when concentrations of diatoms occur on Georges Bank, and was confined strictly to the comparatively shoal waters of the bank (stations 20046 and 20047). *Ch. sociale* was sought in vain in the tow netting over the edge only 20-odd miles distant (station 20045), where *Thalassiothrix nitschioides* and an occasional cell of Guinardia and *Chætoceras diadema* were the only neritic diatoms recognized. The very sparse community of diatoms in the basin immediately to the north of the bank (station 20048) consisted of the same oceanic species of diatoms that characterize the central parts of the gulf generally in February and March—that is, Coscinodiscus, *Chætoceras atlanticum*, *Ch. criophilum*, *Ch. decipiens*, *Ch. boreale*, *Ch. densum*, *Rhizosolenia semispina*, and *Thalassiothrix longissima*.

No tropical phytoplankton was found at our stations outside the continental slope in February or March, 1920 (stations 20044, 20069, and 20077).

Our work for 1913 had already suggested that the diatoms that first commence rapid multiplication in the Cape Ann–Cape Elizabeth region in spring are the forerunners of the vernal flowerings that are the most spectacular event in the yearly planktonic cycle of the Gulf of Maine. These are the several species of Chætoceras that may rival the peridinians here and there along the coast even as early as the last of January or early February, especially in Ipswich Bay. Shortly thereafter the genus Thalassiosira begins flowering, a phenomenon which we have been able to follow through parts of the years 1913, 1915, and 1920.

In 1920 the tow at the mouth of Massachusetts Bay contained Thalassiosira, besides several other kinds of diatoms, on March 1 (station 20050; see list p. 423); and Thalassiosira and Chætoceras must both have commenced flowering actively even earlier than this alongshore between Cape Ann and Cape Elizabeth that year, the "rich" diatom area outlined on the chart (fig. 104) being dominated by these two genera on March 4 and 5.

The list given below (p. 425) for the station near Cape Elizabeth (20059), which was paralleled near the Isles of Shoals (station 20060), and the dominance by Thalas-

siosira may be taken as typical of this part of the coastwise belt during the first half of March. A few miles farther out at sea, however, on the same day, between the Isles of Shoals and Jeffrey's Ledge (station 20061), the several species of Chætoceras, combined, dominated instead of Thalassiosira, though there was also a considerable amount of the latter in the catch; in fact, practically a repetition of the list of species given for station 20059 (p. 425).

In the spring of 1921, when we found the vernal flowering just commencing along the western shores of the gulf during the first week of March, there was a typical though still only moderately plentiful Thalassiosira–Chætoceras plankton in Massachusetts Bay on the 4th (station 10505), dominated by the former, with *Chætoceras debile, Ch. didymum, Ch. diadema, Ch. decipiens, Biddulphia aurita, Ditylium brightwellii,* Coscinosira, Coscinodiscus, *Lauderia borealis,* and *Rhizosolenia semispina. Thalassiosira nordenskioldi,* with *Biddulphia aurita,* also dominated a very sparse diatom plankton in Ipswich Bay that same day (station 10506), with a strong sprinkling of *Ditylium brightwellii,* a few *Chætoceras criophilum,* Lauderia, and Coscinodiscus. North of this (stations 10507 and 10508) and farther offshore (stations 10509 and 10510) the water was still almost clear of diatoms except for Coscinodiscus.

In a tow near Seguin Island, March 4, 1920 (station 20058) *Lauderia glacialis,* not Thalassiosira or Chætoceras, dominated a moderately plentiful diatom plankton, which also included *Chætoceras decipiens, Ch. debile, Ch. diadema,* and other species not yet determined, *Rhizosolenia semispina* and *R. setigera, Thalassiosira nordenskioldi, Thalassiothrix nitschioides,* and Coscinodiscus. The assemblage of species was much the same near Mount Desert Island the day before, though the plankton was extremely scanty (station 20056; see list, p. 426). The inference from this is that Lauderia began flowering in this zone earlier in the season than either Thalassiosira or Chætoceras. We have found no evidence of such a sequence either between Cape Cod and Cape Elizabeth in the one side of the gulf or off western and southern Nova Scotia in the other (the latter marked "sparse diatom" on the chart, fig. 104), where tows during the second and third weeks of March, 1920, shortly antedating the local flowerings of Thalassiosira and Chætoceras, yielded no Lauderia at all but were dominated by Coscinodiscus, the diatom flora, as a whole, still being very sparse, though including a considerable list of species (see list, p. 427; stations 20072, 20078, and 20084).

In the coastal waters of the gulf the genera Thalassiosira and Chætoceras are the most characteristic members of the diatom flora of spring; it is unusual for any other to dominate there after the vernal flowerings are well underway.

Rapid multiplication of Thalassiosira and Chætoceras is responsible for the expansion of the extent of rich diatom plankton which takes place in the western side of the gulf from March on (p. 385). In 1920 *Thalassiosira nordenskioldi, Chætoceras debile,* and *C. decipiens* together dominated the plankton in Massachusetts Bay on April 6 (stations 20089 and 20090), with a considerable list of other species less numerous (see list, p. 424).

The swarms of diatoms off Cape Ann (station 20091), northward past Cape Elizabeth, across the mouth of Casco Bay, and seaward out to Platts Bank (stations 20091 to 20096) also consisted chiefly of Thalassiosira and of various species of

Chætoceras. The lists given below for station 20093 off the Isles of Shoals (p. 425) and station 20095 off Cape Elizabeth (p. 425) may serve as representative.

The two genera, Thalassiosira and Chætoceras, similarly dominated the plankton in the Isles of Shoals region during the April flowerings of the year 1913, as well as in Massachusetts Bay, where the tow on the 3d was chiefly *Thalassiosira nordenskioldi* and *Th. gravida*, with a scattering of *Chætoceras decipiens*, *Ch. densum*, *Ch. atlanticum*, *Ch. contortum*, *Biddulphia aurita*, *Coscinosira polychorda*, *Thalassiothrix nitschioides*, and *Rhizosolenia semispina* (Bigelow, 1914a, p. 405).

Much the same lists of species—chiefly Thalassiosira and Chætoceras—are responsible for the April flowerings of diatoms off western Nova Scotia, in the eastern side of the gulf, and out from Cape Sable across Browns Bank to the Eastern Channel (see lists for stations 20103, 20105, 20106, and 20107, pp. 428, 429. But whereas Thalassiosira is, on the whole, the dominant genus in the western side of the gulf in April and sometimes almost monopolizes the water there (p. 452), it has been entirely overshadowed by a great abundance of Chætoceras in all the hauls in the eastern side. This was also the case with the rich gathering of diatoms made off the southeast slope of Georges Bank on April 16 (station 20109; see list, p. 430). Douthart's tows in 1913 over the northern part of Georges Bank suggest that Chætoceras is also the most characteristic spring flowering diatom there (hence over the offshore banks as a whole), for on April 14 *Chætoceras densum*, *Ch. atlanticum*, and *Ch. decipiens* dominated on the central part of the bank, with smaller amounts of *Thalassiosira nordenskioldi* and *Th. gravida*, besides a scattering of *Ditylium brightwellii*, *Rhizosolenia obtusa*, *Rh. styliformis*, *Rh. semispina*, *Thalassiothrix nitschioides*, *Asterionella japonica*, Coscinodiscus, Coscinosira, and the neritic genus Pleurosigma. The fact that *Rhizosolenia styliformis* instead of Chætoceras dominated an equally productive gathering a few miles to the westward two weeks later illustrates the local fluctuations in the flowerings of different diatoms (Bigelow, 1914a, p. 415).

As the flowerings of diatoms expand eastward along the coast of Maine and offshore over the western half of the basin from April to May (p. 385), Thalassiosira continues to dominate in the coastwise belt (the seasonal expansions and contractions in the range of Thalassiosira are described below, p. 449), and Chætoceras offshore. The very rich gathering in the western side of the basin on May 5, 1915 (station 10267), consisting chiefly of three species of the latter, was one of the most monotonous we have made (see list, p. 429). The rich diatom plankton on the southwestern part of Georges Bank on May 17, 1920 (station 20128), was chiefly *Chætoceras sociale* (p. 430).

The status of the diatoms in summer, autumn, and early winter is discussed above (p. 391) and in the accounts of the several genera. The phenomena chiefly deserving attention are flowerings of Guinardia, Thalassiothrix, and Rhizosolenia on Georges Bank in July (p. 391), of Rhizosolenia in the shoalw ater off Marthas Vineyard in August (p. 431), the very productive flowering of *Asterionella japonica* along the coast of northern Maine in August, 1912 (p. 431), the persistence of an abundance of Thalassiosira and Chætoceras in the region of Mount Desert Island until into autumn (p. 426) and in the eastern side of the basin until late in the summer of 1912 (p. 392), and the flowerings of Skeletonema and *Rhizosolenia alata* in Massa-

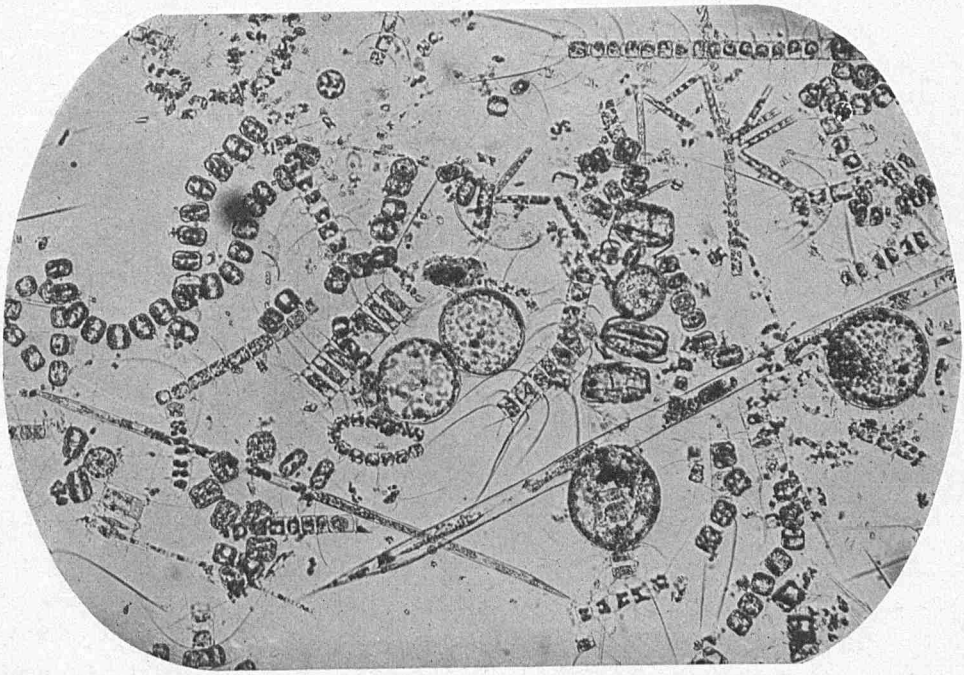

FIG. 117.—Phytoplankton near Seguin Island, March 4, 1920 (station 20058), dominated by *Lauderia glacialis*, Thalassiosira, Chætoceras, Rhizosolenia, and *Thalassiothrix nitschioides*. (See list, p. 425.)

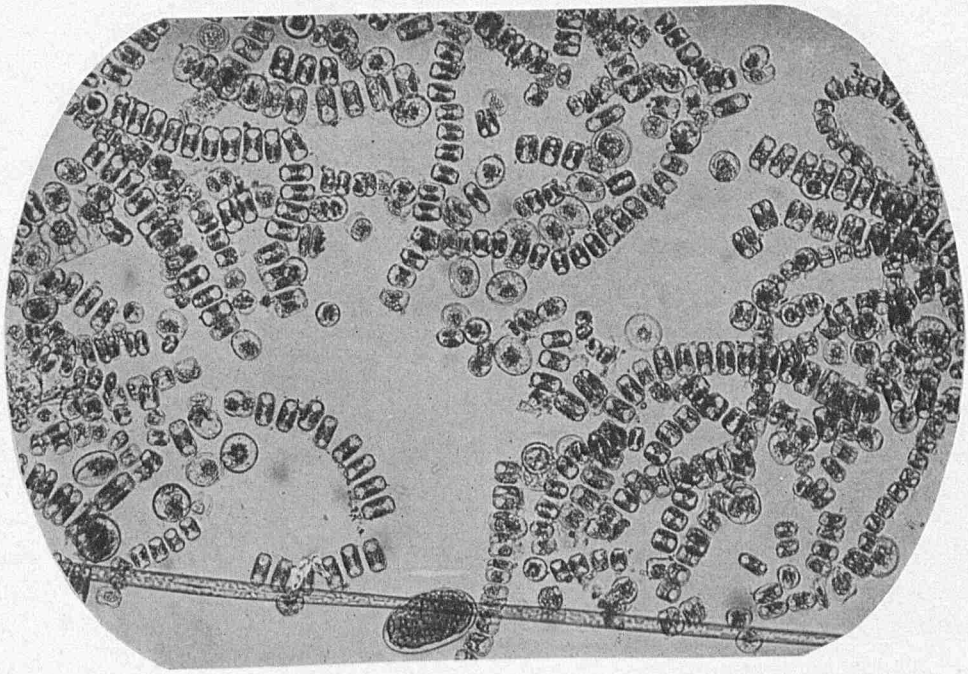

FIG. 118.—Sample of a rich flowering of Thalassiosira from a surface haul off Penobscot Bay, May 12, 1915 (station 10276). × 150

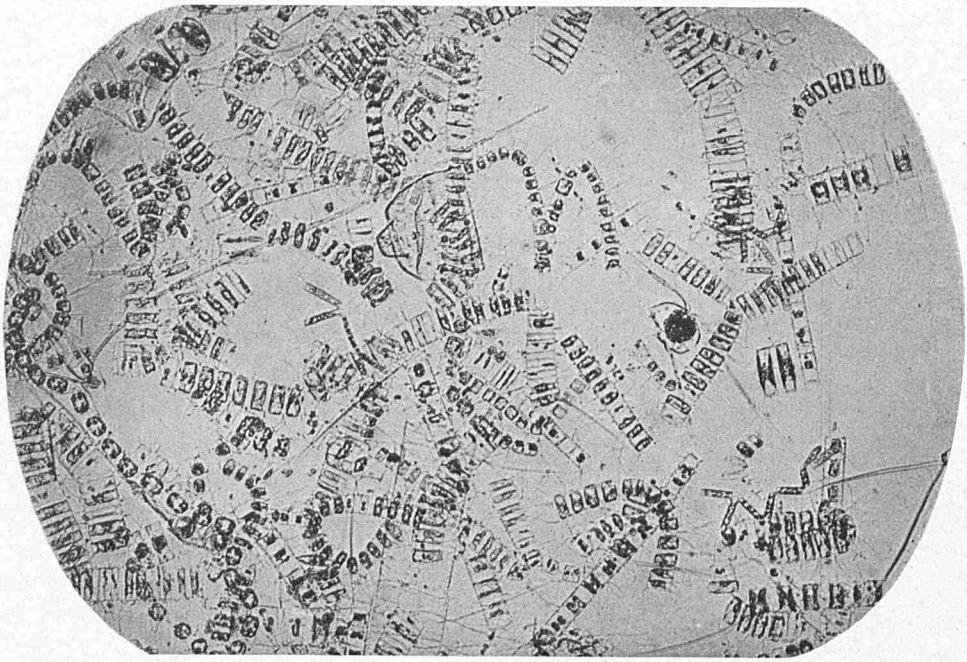

FIG. 119.—Phytoplankton of early spring dominated by neritic species of the diatom genus Chætoceras. Surface haul near Cape Elizabeth, March 4, 1920 (station 20059). × 150. (See list, p. 425.)

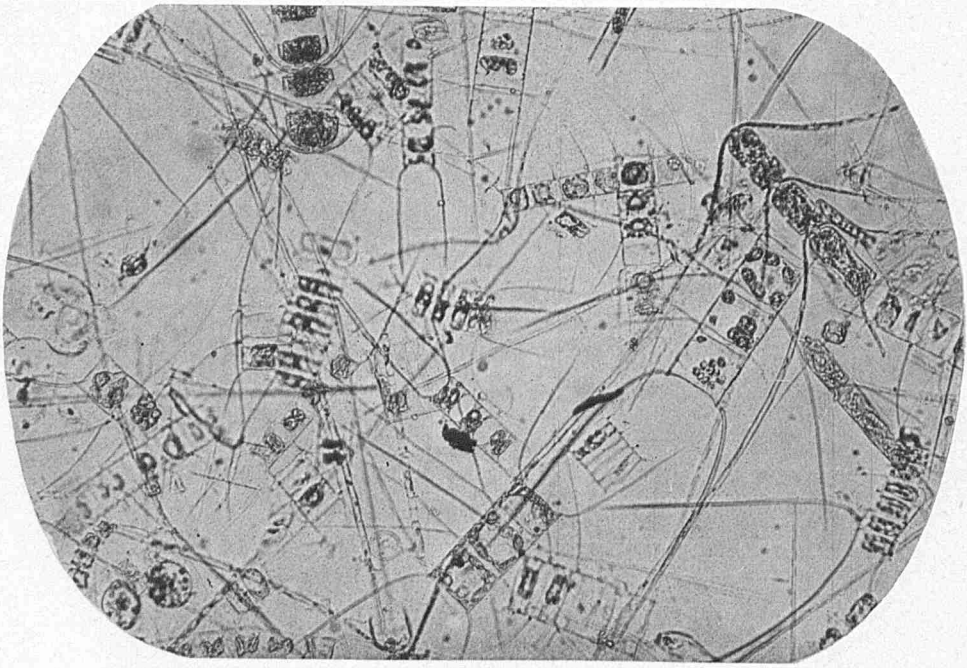

FIG. 120.—Diatom plankton near Lurcher Shoal, April 12, 1920 (station 20101), surface haul, dominated by oceanic species of Chætoceras. × 150. (See list, p. 428.)

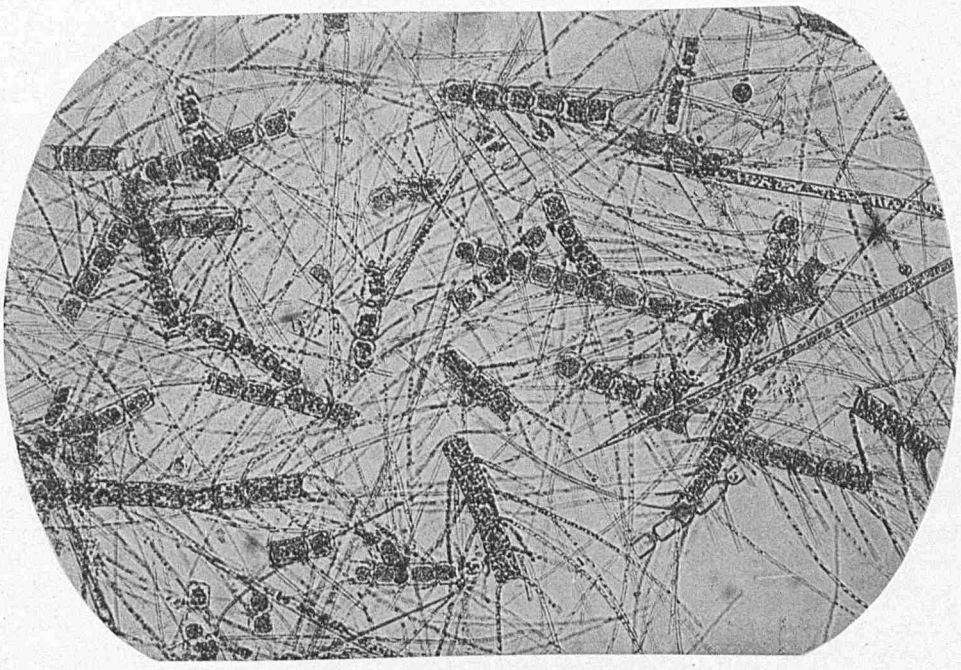

FIG. 121.—Diatom plankton in the western side of the basin of the Gulf of Maine, May 5, 1915 (station 10267, surface), dominated by the oceanic species *Chætoceras densum*. × 150. (See list, p. 429.)

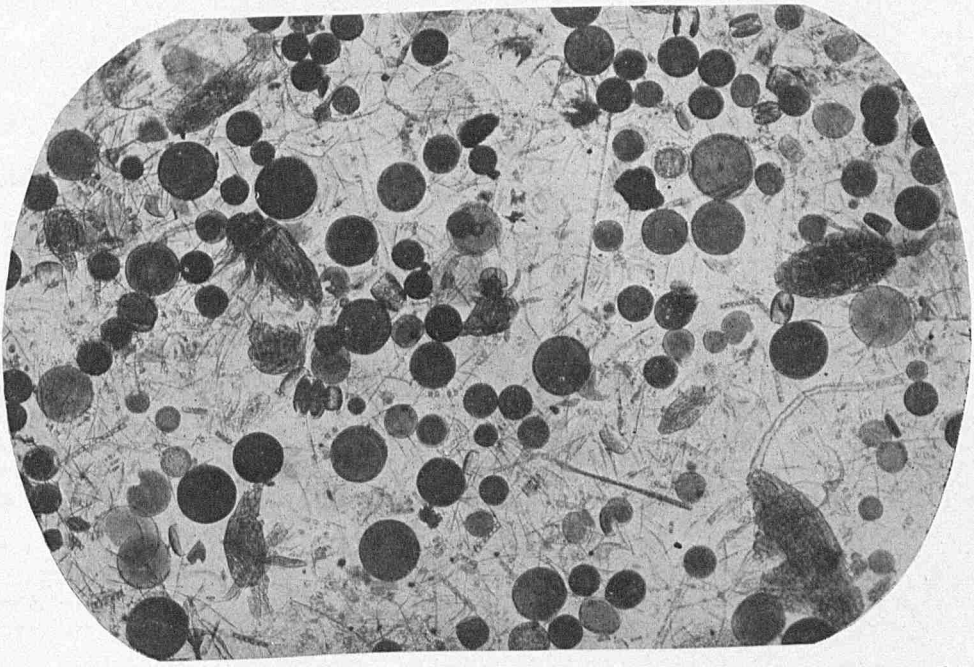

FIG. 122.—Diatom plankton on the northeastern part of Georges Bank, April 17, 1920 (station 20111), dominated by Coscinodiscus, with several species of Chætoceras. × 40. (See list, p. 430.)

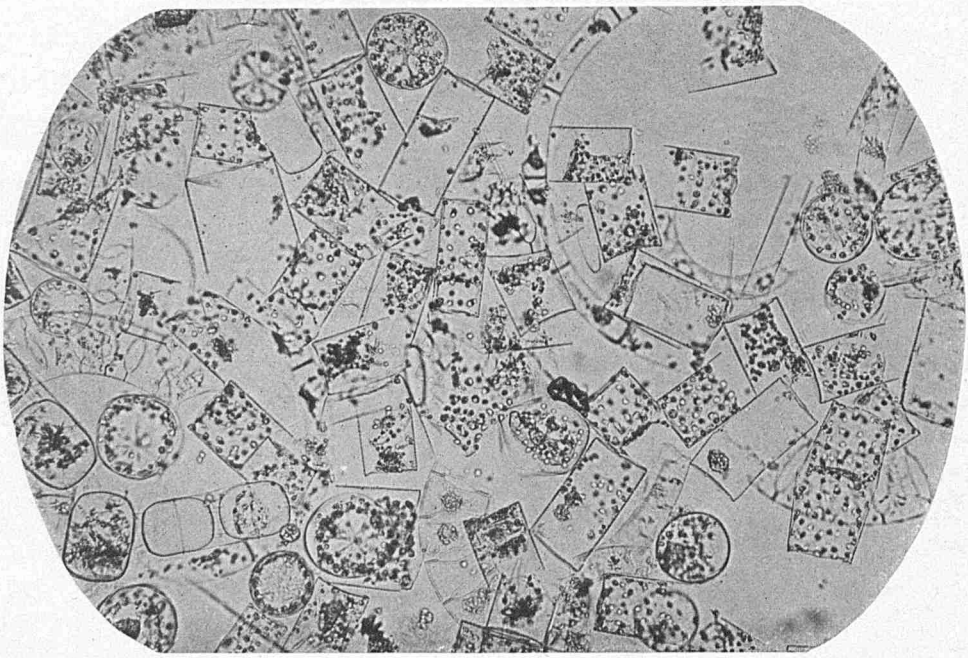

FIG. 123.—Diatom plankton in the western part of Georges Bank, July 9, 1913 (station 10059), dominated by *Guinardia flaccida* and Eucampia. (See list, p. 431.)

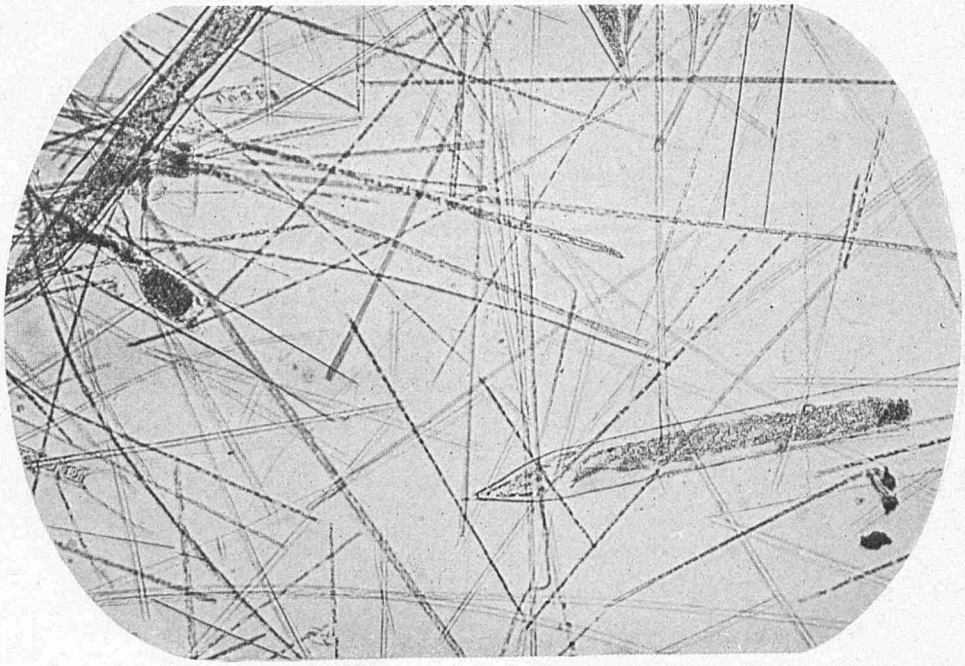

FIG. 124.—Diatom plankton on the western part of Georges Bank, July 23, 1916 (station 10347), dominated by *Thalassiothrix longissima* and *Rhizosolenia styliformis* (see list, p. 431). × 75

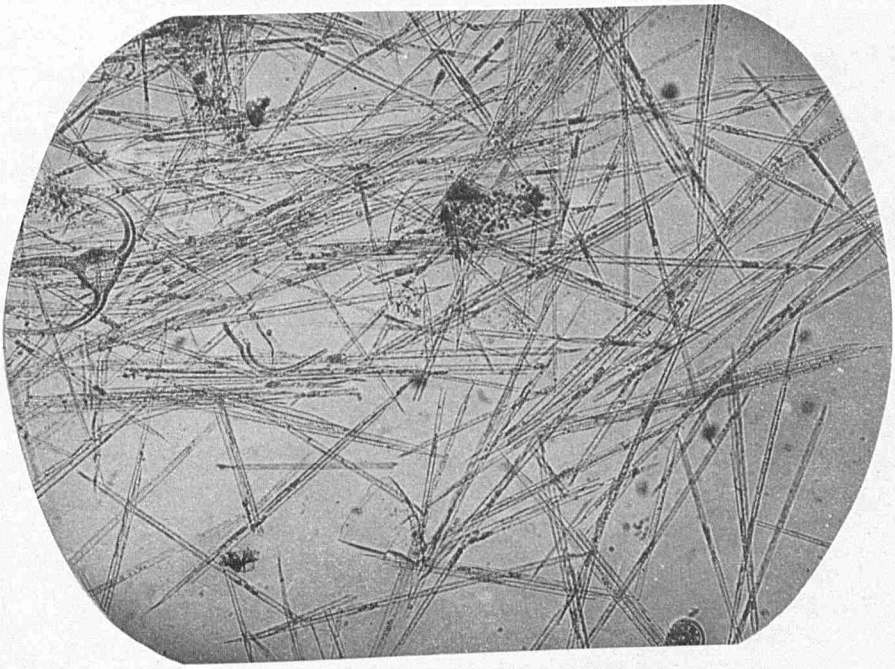

FIG. 125.—Phytoplankton south of Marthas Vineyard, August, 1914 (station 10258), dominated by the diatom *Rhizosolenia semispina*. × 150. (See list, p. 431.)

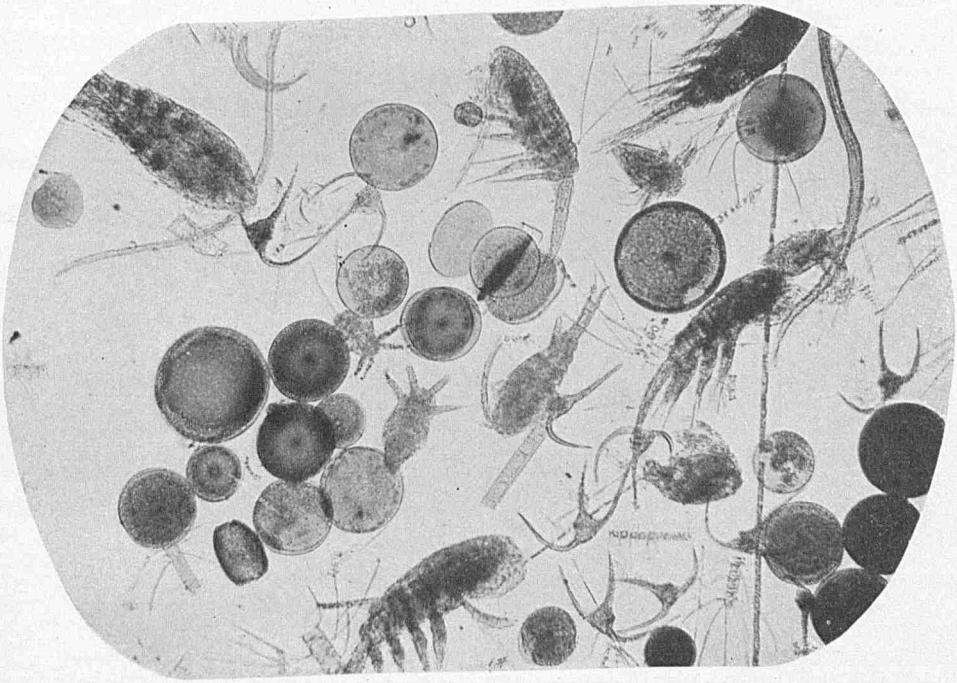

FIG. 126.—Midwinter phytoplankton in the inner part of Massachusetts Bay (station 10488, December, 1920), dominated by the diatom genus Coscinodiscus, with Chætoceras, the peridinian *Ceratium longipes*, and microcopepods. × 40

chusetts Bay and of the former in the Bay of Fundy late in summer and early in autumn (p, 394). Fish (1925) has already called attention to the interesting fact that these, which are summer forms in Massachusetts Bay to the north of Cape Cod, dominated the December catch at Woods Hole. The winter flowering of *Rh. alata* in Cape Cod Bay, described above (p. 396), is also interesting because suggesting a more southerly seasonal cycle there than for other parts of the gulf.

The accompanying photographs (figs. 117 to 126) illustrate the actual associations of the various species of diatoms in different parts of the Gulf of Maine from season to season. Several representative lists for standard stations also follow. The reader is cautioned, however, that in no case do these pretend to be complete, only the more numerous forms, such as would be found by examining a fair sample (but without exhaustive search), being enumerated. Whenever the genus Chætoceras forms any considerable part of the total plankton it has comprised specimens (listed as Chætoceras sp.) the identity of which has not been determined for one reason or another. But this limitation does not interfere seriously with the value of the lists, for it is precisely the more common and therefore ecologically more important species that are of interest to the student of broad oceanographic and biological problems. The samples for each station were examined independently by Dr. Albert Mann and by me unless otherwise noted. Species verified by Doctor Mann are starred. Since no attempt is made to contribute to the systematics of the group, the nomenclature follows Gran's (1908) convenient manual of the planktonic diatoms of northern seas, except in the genus Coscinodiscus, where Doctor Mann recognizes the older species, *asteromphalus* Ehrenberg and *oculus-iridis* Ehrenberg, as distinct from *subbulliens* Jörgensen.

## Lists of diatoms at representative localities

[The most plentiful species for each station are so designated by being located above the dotted line. Species of which only odd examples were noted are marked S. The presence of the starred (*) species was verified by Dr. Albert Mann.]

### 1.—Massachusetts Bay

**A.** Southwest side Cape Cod Bay, November 12, 1925 (*Fish Hawk*, trip 1, station 9):
Diatoms scarce.[49]
Rhizosolenia alata dominant.
---
Chætoceras boreale.
Ch. decipiens.

**B.** Center of Cape Cod Bay, February 7, 1925 (*Fish Hawk*, trip 6, station 7):
Diatoms abundant.[49]
Rhizosolenia alata dominant.
---
Chætoceras decipiens.
Ch. boreale.
Coscinodiscus sp.
Thalassiosira nordenskioldi.
Thalassiothrix longissima.

**C.** West of Stellwagen Bank, February 28, 1925 (*Fish Hawk*, trip 7, station 2):
Diatoms very abundant.[49]
Thalassiosira nordenskioldi dominant.
Thalassiothrix longissima abundant.
---
Biddulphia aurita.
Chætoceras atlanticum.
Ch. decipiens.
Coscinodiscus sp. (?).
Rhizosolenia alata.
Rh. semispina.
Thalassiothrix nitschioides.

**D.** Off Gloucester, March 1, 1920, station 20050:
Diatoms scarce.
Chætoceras decipiens dominant.
*Thalassiosira nordenskioldi dominant.
---

[49] Identified by Dr. C. J. Fish.

**D.** Off Gloucester, March 1, 1920—Continued.
*Chætoceras atlanticum.
*Ch. constrictum.
*Ch. criophilum.
Ch. debile.
Ch. diadema.
*Ch. didymum.
*Coscinodiscus concinnus.
*C. curvulatus.
*Lauderia glacialis.
*Nitschia seriata.

**E.** Off Gloucester, April 9, 1920, station 20090:[50]
Diatoms very abundant.
*Chætoceras debile dominant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum abundant.
*Ch. decipiens abundant.
*Ch. furcellatum abundant.

---

*Biddulphia aurita.
*Chætoceras atlanticum **S.**
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.
*Ch. scolopendra.
*Ch. willei.
*Coscinodiscus asteromphalus.
*Fragilaria cylindrus.
*Navicula sp. (?) **S.**
*Rhizosolenia semispina.
R. setigera.

**E.** Off Gloucester, April 9, 1920—Continued.
*R. styliformis.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

**F.** August 24, 1922, station 10635:
Diatoms moderately abundant.
Skeletonema costatum dominant.
Rhizosolenia alata.
(Skeletonema costatum and Rhizosolenia alata together constituted nearly 100 per cent of the diatoms.)

---

Chætoceras decipiens **S.**
Chætoceras sp. (?) **S.**

**G.** August 24, 1922, station 10640:
Diatoms moderately abundant; many Ceratium.
Rhizosolenia alata nearly 100 per cent of the diatoms.

---

Skeletonema costatum.

**H.** October 1, 1915, station 10323 (near Cape Cod):
Diatoms in medium abundance.
*Skeletonema costatum nearly 100 per cent of the diatoms.

---

*Chætoceras decipiens **S.**
*Coscinodiscus sp. (?) **S.**
*Rhizosolenia shrubsolei **S.**

## 2.—Neighborhood of the Isles of Shoals

**A.** March 4 and 5, 1920, stations 20060 and 20061 combined:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. diadema dominant.
*Thallassiosira gravida dominant.
*Th. nordenskioldi dominant.

---

*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. debile.
*Ch. decipiens.
*Ch. didymum.
*Ch. laciniosum.
*Ch. sociale.
*Ch. teres.
*Coscinodiscus asteromphalus.

**A.** March 4 and 5, 1920—Continued.
*C. concinnus.
*C. curvulatus.
*C. excentricus.
*C. radiatus.
*C. subtilis.
*Detonula cystifera.
*Ditylium brightwellii.
*Lauderia glacialis.
*Melosira borreri **S.**
*Nitschia seriata.
*Pleurosigma stuxbergii.
*Rhizosolenia semispina.
*R. setigera.
*Stephanodiscus astrea **S.**
*Skeletonema costatum.
*Thalassiosira baltica.
*Thalassiothrix nitschioides **S.**

[50] The list of diatoms for a haul in the inner part of the bay on Apr. 6, 1920 (station 20089) is the same except that it includes **Chaetoceras laciniosum*, **Ch. sociale*, and **Ch. teres*, likewise *Rhizosolenia setigera* and **Thalassiosira subtilis*, but lacks *Ch. furcellatum*, Coscinodiscus, Fragilaria, and *Rhizosolenia styliformis*.

**B.** April 9, 1920, station 20093.[51]

Diatoms very abundant.
*Chætoceras decipiens dominant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras debile abundant.
*Rhizosolenia semispina abundant.

---

*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. contortum.
*Ch. criophilum.
*Ch. diadema.
*Ch. furcellatum.
*Ch. scolopendra.
*Ch. sociale.
*Ch. teres.
*Ch. willei.
*Coscinodiscus asteromphalus.
*C. concinnus.
*Pleurosigma stuxbergii.
*Rhizosolenia setigera.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

**C.** Nearer the coast, in Ipswich Bay, April 9, 1920, station 20092:

*Chætoceras contortum dominant.
*Ch. debile dominant.
*Thalassiosira gravida dominant.

---

*Biddulphia aurita.
*Chætoceras atlanticum **S.**
Ch. contortum.
*Ch. decipiens.
*Ch. diadema.
*Ch. furcellatum.
*Ch. laciniosum.
*Ch. teres.
*Ch. wighami.
*Coscinodiscus concinnus.
*Rhizosolenia semispina.
*R. setigera.
Thalassiosira nordenskioldi.
*Thalassiothrix nitschioides.

## 3.—Off Cape Elizabeth

**A.** March 4, 1920, station 20059[52] (fig. 119):

Diatoms abundant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum abundant.

---

Biddulphia aurita.
Chætoceras debile.
*Ch. decipiens.
*Ch. diadema.
Ch. didymum.
Ch. sociale.
Ch. teres.
Ch. sp. ?
*Coscinodiscus curvulatus.
*C. excentricus.
*Ditylium brightwellii. **S.**
Lauderia glacialis
*Pleurosigma stuxbergii **S.**
*Rhizosolenia setigera.
*R. semispina.
Skeletonema costatum.
Thalassiothrix nitschioides.
*Thalassiosira gravida.

**B.** April 10, 1920, station 20095:

Diatoms very abundant.
*Chætoceras debile dominant.

**B.** April 10, 1920—Continued.

*Ch. contortum dominant.
*Thalassiosira nordenskioldi dominant.

---

Biddulphia aurita.
*Cerataulina bergonii **S.**
*Chætoceras atlanticum.
*Ch. decipiens.
*Ch. diadema.
Ch. didymum.
*Ch. laciniosum.
*Ch. scolopendra **S.**
*Ch. sociale.
*Ch. teres.
*Ch. willei.
*Coscinodiscus asteromphalus.
Coscinosira polychorda.
*Eunotia areus **S** (accidentally present).
*Nitschia closterium.
*N. seriata.
*Rhizosolenia semispina.
*R. setigera.
*Skeletonema costatum.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

[51] The list for Platts Bank the next day (station 20094) was the same, except that it included **Chætoceras densum* and *Ch. didymum*, **Coscinodiscus curvulatus*, **Nitschia seriata*, and *Skeletonema costatum*, but lacked *Chætoceras furcellatum*, *Ch. willei*, and *Thalassiothrix nitschioides*.

[52] The list was the same near Seguin Island on that day (station 20058, fig. 117), except that it lacked *Chætoceras diadema*, *Coscinodiscus excentricus*, and *Rhizosolenia semispina*, but included **Chætoceras atlanticum*, **Ch. criophilum*, **Ch. laciniosum*, **Ch. willei*, **Coscinodiscus asteromphalus*, **C. concinnus*, and *C. subtilis*.

**C.** May 13, 1915, station 10277:[53]
Diatoms very abundant.
Thalassiosira nordenskioldi dominant.
Thalassiothrix longissima abundant.

---

Chætoceras contortum.
Ch. debile.
Ch. decipiens.
Ch. didymum.

**C.** May 13, 1915—Continued.
Ch. laciniosum.
Coscinosira polychorda.
Ditylium brightwellii.
Lauderia glacialis.
Rhizosolenia semispina.
R. setigera.
Thalassiosira gravida.
Thalassiothrix nitschioides.

## 4.—Near Mount Desert Island

**A.** March 3, 1920, station 20056:[54]
Diatoms scarce.
Lauderia glacialis dominant.
Coscinodiscus sp.?

---

Chætoceras decipiens.
Ch. didymum.
Ch. atlanticum.

**B.** May 11, 1915, station 10275:
Diatoms very abundant.
*Thalassiosira nordenskioldi nearly 100 per cent of the catch.

---

*Biddulphia aurita.
Chætoceras debile.
*Ch. decipiens.
*Ch. diadema.
*Rhizosolenia setigera.
*Thalassiosira gravida.
(A scattering of each.)

**C.** June 11, 1915, station 10285:
Diatoms abundant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum dominant.
*Ch. debile dominant.

---

Chætoceras constrictum.
Ch. decipiens.
*Ch. furcellatum.
*Ch. laciniosum.
*Ch. scolopendra S.
*Ch. teres.
Ch. sp.?.
*Coscinodiscus concinnus.
Coscinosira polychorda.
Lauderia glacialis.
*Rhizosolenia semispina.
*R. setigera.
*Thalassiosira gravida.

**D.** July 19, 1915, station 10302:
Diatoms in medium abundance.
*Thalassiosira gravida dominant.
*Chætoceras scolopendra abundant.
*Rhizosolenia setigera abundant.

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*Chætoceras contortum.
Ch. debile.
*Ch. decipiens.
*Coscinodiscus asteromphalus.
*Nitschia seriata.
*Rhizosolenia alata.
*Thalassiosira decipiens.
*Thalassiothrix nitschioides.

**E.** August 14, 1914, at a locality off the mouth of Penobscot Bay, station 10250:
Diatoms abundant, with many Ceratium.
*Chætoceras criophilum dominant.
Ch. constrictum dominant.
*Ch. decipiens dominant.
*Ch. diadema dominant.
*Ch. scolopendra dominant.

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*Chætoceras debile.
*Ch. densum.
*Ch. laciniosum.
*Ch. peruvianum.
*Corethron valdiviae.
*Licmophora jurgensii.
*Nitschia seriata.
*Rhabdonema arcuatum S.
*Rhizosolenia setigera.
*Skeletonema costatum.
*Thalassiosira gravida.
*Th. nordenskioldi.

**F.** September 15, 1915, station 10317:[55]
Diatoms in medium abundance.
*Thalassiosira gravida dominant.

[53] Not examined by Doctor Mann.
[54] Not examined by Doctor Mann.
[55] On Aug. 21, 1912, *Asterionella japonica* was nearly 100 per cent of the very abundant phytoplankton in this region (p. 431).

F. September 15, 1915—Continued.
*Coscinodiscus concinnus dominant.

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Chætoceras constrictum.
Ch. decipiens.
*Ch. diadema.
*Coscinodiscus oculus-iridis.
*C. asteromphalus.
*Ditylium brightwellii.
*Melosira crenulata.
*Nitschia closterium.
*Paralia sulcata.
*Pleurosigma normanii.
*Rhizosolenia setigera.
*R. shrubsolei.
*Skeletonema costatum.
*Thalassiosira nordenskioldi.
*Thalassiothrix longissima.

G. October 9, 1915, station 10328:
Diatoms moderately abundant.
*Chætoceras decipiens numerous.
*Rhizosolenia setigera numerous.

G. October 9, 1915—Continued.
*Thalassiosira decipiens numerous.
*Thalassiothrix longissima numerous.

---

*Actinoptychus undulatus.
*Chætoceras breve.
*Ch. didymum.
*Ch. constrictum.
Ch. danicum.
Ch. debile.
*Ch. difficile (with endocysts).
*Ch. laciniosum.
*Coscinodiscus concinnus.
*C. excentricus.
*C. asteromphalus.
*C. oculus-iridis.
Coscinosira polychorda.
*Ditylium brightwellii.
*Paralia sulcata.
*Rhabdonema arcuatum.
*Rhizosolenia shrubsolei.
*Thalassiosira hyalina.

## 5.—Bay of Fundy

A. Petit Passage, Nova Scotia, June 10, 1915:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. decipiens dominant.
*Ch. scolopendra dominant.
*Rhizosolenia semispina dominant.

---

*Actinoptychus undulatus S.
Chætoceras constrictum.
*Ch. criophilum.
*Ch. debile.
*Ch. diadema.

A. Nova Scotia, etc.—Continued.
*Ch. laciniosum.
*Ch. teres (with endocysts).
*Corethron valdiviæ.
*Coscinodiscus concinnus.
*Nitschia seriata.
*Paralia sulcata S.
*Rhabdonema arcuatum S.
*Rhizosolenia alata.
*Thalassiosira gravida.
*Thalassiosira nordenskioldi.

## 6.—Banks off Western Nova Scotia

A. Near Seal Island, Nova Scotia, March 23, 1920, station 20084:
Diatoms scarce.
*Actinoptychus undulatus dominant.
*Biddulphia aurita dominant.
*Coscinodiscus concinnus dominant.
*C. asteromphalus dominant.

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Chætoceras decipiens.
*Paralia sulcata.
*Pleurosigma stuxbergii.
*Rhabdonema arcuatum.
*Rhaphoneis surirella.
*Rhizosolenia setigera.
*R. semispina.
Skeletonema costatum.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

B. South of Seal Island, Nova Scotia, April 15, 1920, station 20104:
Very abundant diatom plankton.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. diadema dominant.

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*Actinoptychus undulatus S.
*Biddulphia aurita.
*Chætoceras criophilum.
*Ch. decipiens.
*Ch. laciniosum (with endocysts).
*Ch. seiracanthum.
*Paralia sulcata.
*Rhizosolenia semispina.
*Thalassiosira gravida.
Th. nordenskioldi.
*Th. decipiens.
*Thalassiothrix nitschioides.

C. Near Lurcher Shoal, April 12, 1920, station 20101 (fig. 120):

Diatoms moderately abundant.
*Chætoceras atlanticum dominant.
*Ch. criophilum dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant.

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Chætoceras debile.
Ch. diadema.
*Ch. seiracanthum.
*Ch. scolopendra.
*Ch. sociale S.
*Coscinodiscus radiatus.
Lauderia glacialis.
*Rhizosolenia semispina.
*Thalassiosira decipiens.
Th. gravida.
*Th. hyalina.
*Thalassiothrix nitschioides.
Th. longissima S.

D. German Bank, April 15, 1920, station 20103.[56]

Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant (with endocysts).

---

*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.

D. German Bank, April 15, 1920—Continued.

*Ch. didymum.
*Ch. scolopendra S.
*Coscinodiscus lineatus.
Coscinosira polychorda.
Lauderia glacialis.
*Pleurosigma longum S.
*Rhizosolenia semispina.
*R. setigera.

*Thalassiosira decipiens.
*Th. gravida.
Th. nordenskioldi.
*Thalassiothrix longissima.
*Th. nitschioides.

E. German Bank, June 9, 1915, station 10290:

Diatoms in medium abundance.
*Rhizosolenia semispina dominant.
*Chætoceras decipiens abundant.

---

*Actinoptychus undulatus.
Chætoceras contortum.
Ch. debile.
*Ch. diadema.
*Ch. laciniosum.
*Coscinodiscus asteromphalus.
*Navicula directa S.
*N. lata S.
*Nitschia seriata.
*Pleurosigma normanii S.,
*P. stuxbergii S.,
*Rhaphoneis surirella S.,
*Rhizosolenia alata.
*R. styliformis.
Thalassiosira sp.?

## 7.—Western Basin abreast of Massachusetts Bay

A. February 23, 1920, stations 20049 and 20058:

Diatoms very scarce.
Coscinodiscus sp. ? dominant.
Chætoceras decipiens.
Ch. atlanticum.
Ch. criophilum.

B. April 18, 1920, station 20115:[57]

Diatoms moderately abundant.
*Chætoceras atlanticum dominant.
*Ch. decipiens dominant.
*Rhizosolenia semispina dominant.

B. April 18, 1920—Continued.

*Thalassiosira nordenskioldi abundant.

---

*Biddulphia aurita.
Chætoceras densum.
Ch. contortum.
Ch. teres.
*Ch. scolopendra.
*Rhizosolenia setigera.
*Skeletonema costatum S.
*Thalassiothrix longissima.

[56] At a neighboring station (20104) Doctor Mann also lists **Actinoptychus undulatus*, **Chætoceras seiracanthum*, and **Paralia sulcata*.

[57] A station (20114) in the center of the basin that same day adds the following species, verified by Doctor Mann: *Chætoceras criophilum, Ch. didymum, Ch. furcellatum, Ch. teres; Rhizosolenia alata; Thalassiosira gravida, Thalassiothrix nitschioides;* also *Ch. densum* and *Ch. contortum* in another sample from station 20115.

**C.** May 5, 1915, station 10267 (fig. 121):
Diatoms very abundant.
*Chætoceras densum fully 50 per cent of the catch.

---

**C.** May 5, 1915—Continued.
Chætoceras criophilum.
*Ch. decipiens.
*Rhizosolenia semispina.
*Thalassiothrix longissima.

## 8. North Channel

**A.** March 20, 1920, station 20078:[58]
Very few diatoms.
Chætoceras contortum.
Ch. criophilum dominant.
Ch. didymum.
Coscinodiscus subbulliens.

---

Rhizosolenia semispina **S.**

**B.** April 15, 1920, station 20105:
Diatoms abundant.
*Chætoceras decipiens dominant.
*Ch. diadema dominant.
*Thalassiothrix nitschioides also abundant.

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Bacteriosira fragilis **S.**
*Biddulphia aurita.

**B.** April 15, 1920—Continued.
Chætoceras contortum **S.**
*Ch. criophilum.
*Ch. debile.
*Ch. laciniosum.
*Ch. teres **S.**
*Coscinodiscus asteromphalus.
*C. denarius **S.**
*Nitschia seriata.
*Pleurosigma stuxbergii **S.**
*Rhizosolenia alata.
*R. semispina.
R. styliformis.
*Thalassiosira decipiens.
*Th. gravida.
*Th. hyalina.
Th. nordenskioldi.

## 9.—Brown's Bank

**A.** March 13, 1920, station 20072.[58]
Scanty diatom and Ceratium plankton.
Coscinodiscus asteromphalus dominant.
Coscinodiscus sp. dominant.

---

Chætoceras diadema.
Ch. debile.
Ch. mitra.
Thalassiothrix nitschioides.

**B.** April 16, 1920, station 20106:
Diatoms moderately abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.

**B.** April 16, 1920—Continued.
*Ch. diadema dominant.
*Thalassiosira gravida abundant.

---

*Chætoceras atlanticum.
Ch. criophilum.
*Ch. laciniosum.
*Coscinodiscus asteromphalus.
Coscinosira polychorda.
*Rhizosolenia semispina.
*R. setigera.
*Thalassiosira decipiens.
Th. hyalina.
*Th. nordenskioldi.
Thalassiothrix nitschioides.

## 10.—Eastern Channel

**A.** April 16, 1920, station 20107:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.
*Thalassiosira gravida dominant.
*Th. nordenskioldi.

---

*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
Ch. diadema.

**A.** April 16, 1920—Continued.
*Ch. laciniosum (with endocysts).
*Coscinodiscus oculus-iridis.
*Fragilaria oceanica.
*Navicula frigida **S.**
*N. vanhöffeni **S.**
*Rhizosolenia alata.
*R. semispina.
*Thalassiosira bioculata.
*Th. hyalina.
*Th. sp. ?
*Thalassiothrix nitschioides.

[58] Not examined by Doctor Mann.

## 11.—Georges Bank, east end

**A.** March 11, 1920, station 20066:
Diatoms not plentiful.
*Coscinodiscus asteromphalus dominant.

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*Actinoptychus undulatus.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. decipiens.
Ch. densum.
*Ch. didymum.
*Coscinodiscus concinnus.
*C. excentricus.
*C. oculus-iridis.
*C. radiatus.
*Melosira sulcata.
*Rhaphoneis surirella.
*Thalassiothrix nitschioides.

**B.** April 16, 1920, station 20109, southeast edge of bank.
Diatoms very abundant.
*Chætoceras debile dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant.

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*Chætoceras atlanticum.
*Ch. contortum.
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.
*Ch. didymum.
*Coscinodiscus asteromphalus.
C. sp.?

**B.** April 16, 1920—Continued.
*Fragilaria oceanica.
Lauderia glacialis.
*Nitschia seriata.
*Pleurosigma stuxbergii.
*Rhizosolenia semispina.
*Skeletonema costatum.
*Thalassiosira gravida, abundant.
*Th. nordenskioldi, abundant.
*Th. hyalina.
*Thalassiothrix longissima.
*Th. nitschioides.

**C.** April 17, 1920, northeast part of bank, station 20111 (fig. 122):
Diatoms in medium abundance.
*Chætoceras atlanticum.
*Coscinodiscus [60] dominant.
*Chætoceras decipiens.
*Ch. densum.
*Coscinodiscus concinnus.
*C. heteroporus (?)

**D.** July 23, 1914, station 10224:
Diatoms abundant.
*Guinardia flaccida dominant.
*Rhizosolenia shrubsolei notably abundant.

---

*Actinoptychus undulatus.
*Cerataulina bergonii.
*Navicula gelida.
Rhizosolenia semispina.
*R. styliformis.

## 12.—Georges Bank, western end

**A.** February 22, 1920, station 20046:
Diatoms abundant.
*Chætoceras sociale dominant.

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*Actinoptychus undulatus.
Chætoceras atlanticum.
*Ch. criophilum.
Ch. decipiens.
*Coscinodiscus crassus.
*C. subbulliens.
Eucampia zodiacus.
*Guinardia flaccida.
Leptocylindrus sp.?
*Navicula gelida.
*Nitschia sp.? abundant.
*Rhizosolenia imbricata.

**B.** May 17, 1920, station 20128:
Diatoms few on surface, abundant at 20 meters.
*Chætoceras sociale dominant.

---

*Chætoceras atlanticum.
*Ch. decipiens.
*Coscinodiscus concinnus.
*C. subtilis.
*Navicula gelida.
*Pleurosigma normanii.
*Thalassiosira decipiens.
*Thalassiothrix longissima.

[60] Doctor Mann states "fully 50 per cent of the diatoms are an intermediate form between *C. asteromphalus* and *C. oculus-iridis*, having the convexity and areolation of the former and the fineness and general delicacy of the latter. Indeed, Rattray and others look on *C. oculus-iridis* as not a valid species."

C. July 9, 1913, station 10059 (fig. 123):
Diatoms very abundant.
*Guinardia flaccida dominant.
*Eucampia zodiacus dominant.

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*Biddulphia alternans.
*Coscinodiscus asteromphalus.
*Pleurosigma normanii.
*Rhizosolenia alata.
*R. shrubsolei.
*R. stolforthii.
*R. styliformis.
Skeletonema costatum.
*Stephanopyxis turris.

D. July 23, 1916, station 10347 (fig. 124):
Diatoms very abundant.
*Thalassiothrix longissima dominant.
*Rhizosolenia styliformis dominant.
(Both together constitute 90 per cent of the phytoplankton.)

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*Actinoptychus undulatus.
*Biddulphia alternans.
*Coscinodiscus concinnus
*C. oculus-iridis.
*C. woodwardii.
*Pleurosigma normanii.
*Rhaphoneis amphiceros.

13.—SHALLOW WATER SOUTH OF MARTHAS VINEYARD [61]

A. August 25, 1914, station 10258 (fig. 125):
Very abundant diatom plankton.
Rhizosolenia semispina 100 per cent of a large sample.

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A. August 25, 1914—Continued.
Guinardia flaccida S.
No other diatoms noted.

## NOTES ON THE DOMINANT GENERA OF DIATOMS

On the following pages such notes are given on the status of the more prominent genera as the preliminary examination of the tow nettings warrant. For convenient reference the genera are arranged alphabetically.

### Asterionella

*Asterionella japonica*, as noted above (p. 392), occurred in extraordinary abundance in August, 1912. During that summer we first found it close to land in Ipswich Bay on July 8 (station 10008; it was not in Massachusetts Bay at that time), again in the coastal zone between Cape Elizabeth and Penobscot Bay the next week (stations 10016 to 10021), and near Lurcher Shoal off Yarmouth, Nova Scotia, on August 15 (station 10031); likewise in the basin near Mount Desert Rock (station 10032) and off (station 10031); likewise in the basin near Mount Desert Rock (station 10032) and off the mouth of the Grand Manan Channel (station 10036) a few days later—captures so widely separated that its range must then have included the whole northern coastal belt of the gulf, though nowhere in any notable abundance. During the last half of August it flowered in such abundance that on the 21st, when "passing Great Duck Island, one of the small islands off Mount Desert, the appearance of the water was noticeably soupy, and immediately the vessel was hove to and a surface haul made with the No. 20 net. When brought on board, the net was filled with a brown slimy mass, which on examination proved to consist almost wholly of countless numbers of chains of *Asterionella japonica* * * *" (Bigelow, 1914 p. 133).

This swarm extended westward, though gradually diminishing in density, right across the mouth of Penobscot Bay to the neighborhood of Seguin Island, where there was such a sudden transition to clear water with very little phytoplankton that the

[61] Not examined by Doctor Mann.

change was plainly visible from the deck of the *Grampus*. Though occasional Asterionella were taken nearly as far west as Cape Elizabeth (station 10040), which seems to have been its southern and southwestern boundary at the time, we have never found Asterionella in the open gulf since then. But according to Bailey, Asterionella (his illustration (1915, pl. 2, fig. 18) identifies it as probably *A. japonica*) is not very uncommon in the St. Andrews' region. He has also reported it from Dead Man's Harbor and from the St. John's River in August, and Fritz (1921) found it occasionally—always in small numbers—in October, 1916, and from April until September, 1917, at St. Andrews. It was likewise noted in the northern part of Georges Bank on April 16, 1913, in the collections made by Douthart (Bigelow, 1914a, p. 415).

Herdman, Scott, and Lewis (1914) have described a similar swarming of *Asterionella japonica* near the Isle of Man in May as an event unprecedented for the Irish Channel. But the occasional presence of an abundance of this diatom at that locality is easily explained, for it is known to occur elsewhere in the waters between Ireland and England in February, May, August, and November, not far from the region covered by the plankton studies of the Liverpool Marine Biological Laboratory (Ostenfeld, 1913, pl. 57), while it flowers abundantly every spring in the English Channel (maximum in April) and throughout the whole southern part of the North Sea.

Whether *Asterionella japonica* is regularly abundant anywhere along the east coast of North America is still to be learned, but its presence in small numbers along the coastal zone between New York and Marthas Vineyard and in Long Island Sound during July and August, 1916 (stations 10360, 10361, and 10396), suggests that it may be more important south and west of Cape Cod than it is in the Gulf of Maine. Fish (1925) reports it at Woods Hole both winter and summer.

### Biddulphia

Because of its dinstinctively neritic habit (it lives planktonic for only a short part of the year), locality records for *Biddulphia aurita* are valuable as indices of movements of water out from the coast. This diatom was found in small numbers among the swarms of Chætoceras and Thalassiosira all around the coastal zone of the gulf during March and April in the years 1913 (Bigelow 1914a, p. 405), 1920 (stations 20054, 20059, 20061, 20084, 20090, 20093, 20095, 20097, 20098, 20099, 20100, 20102, 20114, 20116, and 20117), and 1921 (stations 10505, 10506, and 10508). It is commonest close to the shore, as might be expected from its life history, rivalling Thalassiosira in abundance in a moderately plentiful diatom plankton off the Merrimac River on March 4, 1920 (station 10506), and occurs in some abundance at St. Andrews and elsewhere in the Bay of Fundy (Bailey, 1917, p. 104; McMurrich, 1917; and Fritz, 1921). It was also dominant in the deep off Mount Desert on April 11, 1920 (station 20098), and again off Yarmouth, Nova Scotia, on the 13th (station 20102), but on both these occasions all other planktonic forms were so scarce that the preponderance of Biddulphia was due less to abundance on its part than to an absence of other diatoms. The station off Mount Desert, just mentioned, is our only record for *B. aurita* outside the 100-meter contour; nor have we found it on Georges Bank. These scattered captures show that *B. aurita* is only a very minor

factor in the diatom flora of the offshore waters of the gulf, where it can safely be credited with a coastal origin.

Biddulphia is distinctly a spring species; in fact, we have never found it in the open gulf at any other season. At St. Andrews it occurs only irregularly and sparsely during the October–February period (McMurrich, 1917; Bailey, 1917), but Doctor McMurrich found it regularly, often in abundance, from February 26 until April 23, after which it is rare. Fritz (1921) likewise records an abundance of Biddulphia on April 20, but without naming the species concerned. The seasonal cycle is much the same for *B. aurita* in European seas, where Ostenfeld (1913, p. 500) describes it as living on the bottom for the greater part of the year, to invade the planktonic communities in great numbers during the spring months.

*Biddulphia mobilensis*, a true planktonic form though neritic in nature, has been noted in September and October, 1915 (stations 10316 and 10327), and in March, 1921 (station 10505), always in small numbers. Like *B. aurita*, it is more abundant in the estuarine tributaries of the Bay of Fundy, where Bailey (1917) records it for various dates in January and February and again from August to October, and where he found it very abundant and locally dominant in August.

### Chætoceras

The relationship which the diverse genus Chætoceras bears to Thalassiosira during the spring flowerings of the latter, and the wide distribution of several of its members in the offshore and eastern coastal waters of our gulf at that time, have already been touched upon (p. 418). As a rule, the same species of Chætoceras that precede the Thalassiosira swarms in spring (p. 421) are to be found in some numbers among the masses of the latter later in the season, even when Thalassiosira is most abundant. To enumerate them, station by station, would be repeating entire the lists given above (p. 423), for practically all the species of the genus definitely known from the gulf have been found among the Thalassiosira plankton of April and May. Nor do the lists for the individual stations off the west and north coasts of the gulf for April (stations 20090 to 20096) differ seriously from the March lists (stations 20056 to 20062), *Ch. decipiens* being universal, with the oceanic species *Ch. criophilum* and *Ch. atlanticum*, on the one hand, and the neritic forms *Ch. diadema*, *Ch. laciniosa*, *Ch. contortum*, *Ch. scolopendra*, *Ch. didymum*, and *Ch. sociale* on the other, occurring often enough to show that though they may be overshadowed by Thalassiosira all of them may be expected anywhere along this zone. *Ch. debile* shows decided augmentation in April, when it not only occurred at every coastwise station in 1920 but dominated the phytoplankton locally on Platts Bank on the 10th (station 20094). *Ch. furcellatum*, easily recognized by its peculiar spine-bearing spores, which was not found at all in March, appeared in numbers near Cape Ann, off Cape Cod, and in Massachusetts Bay on April 9, 18, and 20, 1920 (stations 20090, 20116, 20117, and 20119).

Practically the same association of Chætoceras species, barring *Ch. furcellatum*, was likewise encountered off the west coast of Nova Scotia, on Browns Bank, and in the North Channel during April, 1920 (stations 20101 to 20106), and although

the oceanic species *criophilum*, *densum*, and *atlanticum* were more generally represented there than at the inshore stations, others as distinctively neritic—e. g., *diadema* and *debile*—were equally universal, and the latter was dominant at three out of these six stations (stations 20102, 20103, and 20106).

In the offshore deeps of the gulf, where Thalassiosira never dominates the plankton, the augmentation of diatoms characteristic of late spring is chiefly due to these same species of Chætoceras. Thus the April lists for these waters (stations 20097, 20098, 20112, 20113, 20114, 20115, and 20116) are much the same as those for March (p. 418), *Ch. criophilum*, *Ch. atlanticum*, and *Ch. decipiens* being practically universal even in the most oceanic parts of the gulf, with *Ch. diadema*, *Ch. laciniosum*, *Ch. contortum*, *Ch. didymum*, and *Ch. debile* less regular though widely distributed. The latter, in spite of its neritic affinities, dominated a very rich assemblage of diatoms in the Eastern Channel (p. 429, station 20107) and was abundant off the southern face of Georges Bank (station 20109) on April 16, 1920, although *Ch. decipiens*, *Ch. atlanticum*, *Ch. criophilum*, and *Ch. densum* were the only species of Chætoceras noted on the shallows of the bank itself at that time (stations 20110 and 20111). The fact that *Ch. densum*, which was apparently confined to Georges Bank during March, 1920, had spread to the southeast part of the basin by mid-April (stations 20112 and 20113), foreshadows the great abundance to which it attains in May (p. 429).

On the assumption that the status of the various diatoms was essentially the same in the gulf in 1913 and 1915 as in 1920, little change takes place in the general association of Chætoceras species from April until June. For example, the list for a station (10278) north of Cape Ann for May 14, 1915, includes *Ch. densum*, *Ch. decipiens*, *Ch. laciniosum*, and *Ch. debile*, with *Ch. contortum* and *Ch. didymum* nearby (station 10277). Even where *Ch. debile* is the only species of Chætoceras mingled in any abundance with the swarms of Thalassiosira, as is sometimes the case in April and May when Thalassiosira may practically monopolize the plankton, various other species of Chætoceras can usually be detected by sufficient search.

The vernal augmentation of *Ch. densum* just mentioned resulted in such an abundance of this diatom by the first week of May, 1915, that it either dominated the plankton or at least played that rôle jointly with *Ch. criophilum* over the western, central, and eastern deeps of the gulf generally (stations 10267 to 10269). In fact, these two, with smaller amounts of *Ch. decipiens*, were almost the sole components of the rich diatom plankton (fig. 121) at the first-named locality (station 10267); but few if any *Ch. densum* had reached the northeast corner of the gulf (station 10273) by that time, nor have we ever found this oceanic species an important factor in the phytoplankton near the land, where *Ch. decipiens*, *Ch. diadema*, *Ch. contortum*, *Ch. debile*, and *Ch. didymum* have proved the most plentiful representatives of their genus during May.

*Chætoceras sociale* in great abundance dominated the phytoplankton on the western part of Georges Bank in the last week of February (station 20046) and again on May 17 (station 20128) in 1920, suggesting that it continued flowering actively there throughout this period of more than two months. But apparently its season of reproduction was drawing to a close on our second visit to that general locality,

because the diatoms had then sunk from the surface (which was practically barren of them) to a depth of about 20 meters, where they were congregated in such numbers that even the coarse-meshed net came back clogged.

The same neritic species of Chætoceras—*laciniosum*, *contortum*, *debile*, and *diadema*—together with the more oceanic *decipiens*, besides occasional *Lauderia glacialis*, *Thalassiosira gravida*, and Coscinodiscus, were found over the coast banks west of Nova Scotia in June, 1915 (there were few diatoms there in May; p. 387) and dominated the much more abundant diatom plankton of that region in April, 1920 (stations 20103 to 21015).

I may also note that in 1915 the easily recognized cells of *Chætoceras constrictum*, which I have not detected during the spring, appeared in some numbers in the catches near Mount Desert Island on June 14 (station 10285) and in Petit Passage, Nova Scotia, on the south side of the Bay of Fundy on the 10th. Apparently this species reaches its plurimum in the gulf in mid-August, when we have found it dominant off Mount Desert (station 10250, August 14, 1914). On the other hand, the group of oceanic species that includes *Ch. atlanticum*, *Ch. criophilum*, and *Ch. densum* (subgenus Phæoceras of Gran, 1908), have as a rule been represented sparsely in our summer hauls. They were either wanting or at least very rare in all our tow nettings during July and August of 1913 and 1915, although several of the more neritic representatives of the genus (listed above, p. 418), with other diatoms, occurred abundantly along the coast east of Penobscot Bay during those months. In 1914 *criophilum* was an important though not the dominant element in the diatom plankton off Penobscot Bay on August 14 (station 10250), and at the more easterly stations the day before (stations 10247 and 10248), while *Ch. atlanticum* and *Ch. densum* were likewise detected in these hauls. More data are needed to show whether these oceanic species are to be expected regularly in the gulf in August but have been overlooked in the cruises made during that month in other summers.

If Chætoceras plankton is characteristic of the western part of Georges Bank in spring, as the abundance of *Ch. sociale* suggests, it must vanish before midsummer, because no Chætoceras were detected on the bank among the swarms of Guinardia (p. 391) in July, 1913 or 1914; only an occasional *Ch. densum* and *Ch. decipiens* on the southwest part of the bank on July 23, 1916 (station 10348); and no Chætoceras at all among the Thalassiothrix-Rhizosolenia community near by (station 10347, p. 391).

*Chætoceras decipiens* is the only species of the genus that has been detected consistently in the open gulf during the autumn months, and that only in the coastwise belt,[62] the only part of the gulf where diatoms of any kind occur in any number at that season. *Ch. debile*, *Ch. constrictum*, and *Ch. laciniosum* have been recorded locally along the coast of Maine in October (near Mount Desert Island, station 10328, October 9, 1915). *C. danicum* was also detected at this station—so far the only record for this brackish-water species in the gulf outside the Bay of Fundy.

The genus Chætoceras as a whole probably falls to its lowest ebb in the offshore waters of the gulf late in December and early in January, at which season *Ch. decipiens* and *Ch. criophilum* alone were detected at two stations (10488 and 10592)

[62] Stations 10310, 10316, 10317, 10318, 10322, 10323, 10327, and 10328, September and October, 1915.

on the *Halcyon* cruise in 1920 and 1921; but, as pointed out above (p. 396), a comparatively rich collection of Chætoceras was made in Ipswich Bay on January 30, 1913 (see also Bigelow, 1914a, p. 405).

According to McMurrich (1917, and unpublished notes), the genus Chætoceras as a whole is scarcest at St. Andrews during the winter and most abundant between mid-June and September. Fritz's (1921) more detailed counts of the several species of Chætoceras combined, at the same locality, show constantly increasing numbers from the middle of March through April and May, with very abundant flowerings in July and August followed by a decrease during the autumn to the midwinter minimum, when the genus was so scarce that on two occasions (December 27 and January 13) none at all were detected.

McMurrich's, Bailey's (1915 and 1917), and Fritz's lists for St. Andrews, combined, comprise the following species: *Ch. boreale, Ch. constrictum, Ch. contortum, Ch. convolutum, Ch. crinitum, Ch. criophilum, Ch. danicum, Ch. debile, Ch. decipiens, Ch. diadema, Ch. laciniosum, Ch. sociale, Ch. teres,* and *Ch. willei. Ch. debile* begins flowering actively there in April and May, is far the most important species numerically, and was chiefly responsible for the very rich Chætoceras flora of July and August recorded by Fritz. *Ch. sociale,* which yielded her next largest counts, was practically nonexistent in November, December, January, February, and March; appeared in April; flowered actively (207,500 per haul) in May; vanished in July; reappeared in August; and attained its maximum abundance (280,000 per haul) on September 6. *Ch. diadema* and *Ch. laciniosum* have been found at St. Andrews from late winter through spring, summer, and early autumn, both of them having their plurimum in July. *Ch. decipiens* has been found sparsely represented at St. Andrews in late June, July, August, September, October, and early November, and the various other species only between early July and the last week in October. The most notable difference between the status of the genus Chætoceras at St. Andrews, as contrasted with the open gulf, is the scarcity of oceanic species. *Ch. atlanticum* and *Ch. densum* have not been detected there at all. Fritz found *C. criophilum* in only one haul on October 12 at St. Andrews. It is also interesting that in 1917 *Ch. constrictum* did not appear in Fritz's lists at St. Andrews until July 17—i. e., about a month later in the season than on the other side of the Bay of Fundy in 1920 (p. 435). Fritz (1921, p. 53) has remarked that the greatest number of species of Chætoceras was recorded for September, though the plurimum for the genus as a whole and for its two most numerous species fell in August. Fish (1925) reports 20 species of Chætoceras at Woods Hole, but only two of them—*decipiens* and *didymum*—were plentiful enough in his catches ever to be classed as "abundant." These two showed a succession of maxima in winter, summer, and autumn; not, however, in spring.

### Coscinodiscus

The genus Conscinodiscus is very widely distributed in the Gulf of Maine, both in time and space. In midwinter, on the whole, it is the dominant genus of diatoms, both at St. Andrews (McMurrich, 1917; Fritz, 1921) and along the northern and western shores of the gulf generally as off Cape Cod; for example, in Massa-

chusetts Bay and off the mouth of the Merrimac River,[63] and likewise out at sea, as exemplified by the western basin (p. 428). It seems that at this time of year Coscinodiscus is decidedly more numerous near land and on the offshore banks than in the deeper parts of the gulf or over the bank west of Nova Scotia, for during the *Halcyon* cruise of December and January, 1920–1921, our largest catches of Coscinodiscus were made in the Massachusetts Bay region (stations 10488 and 10489) and off the Merrimac (station 10492), whereas only a scattering was taken in our January hauls at sea off Penobscot Bay or in the eastern side of the gulf (stations 10496 and 10499 to 10502). Coscinodiscus was most numerous in the shallow waters over Georges and Browns Banks during the cruises of the *Albatross* in 1920 (stations 20066, 20072, 20110, and 20111); but although this genus may reach its highest development in the gulf in or near comparatively shoal water, its abundance in the Western Basin at the end of February, 1920, and again a month later (station 20049, February 23, 1920; station 20087, March 24, 1920), forbids the assumption that it is distinctively neritic. In fact, one of its commoner members—*C. asteromphalus*—has usually been described as oceanic in other seas.

Coscinodiscus does not exhibit as definite a flowering period in the gulf as do Thalassiosira or the more plentiful species of Chætoceras, nor does it ever rival the enormous numbers in which these latter genera so often appear there. None of our standard hauls has ever yielded more than a few cubic centimeters of Coscinodiscus, contrasted with hundreds of cubic centimeters of Thalassiosira and Chætoceras during their period of greatest abundance (p. 399).

In the open gulf we have made our richest catches of Coscinodiscus during midwinter, in February, March, and April. In fact, this genus has occurred in almost every offshore haul between the end of December and the middle of April, and Fritz (1921) found it constantly throughout the winter and early spring at St. Andrews. Coscinodiscus has been detected only occasionally in the western half of the gulf generally or on the offshore banks during the late spring or early summer. Thus it was found at only 1 out of 14 stations (station 10266) between May 4 and 30 in 1915, at 2 of the 12 June stations for that year, and not at all in the Massachusetts Bay region or off Cape Cod from May 4 to 17, 1920. If Coscinodiscus is not actually nonexistent in midsummer among the peridinian plankton of the basin of the gulf (likewise along the coastwise belt between Cape Ann and the Bay of Fundy) it is at least so overshadowed there by other more plentiful plant cells as to be overlooked easily. Fritz, too, records it as sometimes wanting and usually scarce at St. Andrews during June, July, and early August; but Coscinodiscus was a considerable element in the plankton near Lurcher Shoal, off Yarmouth, Nova Scotia, on August 12, 1914 (station 10245). Apparently this foreshadowed a widespread augmentation of it in the northeastern part of the gulf during the early autumn, for it occurred in considerable numbers at two stations off the eastern part of the Maine coast on September 11 and 15, 1915 (stations 10316 and 10317), again at these same localities on October 9 (stations 10327 and 10328), indicating that it is more

[63] At this locality we found Chætoceras far more numerous than Coscinodiscus as early in the winter as Jan. 16 in the year 1913.

plentiful and more generally distributed in the coastal belt east of Penobscot Bay in autumn than we have found it in August. McMurrich and Fritz have likewise found it comparatively plentiful at St. Andrews during the last half of October; in fact, Fritz's counts locate its plurimum for the year at that season.

We have no evidence that this autumnal augmentation of Coscinodiscus extends to the western part of the gulf, our October and November stations west and south of Penobscot Bay having yielded few or none during the seasons of 1912, 1915, and 1916. Its duration must be short even in the St. Andrews region, also, for both McMurrich (1917, p. 9) and Fritz (1921) found it considerably less plentiful there in November than in October, but it must multiply in early winter, being widespread from late December on.

The several species of Coscinodiscus are so closely allied to one another that the determination of them must await future critical study, wrong identifications being worse than none. The reader will find above (p. 423) lists of those so far determined by Doctor Mann for representative stations and seasons.

### Coscinosira

*Coscinosira polychorda*, a neritic species, has occurred sparingly among the Thalassiosira and Chætoceras at the April and May stations in both sides of the gulf (stations 20090, 20093, 20095, 20096, 20103, 20104, 20106, and 20107 in April, 1920, and 10277 on May 14, 1915) and at one June station (10285, June 14, 1915), always near land. We have never found it an important factor in the spring phytoplankton, but it was relatively abundant, if not dominant, off Swan Island near Mount Desert Island on September 15, 1915 (station 10317), and occasional specimens were also noted at the same general region on the 9th of the following month (station 10328). One well-preserved chain was also noted in a haul off Machias, Me., January 4, 1921 (station 10498). The only Georges Bank record for Coscinosira is for April 15, 1913 (Bigelow, 1914a, p. 415). Bailey (1915, pl. 2, fig. 15; pl. 3, fig. 4) figures it from the Bay of Fundy, and Fritz (1921) includes it under the general heading "Thalassiosira" in her lists of diatoms for St. Andrews.

### Ditylium

The genus Ditylium is never more than a minor factor in the plankton of the open Gulf of Maine, but it deserves a brief word here because it is an excellent indicator of waters of coastwise origin, being strictly neritic, but at the same time able to survive long sea journeys thanks to its powers of flotation, and so easily recognized that it is not apt to be confused with any other diatom.

The Gulf of Maine records for it are confined to the immediate vicinity of the western and northern coasts, mostly inshore from the 100-meter contour (fig. 127). Ditylium is not known either from Nova Scotian waters on the east or from the offshore banks on the south.

As a rule, the records of Ditylium outside the outer islands have been based on occasional specimens only among more plentiful diatoms of other genera. It was comparatively abundant in Massachusetts Bay on March 4, 1921 (station 10505), and Fritz (1921) found it plentiful at St. Andrews in October, with a scattering in November.

Wherever Ditylium is endemic in European seas it occurs throughout the year, though most commonly during the autumn and winter. McMurrich's and Fritz's (1921) data, combined, show it more seasonal at St. Andrews, occurring only from

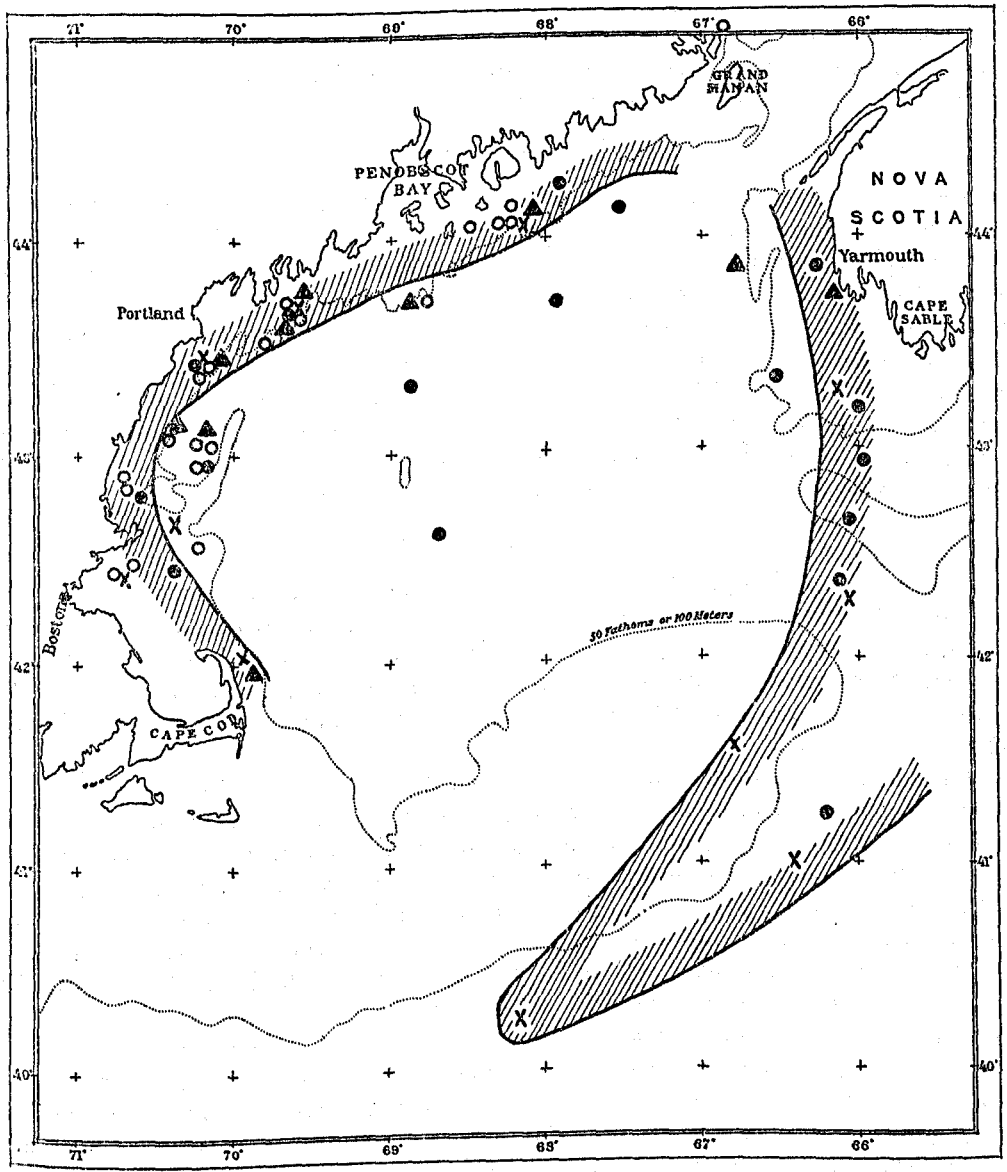


FIG. 127.—Occurrence of the diatoms Ditylium and *Thalassiothrix nitschioides*. ○, locality records for Ditylium; X, for *Thalassiothrix nitschioides*, February and March, 1920; ●, for *Th. nitschioides*, April, 1920; ▲, for *Th. nitschioides*, other seasons and years. The hatched curve bounds the chief area of occurrence of *Th. nitschioides* in March

mid-August until mid-December, with its maximum in October. In the open gulf it has been recognized most often in December and January, when it occurred at about 50 per cent of the *Halcyon* stations in 1920 and 1921 (stations 10488, 10489,

and 10492 to 10497). We have occasional records of it in March (stations 10505, 10506, 20056, 20058, 20059, and 20061), none at all in April, one in May (station 10277), none for June, July, or August, and one each for September (station 10317) and October (station 10328).

Thus Ditylium is chiefly an autumn and early winter form in the coastal zone of the gulf, spreading offshore during the later winter and early spring. Fish (1925) likewise found it a winter diatom at Woods Hole.

### Eucampia

*Eucampia zodiacus*, like Guinardia, has been strictly confined to Georges Bank in our towings, and to the coastal waters farther west and south, though Fritz (1921) found occasional specimens at St. Andrews in one July tow. It shared with Guinardia in the rich diatom flora that occupied the waters over the western part of the bank on July 9, 1913 (station 10059, fig. 123); was sparsely represented in that same general region in July, 1916 (station 10348), and again on February 22, 1920 (stations 20046 and 20047). The Arctic species, *Eucampia grœnlandica*, has not been identified from the Gulf of Maine, but specimens apparently intermediate between it and *E. zodiacus* (cf. Gran, 1908, p. 99, fig. 126b) occurred in some numbers among the Guianardia–Eucampia community just mentioned (station 10059).

### Guinardia

*G. flaccida*, the unique member of this genus, has only once been detected within the Gulf of Maine (occasional specimens near Cape Ann, October 18, 1915, station 10330), and has not been reported at St. Andrews, but, as I have already noted (p. 391), it swarmed locally on the western part of Georges Bank in July, 1913 (station 10059); again on the northeast edge in the same month in 1914 (station 10224).

Guinardia is a summer, not a spring or autumn, diatom there, for it was only sparsely represented on our line across the western end of the bank on February 22 and 23, 1920 (stations 20044 to 20046), and not at all on the more easterly sections for the two months following, or in the collection which Mr. Douthart gathered on the bank during April, 1913. It is irregular in its occurrence on Georges Bank even in July, for in that month in 1914 it was wanting in the region where it swarmed in 1913, though abundant a few miles farther east at the time. It is a question whether Guinardia appears there in such numbers every summer, for it was not detected at all at our July stations on the western end of the bank in 1916 (stations 10347 and 10348), though the water was then full of other diatoms (*Thalassiothrix longissima* and *Rhizosolenia styliformis*). No towings have been made on the bank during autumn, but Guinardia probably occurs there at that season as well as in summer, the *Grampus* having found it flowering along shore west of Newport, R. I., as late as November in 1916 (stations 10405 and 10406). Fish (1925) found it regularly in winter at Woods Hole and only occasionally in summer.

It is not surprising that Guinardia should be at its maximum on Georges Bank during the July to September quarter, which is its flowering season in north European

waters as a whole (Ostenfeld, 1913), but its rarity or absence in the inner parts of the Gulf of Maine contrasts sharply with its status in European coastal waters, such as the English Channel and the North Sea generally, where it is one of the most dominant of diatoms. This difference in its distribution in the two sides of the North Atlantic can not be explained until its life history is better known for American waters, but it is at least suggestive that Guinardia flowers chiefly at a time of year when the Gulf of Maine offers the least favorable environment for the multiplication of diatoms of any sort.

### Lauderia

The brief dominance of *Lauderia glacialis* off the coast of Maine in the very scanty pelagic flora of early March (stations 20056 and 20058) prior to the flowering of Thalassiosira has already been mentioned (p. 421), as has its occurrence near Cape Ann and in Massachusetts Bay at that same season (stations 20060 to 20062). In the western side of the gulf the flowering of Lauderia probably reaches its culmination by the end of March, at the latest, for it was not detected at any of the April stations west of Mount Desert in 1920. It is later in appearing in the eastern side of the gulf, for while none were detected at our several stations off western Nova Scotia on March 23, 1920, it was present there and out to the eastern channel and the southeast face of Georges Bank by April 15 and 16 (stations 20101, 20107, and 20109), accompanying the early flowerings of Chætoceras and Thalassiosira, though nowhere abundant.

Thus Lauderia appears just prior to the rich vernal flowerings of Thalassiosira and Chætoceras, reaches its maximum while these two genera are still in a state of active multiplication, and diminishes or vanishes after the brief period of a few weeks while they are still swarming. We have occasionally found Lauderia among other diatoms in May (station 10285 in 1915), but it is not recorded for later summer or autumn. Neither McMurrich (1917), Bailey (1917), nor Fritz (1921) have detected it at St. Andrews or in the Bay of Fundy. *L. glacialis* (fig. 117; Gran, 1908, p. 23, fig. 23) is the basis of all our records for the genus.

### Nitschia

*Nitschia seriata*, like *Skeletonema costatum* (p. 448), is a summer species in the Gulf of Maine, where it has not been detected during the spring months. Our earliest seasonal record of it is for June 10, when it was represented by occasional examples among the more abundant Chætoceras and other genera off Petit Passage, Nova Scotia, in 1915. Fritz (1921) found it constantly at St. Andrews from July 3 onward throughout the summer; Bailey (1917) records it from the Bay of Fundy in August; and it has appeared with comparative regularity in our July and August tow nettings in those parts of the gulf where diatom plankton persists so late in the season, more especially in the coastal belt between Cape Elizabeth and Nova Scotia. For example, *N. seriata* was present in fair quantity on Jeffreys Bank off Penobscot Bay, as well as close in to the land nearby (stations 10016 to 10021 and 10025),

from July 26 to August 8, 1912; on German Bank, near Mount Desert Island, and off Penobscot Bay from August 12 to 14, 1913 (stations 10095, 10099, and 10101); and again off Penobscot Bay on August 14, 1914 (station 10250). Fritz (1921) found it throughout September and during the first week of October at St. Andrews; Bailey (1917) likewise lists it from the Bay of Fundy for September 18; but occasional specimens in the tow in Massachusetts Bay on October 1, 1915 (station 10322) constitute our only autumnal record for it in other parts of the gulf. *N. seriata* has not been detected in winter either at St. Andrews or in the open gulf, nor in the eastern channel, on Georges Bank, or over the continental slope at any season.

The seasonal fluctuations of *N. seriata* are essentially the same in the Gulf of Maine as in the English Channel, where it attains its maximum abundance in August (Ostenfeld, 1913); but it is described as most plentiful in spring in the northern part of the North Sea and over the northeastern Atlantic generally. Hence, if Ostenfeld's (1913, p. 415) suggestion that this species includes two biologic races—a northern, with maximum in spring, and a more southern, with maximum in August—be well founded, the Gulf of Maine *N. seriata* belongs to the latter. However this may be, *N. seriata* is one of the several diatoms that are summer forms in the gulf but which Fish (1925) found to be characteristic of the winter flora at Woods Hole (p. 423).

This species is of minor importance in the gulf, where it occurs only sparingly even at the time of its greatest abundance, and never, so far as known, in swarms such as have been recorded in European waters. Several other neritic species of the genus have been reported from the estuarine waters at St. Andrews and St. Marys Bay (Fritz, 1921; Bailey and Mackay, 1921), but they are not likely to be found out in the open sea in the gulf except as strays.

### Rhizosolenia

The species of this genus that appears most frequently in the towings in the inner parts of the Gulf of Maine is the variety *semispina* of *Rh. hebetata* (Gran 1908, p. 55, fig. 671b), a form which fortunately is very easily recognized. In March *Rh. semispina* is widely distributed in the coastal belt from Cape Cod to Penobscot Bay on the western side of the gulf (stations 20058 to 20061 and 20088 in 1920; 10505 and 10506 in 1921), and in the shoal water along western Nova Scotia out to the Eastern Channel (stations 20072, 20078, 20079, and 20084) in the eastern; likewise over the outer part of the shelf off Shelburne (stations 20075 to 20077). As a rule Rhizosolenia has proved wanting among the sparse Coscinodiscus–Ceratium plankton that occupies all the central and deeper parts of the gulf during that month, but as a notable exception to this rule it dominated the diatom community of the western basin on March 5, 1921 (station 10510). A few *Rh. semispina* were also noted near the northern edge of Georges Bank on March 11, 1920 (station 20064), and over the slope to the southward on February 22 (station 20044). In April of that year *Rhizosolenia semispina* occurred at nearly all the stations in the gulf proper (stations 20089 to 20098, 20100 to 20107, 20109, 20112, and 20114 to 20117), dominating the plankton in the Western Basin on the 18th (station 20115). It was likewise recorded over the continental slope southeast of Georges Bank on the 16th

(station 20109), and in 1913 it was prominent in the rich diatom flora over the northwest part of the banks during the last few days of the month, as noted above (p. 422). In May, 1915, it was not uncommon among the more plentiful Chætoceras and Thalassiosira in the deeps of the gulf (stations 10267 to 10269) and was dominant locally there on the 10th (station 10273) and near the Isles of Shoals on the 14th (station 10278). It was also recorded in Ipswich Bay on the 8th in 1920 (station 20122), but it was not detected at all on the western part of Georges Bank and neighboring basin, in the Massachusetts Bay region, in the coastal belt north and east of Cape Elizabeth, nor off western Nova Scotia during that month, either in 1915 or 1920.

*Rh. semispina* was not found among the abundant diatom flora of the Mount Desert region in June, 1915 (e. g., station 10285), or in the offshore parts of the gulf during that month, but there was a scattering of it among the Thalassiosira and Chætoceras in Petit Passage on the 10th, and it might fairly be classed as dominant over German Bank on the 19th (station 10290).

Our midsummer records for this species are confined to Georges Bank (where occasional cells were noted in July, 1914, stations 10219 and 10223, but none at all among the *Rh. styliformis*, *Rh. shrubsolei*, and *Thalassiothrix longissima* that swarmed on July 23, 1916); to the Eastern Channel (station 10227), Browns Bank (station 10228), the neighborhood of Lurcher Shoal (station 10245), the northeast corner of the gulf (stations 10247 and 10248), the waters off the coast of Maine east of Cape Elizabeth (station 10258); and to the shelf off Marthas Vineyard, where it swarmed on August 25, 1914 (station 10258; fig. 125). Like diatoms generally, *Rh. semispina* practically vanishes from the central deeps of the gulf during the summer. Nor is there any reason to look for a considerable augmentation in its numbers there during the autumn, for it has appeared only sparingly in our September, October, and November hauls (station 10047, November 20, 1912; stations 10317 and 10336, September 15 and October 26, 1915; and stations 10400 and 10403, November 1 and November 8, 1916). It was widely distributed over the northern half of the gulf (always, however, in very small numbers) in the midwinter of 1920–21, when it occurred at about 50 per cent of the stations (stations 10490, 10491, 10494, 10495, 10496, 10497, 10500, and 10502). Fritz (1921a) records a scattering of "*Rh. hebetata*," which probably were this variety, at St. Andrews in every month except November.

The most notable feature of the occurrence of *Rh. semispina* in the Gulf of Maine, as outlined by our data, is its irregularity; no definite succession of flowerings is demonstrated. On the whole, however, it can be described as at its maximum during the spring and summer (this half of the year includes all the rich flowerings we have encountered), and at its minimum in autumn and winter. At Woods Hole, too, Fish (1925) reports the richest flowerings of this species as occurring in summer. This parallels its seasonal status in northern European seas, where it is most abundant from April until June, flowering earliest in the more southern and latest in more northern waters.[64] But no definite correlation between flowering periods and latitude or temperature is yet apparent for the Gulf of Maine.

[64] Flowers most abundantly in the North Sea in May, but not until August in Greenland waters and in Barents Sea.

*Rh. semispina* certainly is no more neritic in the Gulf of Maine than it is off north European coasts, where it is commonly regarded as oceanic, and I may hazard the guess that its occasional abundance in waters as shoal as those of German and Georges Banks and off Marthas Vineyard reflects local hydrographic conditions exceptionally favorable for its growth and reproduction, not any dependence on its part on the bottom below or on the neighboring coast line. Nevertheless, the presence of *Rh. semispina* is not a reliable index to offshore water, because it may be able to thrive in coastwise regions "several years after the inflow of oceanic water has taken place," as Ostenfeld (1913, p. 443) has remarked. In short, from the distributional standpoint *Rh. semispina* is intermediate between the typically oceanic *Rh. styliformis* and the strictly neritic *Rh. setigera* (p. 446), these three species bearing the same relationship to one another in the Gulf of Maine as on the other side of the North Atlantic. A fuller knowledge of the degree to which *Rh. semispina* is endemic within the limits of the gulf, or is immigrant thither from elsewhere, is much to be desired.

Only two other species of Rhizosolenia have so far been detected with any regularity in the collections from the open Gulf of Maine—*Rh. styliformis* and *Rh. setigera* (fig. 128). *Rh. styliformis* has been but sparsely represented in the tow nettings north of Georges Bank. In March, 1920, it was not found there at all; in April of that year it was noted (occasional specimens) off Cape Cod (station 20088), at the mouth of Massachusetts Bay (station 20090), and in the Northern Channel (station 20105). We did not detect it at all in the gulf north of the banks in May either in 1915 or in 1920, and only once in June, 1915 (station 10290), and have only one summer record of it in the inner parts of the gulf—viz, off Lurcher Shoal on August 12, 1914 (station 10245). It appeared in small numbers at three out of five stations near Massachusetts Bay from November 1 to 8 in 1916 (station 10400 north of Cape Ann and stations 10401 and 10403 off Massachusetts Bay), likewise off Cape Ann, off Cape Cod, and in the Western Basin on December 29 and 30, 1921 (stations 10489, 10490, and 10491), suggesting a period of augmentation in autumn and early winter either by propagation within the gulf or, as is more likely, by immigration from offshore. Similarly, Fish (1925) found it only in winter at Woods Hole, and very scarce even then. Evidently it is rare in the Bay of Fundy, for while Bailey (1915) notes it for St. Andrews, McMurrich found it on one occasion only, and Fritz (1921) does not list it there at all.

*Rh. styliformis* is far more important in the plankton over the offshore banks than it is in the inner parts of the gulf, as might be expected from its typically oceanic nature. For example, the *Grampus* found it in abundance on the western part of Georges Bank in July, 1913 (station 10059), and again in July, 1916 (stations 10347 and 10348), and likewise over the northeast part of the bank in that same month in 1914 (station 20223). It also occurred generally from off Nantucket out to the continental slope of Georges Bank in July, 1916 (stations 10349, 10351, and 10354 to 10356). Although we did not detect *Rh. styliformis* anywhere on the bank (or on Browns Bank either, for that matter) in March, April, or May of 1920, it dominated the pelagic flora over the northern part of Georges Bank on the 27th of April in 1913, when "many of the specimens were so large (1.1 millimeters) as to be easily

visible with the naked eye" (Bigelow, 1914a, p. 415). Curiously enough, this species has not been detected in our tows over the offshore slope of the bank in summer, though represented there in March, 1920 (station 20069).

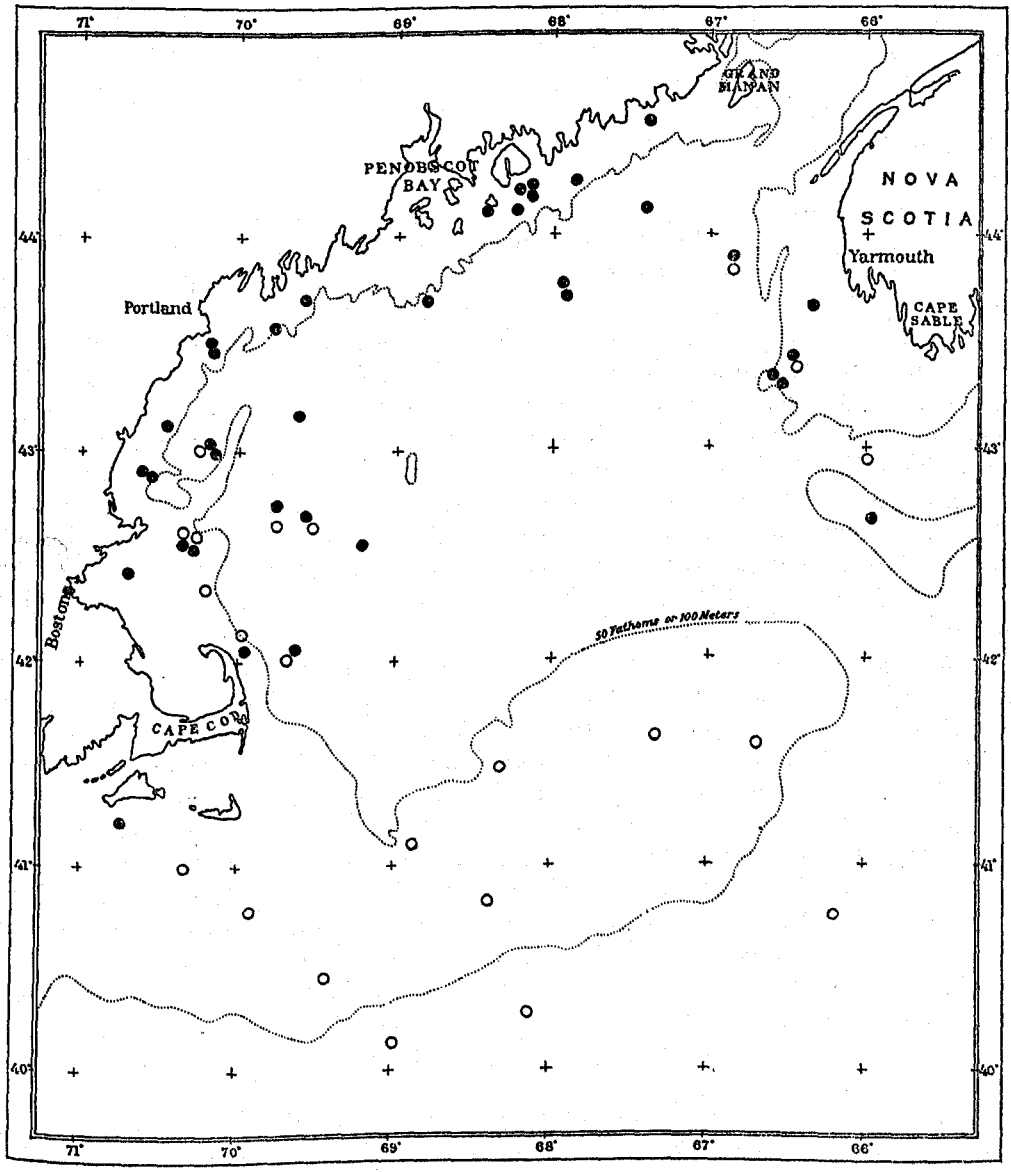


FIG. 128.—Locality records for *Rhizosolenia setigera* (●) and *Rh. styliformis* (○)

The comparative scarcity of *Rh. styliformis* in the inner parts of the Gulf of Maine, contrasted with its abundance over large areas of the open north Atlantic in summer (Cleve, 1897; Ostenfeld, 1913), suggests that the optimum salinity for

it is high (over 35 per mille, as Ostenfeld suggests) and that water less saline, say, than 33 per mille operates as an actual bar to its dispersal and propagation. Otherwise it would be hard to explain its failure more completely to colonize the Gulf of Maine, which is fully as accessible to it, both by temperature, by the influx of offshore water, and by its geographic location, as the northern part of the North Sea is, where *Rh. styliformis* occurs in abundance throughout the half year from May to November.

Inasmuch as *Rh. styliformis* occurs chiefly as an immigrant in the Gulf of Maine, where its presence is indicative of ocean water, it is one of the diatoms for which a sharp lookout should be kept, a lookout facilitated by its large size and precise structural characters.

*Rhizosolenia setigera* is the antithesis of *Rh. styliformis* in its relation to the coast line, for it is neritic instead of oceanic and produces resting spores, corresponding to which difference it occurs more regularly in the Gulf of Maine. Its period of greatest abundance falls in spring. Its richest flowerings roughly correspond with those of the abundant Thalassiosira–Chætoceras flora in their geographic locations, having been limited in 1920 to the Cape Ann–Cape Elizabeth belt (stations 20058, 20059, and 20061) and to one locality off Yarmouth (station 20083) in March, spreading to Massachusetts Bay on the one side of the gulf (stations 20089, 20116, and 20117) and to the banks off Nova Scotia, to Browns Bank, and to the northeast corner of the gulf on the other (stations 20098 and 20099) by the last week of April. McMurrich (1917), too, found this species attaining its maximum abundance in the St. Andrews region in April, though Fritz (1921) does not list it at all from that locality. At Woods Hole, however, Fish (1925) found rich flowerings in late summer as well as during the winter and early in spring.

*Rh. setigera* either diminishes in numbers in the open gulf during May and June or has been overlooked there among the more numerous diatoms of other genera, for we have only one definite record of it for each of these months (station 10277 on May 13, 1915, and station 10299 on June 26, 1915). But it occurs occasionally throughout the summer and at least until early October in coastal areas wherever diatoms persist so late in the season in any quantity; off Penobscot Bay and in the Mount Desert region, for example; near Machias, Me.; and on German Bank (stations 10029 and 10030 in 1912; 10248 and 10250 in 1914; and 10301, 10305, 10317, and 10318 in 1915). In the Bay of Fundy this species apparently passes through a period of abundance in September and October (Bailey, 1917), an interesting phenomenon paralleling its occurrence on the other side of the Atlantic, where it has two maxima—one in spring and the other in autumn (Ostenfeld, 1913). We have found nothing to suggest this in other parts of the Gulf of Maine, however, or in Massachusetts Bay.

*Rh. setigera* was recognized at only two stations during the December to January cruise of 1920–1921 (stations 10490 and 10502), and not at all in Massachusetts Bay during the winter of 1912–13. *Rh. setigera* has not been found on Georges Bank, on Browns Bank, in the Eastern Channel, or over the continental slope to the south. The chart (fig. 128) illustrates the sharp contrast between the distribution of the neritic species, *Rh. setigera*, and that of its oceanic relative, *Rh. styliformis*.

*Rhizosolenia shrubsolei* was sparsely represented off Cape Cod and near Mount Desert Island early in October, 1915 (stations 10323 and 10328), and on the northeast and southeast parts of Georges Bank in July, 1914 (stations 10220 and 10224); it swarmed on the western end of the bank on July 23, 1916 (station 10348), and likewise in Nantucket Sound on October 25, 1915 (station 10335). Fritz (1921) lists it regularly from St. Andrews through October and November, occasionally in December, and not at all during the other months of the year, but Fish (1925) found it flowering in midsummer at Woods Hole, as well as in winter. *Rh. imbricata,* if it be actually separable from *shrubsolei,* which Gran (1908) doubts, was detected by Doctor Mann at one station on the western part of Georges Bank on February 22, 1920 (station 20046).

We have found Rhizosolenias of the *alata–obtusa* group (critical examination of them is needed before they can be referred definitely to one or the other species or variety) in small numbers on and south of Georges Bank in July (stations 10215 and 10220 in 1914, and 10348 in 1916), and once in abundance in the deep water a few miles to the north of the bank during that month (station 10058, July 8, 1913). There are no other summer records for them in the basin of the gulf, but they dominated the moderately abundant diatom plankton at most of the stations occupied by the *Halcyon* in the outer part of Massachusetts Bay from August 22 to 24 in 1922 (stations 10631 to 10642), though not in Cape Cod Bay (stations 10643 and 10645); likewise off Mount Desert Island on July 19, 1915 (station 10302). Fritz (1921) noted them (occasional cells) at St. Andrews on August 28, regularly during the last half of September, October, and November, but not in any other month. We have no autumnal record for the *alata–obtusa* group in the open gulf but they were detected at three stations (10493, 10496, and 10497) along the coast between Cape Ann and Mount Desert from December 30, 1920, to January 1, 1921. In 1925 they were flowering in great abundance in the eastern side of Cape Cod Bay and in the channel between Cape Cod and Stellwagen Bank from December 16 to February 6 to 7 (*Fish Hawk* stations 2, 4, 6, and 7, trips 3, 5, 6, and 7, p. 396), after which date they were only occasional, being succeeded by Thalassiosira (p. 396). We also have record of them in the North Channel (station 20105), in the Eastern Channel (station 20107), and in the center of the gulf (station 20113) in April, 1920.

This completes the list of Rhizosolenias so far recognized in the towings from the outer waters of the Gulf of Maine. Fritz (1921), however, also lists *Rh. faroensis* occasionally in August and October at St. Andrews. In general, the genus Rhizosolenia is far less important a factor in the phytoplankton of the offshore waters of the Gulf of Maine than in the open North Atlantic, where, as Cleve (1900) long ago pointed out and as Ostenfeld (1913, p. 444) has recently remarked afresh, this genus may be its most abundant member, a difference to be expected because most of the species of Rhizosolenia, and especially *Rh. styliformis* (p. 444), are oceanic in nature. As noted above (p. 396), however, rich flowerings of the genus (*Rh. alata*) in the inner parts of Massachusetts Bay during the winter of 1924–25 suggest greater importance for its neritic members close to the coast.

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**Skeletonema**

*Skelteonema costatum* is an interesting species because it reaches its maximum abundance in the Gulf of Maine during the summer and early autumn, not in spring, as most other diatoms do, whereas Fish (1925) found it a winter form at Woods Hole and occurring only occasionally during the warm months. Skeletonema is typically neritic and has been found flowering actively in Massachusetts Bay, the Bay of Fundy, and on Georges Bank, but not in the deeper parts of the Gulf of Maine. Bailey (1917) found it occasionally in estuarine situations on the north shore of the Bay of Fundy in January and February and again in July and August, but not at all during March, April, May, June, or October. In the open bay near Grand Manan he describes it as abundant on September 18. Fritz's (1921) more extensive lists note Skeletonema as occurring irregularly (always in small numbers) at St. Andrews during the winter and early spring of 1917, multiplying in April, and reaching its maximum in July and early August. In Massachusetts Bay we have not detected it at all at any October, November, winter, spring, or early summer station, nor in any of the hauls made in this region in 1916—July, August, October, or November. In 1915 it appeared at the mouth of the bay, near Provincetown, and off Cape Cod from September 29 to October 1 (stations 10320 to 10323) in sufficient abundance to give a characteristic aspect to the phytoplankton (p. 394), though the period of reproduction must have been brief, for no Skeletonema were found at three stations across the mouth of the bay on October 26 and 27 (stations 10337 to 10339).

It would be interesting to know how far offshore this autumnal flowering extended, but unfortunately we have no data bearing on this. In 1922, however, when it again dominated the phytoplankton at six stations around the shore of Massachusetts Bay from Gloucester to the neighborhood of the Cape Cod Canal on August 24 (stations 10634, 10635 to 10637, 10639, 10642, and 10643), the belt that it occupied extended only 4 to 5 miles out from land, none having been detected at the eight other stations in the outer parts of the bay which the *Halcyon* occupied on that day and two days previous. Unfortunately no plankton hauls were made later in the season during that year.

Skeletonema was also abundant on the western part of Georges Bank on July 9, 1913 (station 10059)—our only record of it on the offshore banks—among the Guinardia and Eucampia, which at the time dominated the local phytoplankton. The only other records for it in the open gulf, outside the outer headlands, are for occasional chains off Cape Sable, off Cape Cod, near Cape Ann, off Mount Desert Rock, and in the northeastern corner of the basin in March and April, 1920 (stations 20084, 20088, 20091, 20098, and 20100).

Evidently the flowerings of this genus are closely confined to the immediate vicinity of the land in the Gulf of Maine and to the shallow water of the banks, where it flowers irregularly during summer and early autumn; and probably it will be found to occur as abundantly along the coasts of Maine and Nova Scotia as it does in Massachusetts Bay and at St. Andrews, when the diatoms of the other harbors and bays are studied.

*Skeletonema costatum*, a form of wide distribution, mainly northern, but, as Ostenfeld (1913) remarks, including the coasts of almost all countries, is similarly

neritic in other seas and usually confined to the neighborhood of the coast. In north European waters it has its maximum in spring but has been found flowering in autumn as well at many localities.

### Thalassiosira [65]

The spring flowerings of Thalassiosira (fig. 129) are perhaps the most notable event in the phytoplanktonic cycle of the coastal belt of the Gulf of Maine. In 1920 these commenced first in the coastal belt between Cape Elizabeth and Cape Ann, probably during the last week of February, and they progressed so rapidly that by March 5 (stations 20059 and 20060) a tow of a few minutes clogged the nets with brownish masses of *Thalassiosira nordenskioldi* (*Th. gravida* only occasionally appears in these catches, and *Th. decipiens* still more rarely), with smaller amounts of *Chætoceras criophilum, Ch. decipiens, Ch. didymum, Ch. diadema, Ch. atlanticum, Ch. laciniosum, Ch. debile, Rhizosolenia semispina, Rh. setigera, Thalassiothrix nitschioides, Coscinodiscus,* and *Lauderia glacialis*. Thalassiosira also commenced to flower at about this same date in the Massachusetts Bay region in 1925, when it was not detected in Cape Cod Bay in December or January, but was extremely abundant near Stellwagen Bank on February 24, in Cape Cod Bay and near the tip of Cape Cod during the first week of April, and still plentiful in the northern side of Massachusetts Bay during the last week of the month.

Thalassiosira is a characteristically neritic genus, and at first its flowerings are closely confined to the immediate vicinity of the land. Thus it was overshadowed by Chætoceras 22 miles out at sea on March 5, 1920 (station 20061), though diatoms were in as great volume there as close inshore, with practically the same list of species plus the more oceanic *Chætoceras atlanticum* but lacking the neritic *Thalassiothrix nitschioides*.[66] During the first week of March in 1920, Jeffreys Ledge marked roughly the offshore boundary for the flowerings of Thalassiosira in the western side of the gulf; in fact, it did not spread out over the western basin until some time between March 24 and April 18 in that spring.

Thalassiosira may be expected to commence multiplying one or two weeks later in the season in Massachusetts Bay than it does just north of Cape Ann, for only occasional specimens were noted off Gloucester on March 1 and at the head of Massachusetts Bay on the 5th in 1920;[67] but it was extremely abundant at both these localities from April 6 to 9 (stations 20089 and 20090).

In the northern side of the gulf the first flowerings of Thalassiosira hardly spread beyond Cape Elizabeth, it being only sparsely represented near Seguin Island on March 4, 1920 (station 20057), though other diatoms were moderately abundant there (p. 425), and it was not found at all off Mount Desert Island the day before (station 20056). On April 10 (station 20096), however, it dominated a moderately abundant assemblage of diatoms at the first of these localities, evidence

[65] For records of Thalassiosira during the spring of 1913 see Bigelow, 1914a. It has since been recognized at station 10250 in August, 1914; stations 10275 to 10278, 10280, 10281, 10285, 10287, 10290, 10301, 10302, 10322, 10328, 10329 and off Schoodic Head on June 3 and Petit Passage on June 10, 1915; stations 20050, 20058 to 20061, 20072, 20088 to 20107, 20109, 20114 to 20117, and 20122 in 1920; and stations 10505 to 10507 in 1921.

[66] Halosphæra was likewise detected at this station (p. 459).

[67] At this station (20062) no peridinians were detected and but few diatoms, chiefly *Th. nordenskioldi* with occasional cells of *Chætoceras decipiens, Ch. atlanticum, Ch. criophilum,* and *Lauderia glacialis*.

of an eastward expansion of its flowering area; and although the waters farther east along the coast supported only a scattering of Thalassiosira on the 12th (station 20099, April 12), it is probable that this genus is flowering actively all along the northern

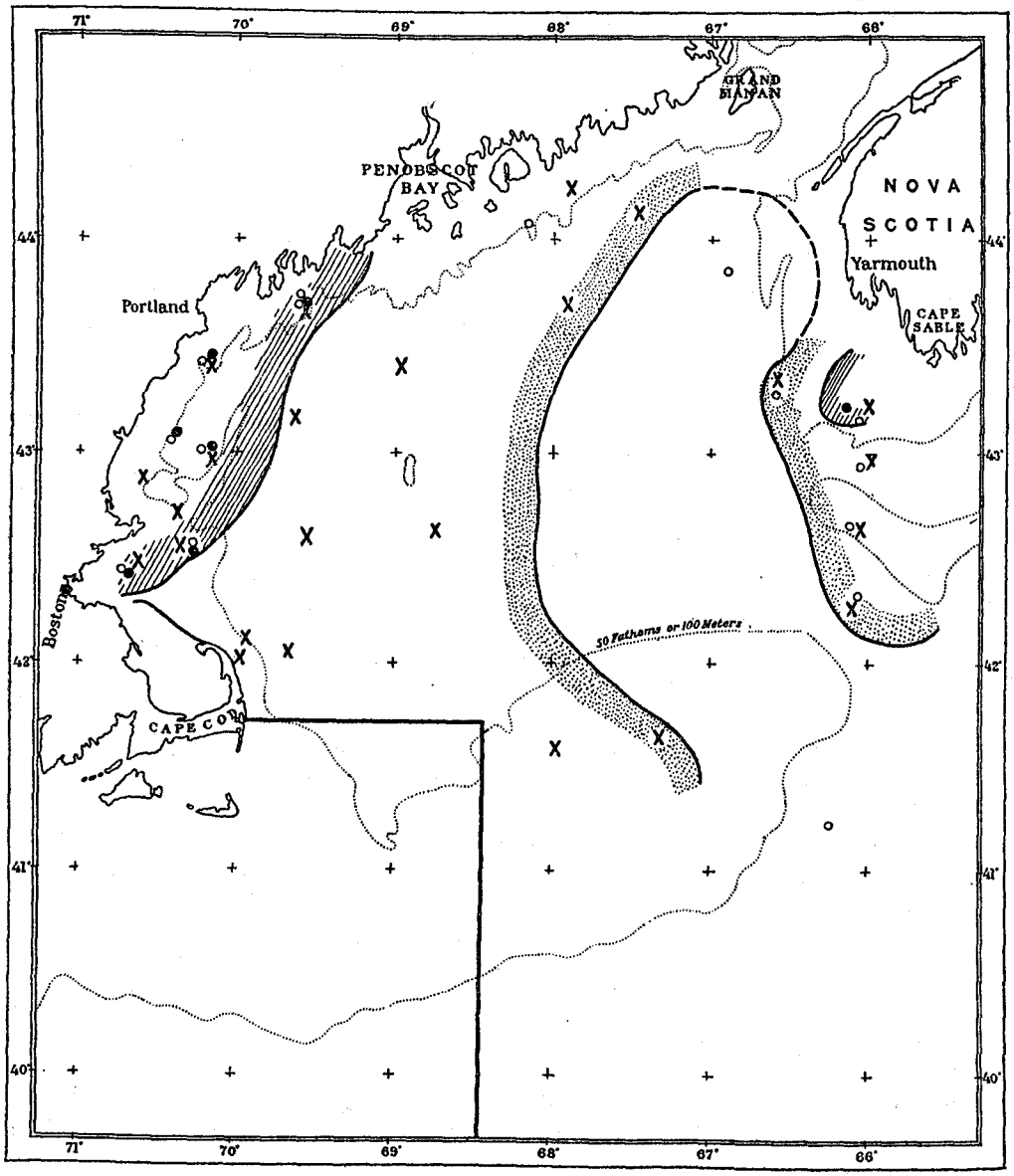


FIG. 129.—Distribution of the diatom genera Thalassiosira and *Lauderia glacialis*. ●, locality records for Thalassiosira for March; X, for April; O, for *Lauderia glacialis*. The hatched curve marks the offshore boundary to the abundant flowerings of Thalassiosira up to mid-March; the stippled curve incloses its flowerings up to the last week of April for the years 1913 and 1920

shores of the gulf by the middle of the month in most years. It is also likely that the harbors and bays along this part of the coast see a great production of Thalassiosira commencing a week or two earlier, judging from conditions at St. Andrews.

Thus Fritz (1921) found no Thalassiosira during November, December, or January, but a scattering appeared in her tows in February and early March; it was flowering actively by the end of that month, reaching its plurimum during the last half of April and first half of May. Similarly, McMurrich (1917) did not detect it at St. Andrews until March nor regularly until April in 1916.

Thalassiosira likewise spreads seaward over the whole western half of the gulf from mid March to mid April (fig. 129). And while we found no Thalassiosira on Georges Bank in February, March, or April of 1920, except for occasional examples at one station on the southeastern slope (station 20109) on the 16th of the latter month (flotsam, perhaps, from the Thalassiosira flowerings then under way from Cape Sable out to the Eastern Channel), this genus is to be expected to appear over the western half of the bank during the last half of April, Douthart having collected masses of it over the north central part on the 14th of the month in 1913 and in less abundance at various locations in that same general region on the 27th (Bigelow, 1914a, p. 415).

It is not clear whether this Georges Bank flora is primarily driftage from the inner parts of the gulf which multiplies actively in the shoal waters over the bank, or whether it represents the local flowerings of Thalassiosira that have survived there since the last preceding period of multiplication as resting spores on the bottom. In any case the result is that the range of Thalassiosira extends from the north shore of the gulf right out across the western side of the basin to Georges Bank by the last week in April, and Douthart's rich gatherings point to the northwestern part of the latter as the site of very productive flowerings.

The flowerings of Thalassiosira that take place in the shoal waters off Cape Sable and out to Browns Bank arise entirely independent of those in the western side of the gulf. They do not commence until later in the season, for only an occasional specimen was found off the Cape on March 23 in 1920 (station 20084), and none on Browns Bank or in the northern channel a few days earlier (stations 20072 and 20078). However, production must have been under full headway there soon after that, because the genus occurred in abundance at all the stations off Cape Sable, on German Bank, and right out to the Eastern Channel by April 15 and 16 (stations 20103 to 20107).

At this time the Eastern Channel marked the extreme limit of the shoals of Thalassiosira in this direction, there being none in our towings on the neighboring parts of Georges Bank on April 16 and 17 (stations 20108 to 20111), although there was a very abundant community of Chætoceras over the seaward slope (station 20109). But what is known of the expansion of the Nova Scotian current during the later spring makes it probable that Thalassiosira would have been found generally dispersed over the eastern half of Georges Bank a week or two later, thus making its range continuous over the whole of the latter at some time late in April.

It is at about this date that Thalassiosira attains its widest distribution as an important factor in the plankton of the gulf, as outlined on the chart (fig. 129). It is doubtful whether it ever spreads in any abundance over the western side of the basin, for we found a belt of considerable breadth entirely free from it there

from April 12 to 17 in 1920; nor did we find it at all in the eastern side of the gulf in the first half of May in 1915.

Considering the gulf as a whole, Thalassiosira attains its plurimum abundance as well as its widest range during the last half of April, but it remains so typically neritic throughout its vernal flowering period that it is always most plentiful close in to the land, where it may monopolize the surface waters locally. Such, for example, was the case off Gloucester on April 3, 1913 (station 10055), when the mass of diatoms taken in a short tow was almost exclusively composed of two species of Thalassiosira—*T. gravida* and *T. nordenskioldi*—with only occasional examples of *Chætoceras densum*, *Ch. atlanticum*, *Ch. contortum*, *Biddulphia aurita*, *Coscinosira polychorda*, *Thalassiothrix nitschioides*, and *Rhizosolenia semispina*. Even more monotonous and equally abundant catches of Thalassiosira were made by Welsh between Cape Ann and Cape Elizabeth early in May, 1913. On the 2d he wrote:[68] "The water yesterday and to-day full of green slime," and on the 3d, "the water is full of greenish-brown algæ," which on examination proved to consist almost altogether of Thalassiosira (in Bigelow 1914a, p. 406). This genus was equally predominant, and in great abundance, off Penobscot Bay on May 12, 1915 (station 10276), and at St. Andrews Fritz found it far outnumbering all other diatoms combined on April 20 and May 1, 1917, the dates of its maximum abundance.

Even in the centers of greatest abundance for Thalassiosira along the western and northern shores of the gulf we have usually found a considerable mixture of the several species of Chætoceras in the catches of the tow nets, especially of *Ch. debile*, *Ch. decipiens*, *Ch. diadema*, and of various other diatoms as well. Farther out at sea, in the basin of the gulf, Thalassiosira has never been notably abundant and has been both outnumbered and outbulked by Chætoceras at most of the stations. This was the case on Platts Bank (station 20094) on April 10 and in the western side of the basin (station 20115) on the 18th in 1920. Near Cashes Bank, however, Thalassiosira was a large element in the plankton—though hardly to be described as dominant—the day previous (station 20114). Possibly this shoal ground is a local flowering center.

These observations suggest that Thalassiosira first spreads to the basin of the gulf as flotsam from the coastal zone and to some extent from Georges Bank, but that it continues to multiply as long as the physical state of the water with which it drifts continues favorable for its existence and reproduction.

Thalassiosira did not dominate the diatom community at any of our stations off western and southern Nova Scotia during the spring of 1920, though it was both plentiful and widespread there in April, as I have just remarked.

It is probable that the geographic range of Thalassiosira in the Gulf of Maine begins to contract, from the sea shoreward and from south to north along the western shore, about the 20th to the 25th of April in most years. Our stations for 1915 and 1920 combined show that it entirely vanished from the Cape Cod-Massachusetts Bay region by the first week of May. It was confined to the northern coastal zone, from Cape Ann to the Bay of Fundy, by the second week of the month in 1915. In the zone between Cape Ann and Cape Elizabeth, where it was so

[68] In his field notes.

abundant during the first days of May, 1913, that the streaks in which it occurred were dense enough to discolor the water, the proportion of living cells and chains rapidly diminished and dead débris increased after the 1st of May.

In 1915 Thalassiosira, like most other diatoms, had likewise entirely disappeared from the banks off western Nova Scotia by May 7 to 10 (stations 10271 and 10272), where our tows for the spring of 1920 proved it plentiful in April, though it may persist until later close in to the coasts. It is also probable that it vanished by May from the parts of Georges Bank where it flowers in April, none having been found on the western end on May 16 and 17 in 1920 (stations 20127 to 20129), nor in any of our summer tows on the bank.

As the spring draws to a close the range of Thalassiosira continues to contract, until by the middle of June it is confined to the immediate vicinity of the land from Cape Elizabeth on the west to the northern shores of Nova Scotia on the east[69]; but notwithstanding this shrinkage in the area occupied by it, it continues flowering actively along the northern shore of the gulf. Thus we made almost pure catches of *Thalassiosira nordenskioldi* and *Th. gravida* and in great abundance near Mount Desert Island, off Penobscot Bay, and off Casco Bay on May 10 to 13 in 1915 (stations 10275 to 10277), and again off Schoodic Head, a few miles east of Mount Desert Island, on June 3. It was also fairly plentiful off the mouth of Penobscot Bay on June 14 (station 10287), and in 1912 *Th. gravida* was a considerable element in the plankton at two stations between Casco Bay and Penobscot Bay as late in the season as July 26 to August 2 (stations 10016 and 10022).

In 1915 it was not uncommon near Mount Desert Island and off Machias, Me., as late as July 15 and 19 (stations 10301 and 10302), while Bailey (1917, p. 98) records it from Eastport on July 29 and locally along the shores of the Bay of Fundy during the first half of August.

Thalassiosira was not detected at any station outside the 100-meter contour in the northern and eastern deeps of the gulf in August, 1913, 1914, or 1915, but in 1912 we found it at two stations and in some numbers in the Eastern Basin as late as the 14th of that month (stations 10027 and 10028). Evidently its summer status varies from year to year in this part of the gulf. This is also the case at St. Andrews and probably in all estuarine situations generally along the coast line east of Mount Desert Island. Thus Doctor McMurrich's notes give it as dominant only until about June 8 at St. Andrews in 1916 and scattering until July 6, but in 1917, when Fritz (1921, p. 53) found its flowering culminating early in May, with "the enormous total of 8,750,000 frustules" in her tow on the 1st, it persisted in moderate numbers throughout June. She noted a second maximum (1,760,000 in the tow) on July 3, and while only small numbers of Thalassiosira were taken after that date, the genus persisted, among more numerous diatoms of other genera, right through the late summer and early autumn until October 24, which was her latest date for it. Thus there is a marked contrast between the seasonal periodicity of Thalassiosira at St. Andrews on the one side of the gulf and in Massachusetts Bay in the other, where,

[69] During June, 1915, Thalassiosira was detected at stations 10281, 10284, 10285, 10287, 10290; also half a mile off Schoodic Head on the 3d, where it was extremely abundant, and off the entrance of Petit Passage, Nova Scotia, on the 10th.

though dominant and extremely plentiful in April, it practically vanishes by the first week of May.

Neither of the two most abundant species of Thalassiosira (*Th. nordenskioldi* or *Th. gravida*) exists planktonic in the surface waters of the open gulf in any numbers after August, nor are they recorded for the outer parts of the Bay of Fundy after August 10 by Bailey (1917). The fact that we found a scattering of *Th. nordenskioldi* close to Swan's Island off the mouth of Penobscot Bay on September 15 (station 10317), and again in Massachusetts Bay on October 1 (station 10322), during the autumn of 1915, shows that they may persist in small numbers here and there along the coast until well into the autumn; but the genus has not been detected in any haul in any part of the open gulf between the last week of October and the first week of February.[70]

The seasonal lists of Thalassiosira in northern seas generally (especially the well-marked periodicity in its appearances and disappearances), and the certainty that its abundance in the Gulf of Maine results from local flowering and not from immigration, makes it probable that is passes the balance of the year, from the close of the summer flowerings until its reappearance in the plankton in early spring, on the bottom as resting spores. But so far as I am aware these have not actually been seen in this genus.

The relative numerical proportions in which the two commoner species of Thalassiosira—*Th. nordenskioldi* and *Th. gravida*—occur in our spring and summer samples have not been worked out fully, but the preliminary examination suggests that on the whole *Th. nordenskioldi* is the more important in March, April, and May (as might be expected from the experience of European students), and that *Th. gravida* increases in relative abundance as the season advances. A third species of Thalassiosira, *Th. decipiens*, which has been rare in the spring tow nettings (stations 20059, 20101, and 20104 to 20106), appeared in numbers near Mount Desert Island (station 10328) and off Penobscot Bay (station 10329) on October 9, 1915. *Th. hyalina* has been detected at several widely separated localities during the spring of 1920 (occasional specimens only)—viz., off Cape Cod on March 24 (station 20088), in the Northern Channel (station 20105), over Browns Bank on April 16 (station 20106), off the southeast face of Georges Bank on April 16 (station 20109), and in the Eastern Channel (station 20107). *Thalassiosira baltica* is recorded from one station (20061) and may well have been overlooked elsewhere among the swarms of *Th. nordenskioldi*. There is also one locality record each for *Th. clevei* (station 10328), *Th. subtiles* (station 20089), and *Th. bioculata* [71] (station 20107).

### Thalassiothrix

This genus is represented in the Gulf of Maine hauls by two species—*longissima* and *nitschioides*. The records for *Th. longissima* are too scattered to outline its seasonal fluctuations in our waters in a satisfactory way. It appeared only twice in the catches for March, 1920—that is, in the southeast corner of the basin (station 20064) and on Georges Bank (station 20066). McMurrich (1917), too, found it only once at St. Andrews during that month (March 4); then, however, in abundance. It was not detected among the Thalassiosira-Chætoceras flowerings in the north-

[70] Fritz (1921) records it on Feb. 9.

[71] Identified by Dr. Albert Mann.

western side of the gulf during April, 1920, nor did Fritz find it at St. Andrews at any time during the spring or until the end of August. But it occurred sparingly at two of our April stations in the northeast corner of the gulf and off the Nova Scotian coast (stations 20101 and 20103), likewise locally off Georges Bank (station 20109), in the basin (stations 20114 and 20115), and off Cape Cod (station 20116) during that month in 1920. We have twice made rich catches of Thalassiothrix between Cape Elizabeth and Penobscot Bay in May (station 10277, May 13, and station 10280, May 31, 1915). It likewise dominated the diatom plankton on the western end of Georges Bank and southeast of Nantucket Shoals on July 23, 1916 (stations 10347, 10348, and 10354), but we have not found it elsewhere in the open gulf during June, July, or the first half of August, though Fritz (1921) records it at St. Andrews on August 28.

*Th. longissima* was present in small numbers off Penobscot Bay on September 15, 1915 (station 10317), and irregularly at St. Andrews during that month in 1917, according to Fritz. It flowers abundantly in the Bay of Fundy and along the coast of Maine in October, for Fritz counted over half a million in her standard haul at St. Andrews on October 6, 1917. It was abundant near Mount Desert Island on October 9, 1915 (station 10328), and a corresponding augmentation of this species extended southward at least as far as Cape Ann during the last 10 days of that month (stations 10329 and 10330).

Fritz found few *Th. longissima* at St. Andrews after the middle of October and none in January or February. Neither have we found it anywhere in the open gulf during the winter. McMurrich (1917) describes it as present in great numbers at St. Andrews on February 26, 1915.

On the whole these data suggest two maxima for *Th. longissima*—one late in the spring and the other in October,[72] paralleling its seasonal history in the North Sea region, where its chief flowering time is May, though it may also occur in great quantities around Scotland in August and November (Ostenfeld, 1913, p. 408). At Woods Hole Fish (1925) found it regularly in late winter and spring but only occasionally at other seasons. The flowerings of Thalassiothrix observed by McMurrich in February and March show that its seasonal cycle is less regular than that of Thalassiosira, Biddulphia, etc.

*Th. longissima* is usually a minor element in the phytoplankton of the inner parts of the gulf, where its flowerings are not only local but brief in duration. But it was extremely plentiful on the western end of Georges Bank on July 23, 1916, at the stations just mentioned, where with fewer *Rhizosolenia styliformis* it formed a very rich and monotonous diatom community (fig. 124), and when its center of abundance extended over a considerable area, out to the continental slope on the south and to Nantucket Shoals on the west.

We have never seen this flowering of Thalassiothrix rivaled within the gulf, and a single occurrence of this sort does not necessarily establish Georges Bank as a major center of production for it. This species is so large and so easily recognized that it may finally prove of great value for the study of ocean currents, as Ostenfeld

[72] Probably the "Thalassema" mentioned by Bailey (1917, p. 107) as dominating some of the October gatherings in Passamaquoddy Bay were actually *Thalassiothrix longissima*.

(1913) points out, but before it can be used in this way for American waters a far clearer insight must be gained into its hydrographic and geographic relationships. In fact, it is still an open question whether *Th. longissima* is oceanic or neritic in the western Atlantic, or as indifferent to the proximity of coasts or shallows as it is on the European side.

*Thalassiothrix nitschioides*, although one of the most characteristically neritic of all pelagic diatoms, has occurred far more often in our tow nettings than has its relative, *Th. longissima*. Fritz (1921) found *Th. nitschioides* at St. Andrews throughout the year except between October 15 and December 13, and the numbers counted were usually so small that its absence from the hauls made during that period is perhaps not significant. Probably it occurs irregularly the year round in similar situations all along the coast line of the gulf, and its presence or absence and its relative abundance out at sea may depend more on the currents sweeping it out from these sources of supply around the coast line than on local flowerings.

It seems that few drift out to sea during the winter, for it was detected at only one station—off the mouth of the Merrimac River (station 10492)—during the midwinter cruise of the *Halcyon* in 1920 and 1921, and not at all in our tows off Gloucester from November, 1912, to February, 1913. But we had it off the western part of Georges Bank on February 22, 1920 (station 20045), and during that March it was found at four stations in the coastal belt between Cape Cod and the Bay of Fundy; also in the Eastern Channel, on the southeastern slope of Georges Bank, and at two stations off Shelburne, Nova Scotia (stations 20056, 20058, 20059, 20064, 20066, 20068, 20071, 20075, 20076, 20084, and 20088; fig. 127). *Th. nitschioides* attains its widest distribution in the gulf in April, during which month in 1920 it not only occurred more regularly in the coastal belt than in March (in fact, at almost every inshore station where diatoms of any sort were plentiful), and off Nova Scotia out to the southeastern slope of Georges Bank, but likewise at four localities in the central basin of the gulf (stations 20089 to 20093; 20095 to 20098; 20100, 20102 to 20107, 20109, 20114, and 20117).

Our records suggest that *Th. nitschioides* practically disappears again from the offshore parts of the gulf after the end of April, for it was detected at only one station off Cape Elizabeth (10277) during the May cruise of the *Grampus* in 1915, not at all at the 10 stations occupied by the *Albatross* on the western side of the gulf and on Georges Bank from May 4 to 17, 1920 (stations 20120 to 20129). We have not found it at sea in the gulf during the summer and only once during the autumn, viz, off Penobscot Bay on October 9, 1915 (station 10329).

*Th. nitschioides* follows much the same seasonal cycle in north European waters, where it flowers most abundantly from February until April, according to locality, diminishing in abundance during May, and with its annual minimum in August. It is far less important as a member of the plankton in the Gulf of Maine, where we have never found it abundant, than it is in the North Sea region, where it occurs at all times of the year (Ostenfeld, 1913, p. 409), very generally over the entire area, and at times in great numbers.

The occurrence of *Th. nitschioides* so far offshore off Nova Scotia and over the southeastern slope of Georges Bank, contrasted with our failure to find it in any of

our other towings on the bank irrespective of season, is best explained as due to a drift of the Nova Scotian current moving southwestward in spring from the Scotian banks across Browns Bank and the eastern channel and along the outer part of Georges Bank. This is corroborated by sundry other lines of evidence, planktonic as well as hydrographic.

As there is some confusion between this species and the closely related *Th. frauenfeldi* in the European lists published by the International Committee for the Exploration of the Sea (Ostenfeld, 1913), I may note that only such cells as were attached to one another in their characteristic zigzag chains are recorded here as *nitschioides*, these being quite different in appearance from the chains of *frauenfeldi*. The latter species has not been identified in any of the Gulf of Maine tow nettings.

### Other diatoms

The genera so far discussed include all that we have found important in the plankton of the outer waters of the Gulf of Maine, and while the station lists (p. 423) include various others, none of them occur regularly or abundantly enough to color the plankton. I may emphasize especially the universal rarity of brackish-water, littoral, and bottom-dwelling diatoms out at sea. Pleurosigma, for example, is never represented by more than occasional examples, though detected at many localities far and wide. Under estuarine conditions, however, as in the tributaries of the Bay of Fundy, littoral diatoms of many genera are much more abundant (Bailey, 1917; Fritz, 1921; Bailey and Mackay, 1921).

Finally, I may emphasize our failure to find any diatoms in the gulf to which it is safe to ascribe either a Tropic or an Arctic origin, except, perhaps, for *Fragilaria oceanica*, occasional examples of which were detected in the tows in the Eastern Channel and over the southeast slope of Georges Bank on April 16, 1920 (stations 20107 and 20109). The absence of other arctic diatoms in the Gulf of Maine is the more striking if contrasted with their abundance and frequent dominance in the Gulf of St. Lawrence in spring, as is illustrated by the following table based on Gran's (1919) list for May 11, 1915. This Arctic community proved so shortlived there, however, that it had entirely disappeared in June, to be replaced by a typically boreal assemblage, most of whose members—*Rhizosolenia setigera*, *Nitschia seriata*, Coscinodiscus, and *Chætoceras laciniosum*—are equally characteristic of the spring plankton of the Gulf of Maine.

| St. Lawrence diatoms, May 11, 1915 | Arctic[1] | Gulf of Maine | St. Lawrence diatoms, May 11, 1915 | Arctic[1] | Gulf of Maine |
|---|---|---|---|---|---|
| Acnanthes tæniata | × | | Fragilaria cyclindrus | × | |
| Amphiprora hyperborea | × | | Fragilaria oceanica | × | × |
| Bacteriosira fragilis | × | | Navicula pelagica | × | |
| Biddulphia aurita | | × | Navicula septentrionalis | × | |
| Chætoceras atlanticum | | × | Navicula vanhöffeni | × | |
| Chætoceras compressum | | × | Nitschia closterium | | × |
| Chætoceras criophilum | | × | Nitschia frigida | × | |
| Chætoceras debile | | × | Pleurosigma stuxbergi | | × |
| Chætoceras decipiens | | × | Rhizosolenia hebetata | | × |
| Chætoceras diadema | | × | Thalassiosira bioculata | | |
| Chætoceras scolopendra | | × | Thalassiosira gravida | | × |
| Chætoceras teres | × | × | Thalassiosira hyalina | × | × |
| Detonula confervacea | × | | Thalassiosira nordenskioldi | | × |
| Eucampia grœnlandica | × | | Thalassiothrix longissima | | × |

[1] Species that are endemic in the Polar seas, where ice forms in winter, and in the Gulf of St. Lawrence, but which occur only as immigrants farther south.

## NOTES ON OTHER UNICELLULAR PLANTS AND ANIMALS

The flagellates Phæocystis and Halosphæra and the tintinnid infusorians and acantharian radiolarians are secondary in importance to the peridinians and diatoms in the plankton of the Gulf of Maine, but are still sufficiently abundant there at times to call for brief notice. The last two are grouped here with the phytoplankton for convenience sake, though they are animals and consequently consumers and not producers.

### PHÆOCYSTIS

The brown unicellular alga Phæocystis is the only organism that we have ever found rivaling the vernal flowerings of diatoms in the Gulf of Maine either in abundance of floating vegetable matter produced or in actual numbers. Its identity is established by the simple structure of its cells, together with their green color and association into slimy colonies. But whether we have to do with *Ph. pouchetii*, *Ph. globosa*, or with both these species, has not been determined, the precise character by which the two are separable—i. e., the form of the colonies, whether lobate (*pouchetii*) or globose as in *globosa* (Lemmermann, 1908)—having been destroyed either by preservation or by the churning which they underwent in the nets. This is unfortunate, because *pouchetii*, with a range hardly extending south of 55° N. latitude in European waters, is decidedly a more northern form than *globosa*, which occurs in maximum abundance in the southern part of the North Sea and in the English Channel (Ostenfeld, 1910).

The Gulf of Maine records for Phæocystis have been confined to April 18 to 20, 1920, when it was sparsely represented in the western basin (station 20115) but so plentiful off Cape Cod and in the southern part of Massachusetts Bay (stations 20116 to 20118) that the fine-meshed silk nets used on the surface were clogged with its slimy masses after a few minutes towing, making it impossible to obtain a representative catch of diatoms or of other members of the phytoplankton. The Phæocystis colored the water brown; in fact, the appearance of the nets as they are lifted dripping with brown slime of offensive odor betrays the presence of this alga at once.

Plentiful though Phæocystis was at this time, its flowering period must have been brief, because it was not found in the region in question three weeks earlier (stations 20087 to 20090) or off Massachusetts Bay and Cape Cod two weeks later (stations 20120 to 20125), and it was not found anywhere in the gulf during the first weeks of May, 1915.

These few records show that Phæocystis fills much the same biologic niche in American as in north European waters. The region of its occurrence in the gulf is reconcilable, without discussion, with the neritic habit with which Gran (1902 and 1912) and Ostenfeld (1910) have credited it, and which its European distribution as a whole demands, though it is not confined to the immediate neighborhood of the coast in either side of the North Atlantic. It seems a regular event for Phæocystis to appear suddenly in tremendous quantities, and while its maximum flowering falls later in the northern than in the southern part of its range, it is characteristic of it to dominate the plankton for only a short time at any given region. Off the Norwegian

coast, according to Gran (1902, p. 17), Phæocystis reaches its maximum after the diatoms have passed their apex of abundance, with a monotonous Phæocystis plankton succeeding them for a very short period. Apparently it bears much the same temporal relationship to the vernal diatom flowerings in Massachusetts Bay, but in the western basin farther offshore it seems that Phæocystis precedes instead of succeeds the greatest seasonal abundance of diatoms.

The records of the International Committee point to May as the month in which Phæocystis is at its maximum in the North Sea—that is, about the same season as in the Gulf of Maine. Judging from the general geographic distribution of Phæocystis, the latter is probably its most southerly center of abundance in the western side of the North Atlantic, but the optima of temperature and salinity for this alga can not be established for American waters until more records are available. It may, however, be of interest to note that the Gulf of Maine collections (being from water of 3 to 4.5°) have been well within the temperature limits of *Ph. pouchetii* in European waters. But the salinity in which we have found it (31.43 to 32.45 per mille) is far less than the mean of the European records, which is given by Ostenfeld (1910) as about 34.8 per mille for *pouchetii* and as 34.89 per mille for *globosa*, though the former also occurs at the mouth of the Baltic in waters less saline than those of the Gulf of Maine.

## HALOSPHÆRA

The unicellular pelagic alga *Halosphæra viridis* Schmidt[73] has been found at many of our stations, sometimes in considerable numbers, though it is not sufficiently prominent in the Gulf of Maine to have received a local vernacular name as it has in the Mediterranean (Steuer, 1910, p. 2). Halosphæra was first detected in the gulf in 1915, when it was widely distributed over the eastern basin of the gulf in May (stations 10269, 10270, 10271, 10272, and 10273), though nowhere abundant, and occurred locally off Mount Desert in June (stations 10284 and 10286); also at one station (10310) in August. It was likewise found across the whole breadth of the continental shelf south of Nova Scotia in June (stations 10291, 10293, 10294, and 10296), and off Shelburne in September (station 10313); likewise on German Bank on September 2 of that year (station 10310) and in the Massachusetts Bay region early and late in October (stations 10322, 10336, and 10337). During the spring cruises of the *Albatross* in 1920 Halosphæra was detected at some thirty stations in the gulf widely distributed both in time and space (stations 20044, 20045, 20048, 20054, 20057, 20064, 20067, 20069, 20070, 20072, 20073, 20074 to 20076, 20078 to 20080, 20086, 20097, 20098, 20100, 20105, 20112, 20120, 20123, 20124, 20126, and 20129). These records, combined, suggest that Halosphæra attains its maximum in the gulf late in the spring, practically disappearing again in midsummer,[74] though it has been described as plentiful at that season in the colder waters about Cape Breton, Nova Scotia (Wright, 1907). Doctor McMurrich found Halosphæra in late spring and early summer (April 17 to July 6) at St. Andrews, which corresponds to the May–June maximum in the open Gulf of Maine.

[73] Identification according to Lemmermann, 1908, p. 21.

[74] Our failure to find Halosphæra previous to 1915 was probably due to the fact that most of our stations in previous years were in late July and August when Halosphæra is rare in the Gulf of Maine.

We have never found Halosphæra dominant in the plankton of the gulf. The richest catches have been over the outer part of the shelf off Nova Scotia (fig. 130; stations 10293 to 10295) and off Mount Desert Island (station 10284) in June, 1915. Most of our records are based on the vegetative stage and on stages in division of the protoplasm (Lemmermann, 1908, p. 21, figs. 71 and 72). Cells with aplanospores have been detected only once in our towings—that is, near Shelburne, Nova Scotia, June 23, 1915 (station 10293), and no attempt has been made to trace the life history of Halosphæra in American waters, as Gran (1902, p. 12) has done so carefully for the Norwegian Sea.

The seasonal fluctuations of Halosphæra in the Gulf of Maine generally parallel its occurrence in the North Sea, where it is at its maximum in May and its minimum in August. But east of Cape Sable it evidently reaches its greatest abundance later in the season, for Wright (1907) describes it as an important factor in the plankton at Canso, eastern Nova Scotia, in June and July.[75]

It is now well established that Halosphæra is not endemic in the North Sea but occurs there only as an immigrant from the Atlantic via the northern route around Scotland; and it is primarily of southern—Atlantic—origin in the Norwegian Sea, though it may also be endemic there to some degree. Whether it is equally an immigrant in the Gulf of Maine is yet to be determined, but the facts that our largest catches of it have been made over the outer part of the continental shelf and that we have never found it in any great numbers in the inner part of the Gulf point in this direction.

## ACANTHARIAN RADIOLARIANS[76]

The swarming of radiolarians, represented by the genus Acanthometron, is a decidedly sporadic event in the Gulf of Maine, as it is in North European waters also (Mielk, 1913), but on such occasions they are extremely conspicuous among the plankton, thanks to their large size, distinctive appearance, and reddish color. Up to the present time we have only once found Acanthometron dominant—that is, on August 22, 1914 (station 10253, fig. 131), when it swarmed off Cape Ann and in the western basin. We have never found Acanthometron before or since in midsummer in the gulf. Apparently it occurs more regularly in early autumn and is more generally distributed then, for it was comparatively plentiful in the center of the gulf (station 10309), in the northeast corner (station 10316), off Penobscot Bay (station 10318), and off Shelburne, Nova Scotia (station 10313), during the first and second weeks of September in the year 1915. It was a conspicuous element in the plankton of Massachusetts Bay during the last week of that month (stations 10320 and 10321; fig. 132), but its presence there was short-lived, for none were found a month later (stations 10337, 10338, and 10339, October 26 and 27). Acanthometron has been detected in only one October tow elsewhere in the gulf (a few miles off Penobscot Bay, October 9, 1915, station 10329). It was not found at any of the stations in the western part of the gulf in the late autumn, winter, or spring, but a few specimens were noted on German Bank and in the North Channel on April 15, 1920 (stations 20103 and 20105).

[75] For notes on the temporal occurrence of Halosphæra in the open Atlantic, the Norwegian Sea, and in the Mediterranean see Cleve (1900), Gran (1902), Steuer (1910), and Ostenfeld (1910).

[76] For an excellent account of the northern acantharians see Popofsky, 1905.

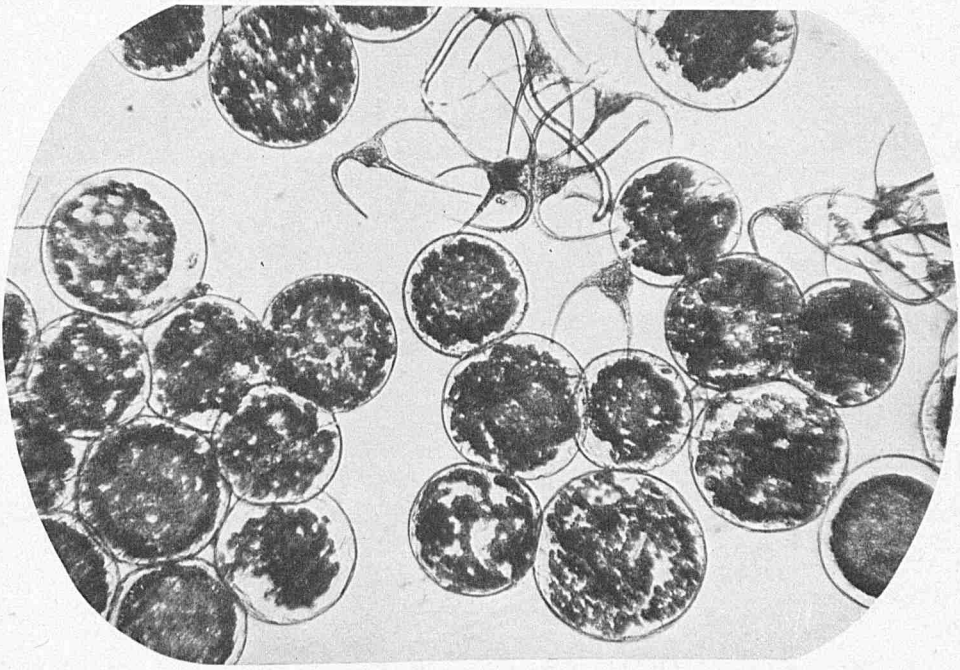

FIG. 130.—Phytoplankton dominated by Halosphæra, with *Ceratium longipes*. Surface haul off Shelburne, Nova Scotia, June 23, 1911 (station 10293). × 40

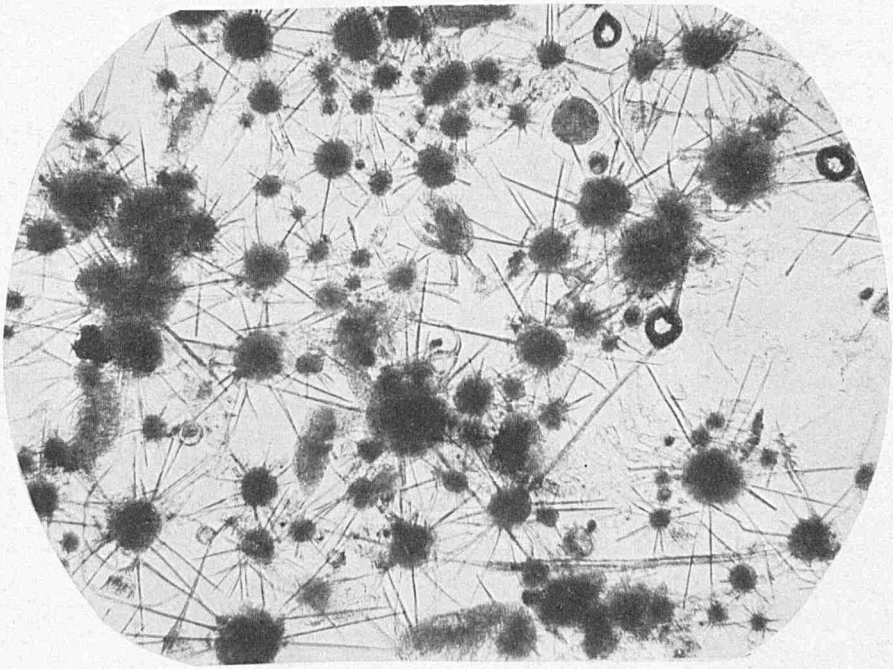

FIG. 131.—Plankton dominated by the radiolarian genus Acanthometron. Surface haul off Cape Ann, August 22, 1914 (station 10253). × 50

These scattered records point to late summer and early autumn as its season of greatest abundance in the Gulf of Maine, and they suggest, though hardly prove, that its chief center of distribution lies in the western part of the gulf with a second-

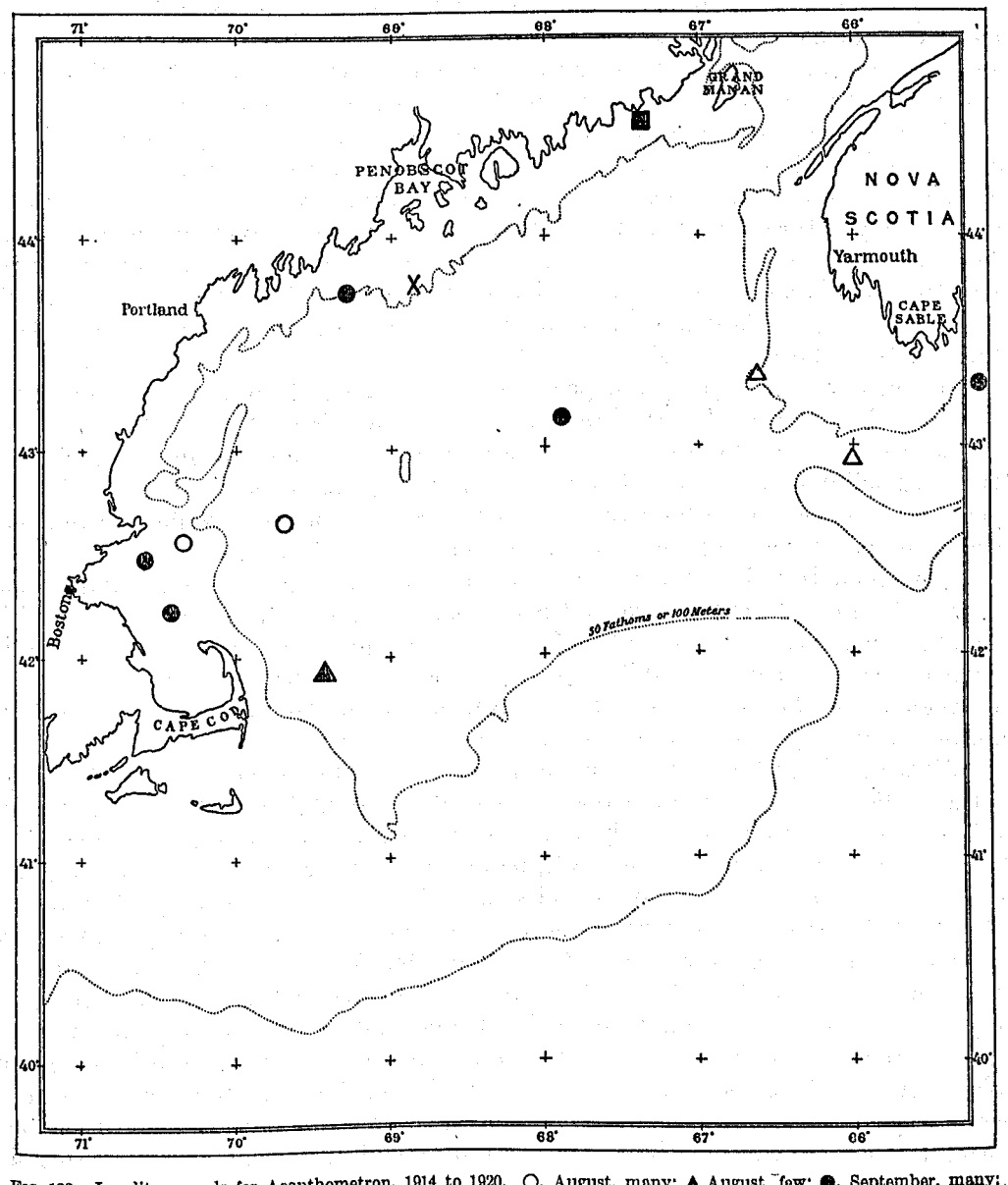


FIG. 132.—Locality records for Acanthometron, 1914 to 1920. ○, August, many; ▲ August, few; ●, September, many; ■, September, few; ✕, October, few; △, April, occasional

ary center somewhere off southern Nova Scotia, for which its presence off Shelburne on September 6, 1915, is evidence. Furthermore, the areas of abundance for Acanthometron have been small in extent, with neighboring stations yielding

few or none even on the same day. The August swarm just mentioned was so concentrated that only odd specimens appeared in the tow at the station next to the south (station 10256) and none at all at those to the east or north. On September 1, 1915, when it was abundant at station 10309, none were taken 40 miles to the southwest (station 10308), 35 miles to the east (station 10310), or 60 miles to the northeast (station 10315). Similarly, none were taken off Cape Elizabeth on September 20, 1915 (station 10319), nor off Mount Desert Island on the 15th (station 10317), though it was plentiful at an intervening station (10318) on the 16th, with no notable hydrographic difference in the state of the water. There is no apparent correlation between the presence or absence of Acanthometron in the gulf and the precise temperature, for while the August swarms of 1914 were living in water of about 18 to 20° off Cape Ann, the Nova Scotian collections for September, 1915, were from a temperature colder—and perhaps very much colder—than 15°. We have one record of Acanthometron from water of only about 4° (German Bank, station 20103, April 15, 1920).

Its occurrence is equally independent of salinity within broad limits, for it was most abundant in the Western Basin and off southern Nova Scotia when the water was near its freshest for the year, but we have not detected it in Massachusetts Bay until salinity has increased considerably from its seasonal minimum. Broadly speaking, however, Acanthometron is plentiful in the gulf only while the temperature is comparatively high and the salinity comparatively low.

Acanthometron likewise attains its seasonal maximum in late summer and autumn off north European coasts, with a general increase from August on, and its minimum in May. On both sides of the Atlantic the richest catches of this radiolarian have been from the eddies of cyclonic currents—that is, from the southern Norwegian Sea (May), Irminger Sea (July), middle of the North Sea (November), and in our gulf from the Western Basin (August).

Although Acanthometron occurs at times and locally in even greater abundance in the shallow coastal waters of the eastern side of the Atlantic than in the Gulf of Maine, it is essentially an immigrant there from the open ocean. The records of the International Committee for the Exploration of the Sea prove that although it is independent of actual temperature and salinity for its ability to exist, its abundance in the North Sea depends more or less on the amount of warm, highly saline ocean water entering around the north of Scotland (Mielk, 1913). Its chief centers of abundance in the Gulf of Maine have been in the regions farthest removed from such oceanic influence—that is, close in to land and in the semistagnant Western Basin. Furthermore, we have never found it in the zone of mixture between cool coast waters and warmer ocean waters along the continental slope, and its absence there is particularly significant because Acanthrometron centers have often been encountered in the contact zone between Atlantic and Arctic waters on the other side of the North Atlantic.

Here we must leave the question of the distribution of Acanthrometron for the present; but in passing I may point out that more data on this point are particularly desirable, not so much for the sake of mere completeness of local information as because of a very interesting phenomenon exhibited by this form, namely, the sharply

circumscribed areas in which it occurs when it does swarm and the suddenness of its appearances and disappearances, the causes of which are totally unknown.

## TINTINNIDS

The tintinnids of the Gulf of Maine offer an interesting field for study because the several members of Cyttarocylis—the chief genus—have rather precise geographic characteristics (Jørgensen, 1899; Brandt, 1906). The records for 1914, 1915, 1916, and 1920 show that tintinnids may be expected anywhere in the gulf; only rarely, however, have they formed any considerable part of our catches of phytoplankton. As a rule, they are decidedly scarce, often absent, or at least so rare as to be overlooked, though they are conspicuous objects in the field of the microscope. In1920 they were found at most of the March stations in the eastern side of the gulf from the coast of Nova Scotia out to the Eastern Channel and across the continental slope off Cape Sable (fig. 133; tintinnids sufficiently numerous to be recorded at stations 20071, 20072, 20074 to 20079, 20083, 20084, and 20086); but none were detected on Georges Bank or in the western half of the gulf during that month. By mid-April [77] the tintinnids, like the peridinians, had practically disappeared from the waters where they occurred in March, with no compensating augmentation elsewhere in the gulf. In 1915 we found tintinnids in some numbers on German Bank and off Lurcher Shoal on the 7th and 10th of May (stations 10271 and 10272), as well off as Penobscot Bay two days later (station 10276). Apparently (though our records are insufficient) they gradually spread westward from May on, with the advance of the season, for we took them in large numbers off Cape Cod on July 22, 1916 (station 10346).

In August and September, 1915, tintinnids were recognized in the Eastern Basin, in the center of the gulf, and alongshore from Penobscot Bay to Cape Elizabeth (stations 10304 to 10306, 10310, 10311, and 10316 to 10319). In October of that year they occurred in localities as widely separated as the Massachusetts Bay region (stations 10320, 10323, and 10336), the neighborhood of Mount Desert Island (station 10328), and off the Grand Manan Channel (stations 10316 and 10327). McMurrich found them at St. Andrews from late August until October 9, in 1916. In short, they may be expected anywhere in the gulf in summer and early autumn.

Only three times have we found tintinnids an important factor in the plankton of the gulf—that is, at the Cape Cod station just mentioned, July 22, 1916, where there were about half as many Cyttarocylis as Ceratium in a sample taken at random; off Cape Elizabeth on September 20, 1915 (station 10319); and off the southeast slope of Georges Bank on July 22, 1914 (station 10220). But the group is evidently more important east of Cape Sable, for they appear at times in great numbers in the cold water along the outer coast of Nova Scotia, this being the case at several of our stations in July and August, 1914 (Bigelow, 1917, p. 329). Wright (1907) records both Tintinopsis and Cyttarocylis as common at Canso, Nova Scotia, during the summer.

[77] There are only two April records for the group in the gulf—stations 20098 and 20101. Elsewhere during that month they were at least so rare as to be overlooked.

I can give only the briefest of notes on the species of tintinnids concerned, though these are not hard to identify, thanks to Jørgensen's (1899) and Brandt's (1906) beautiful figures. Most of the Gulf of Maine records listed above are based

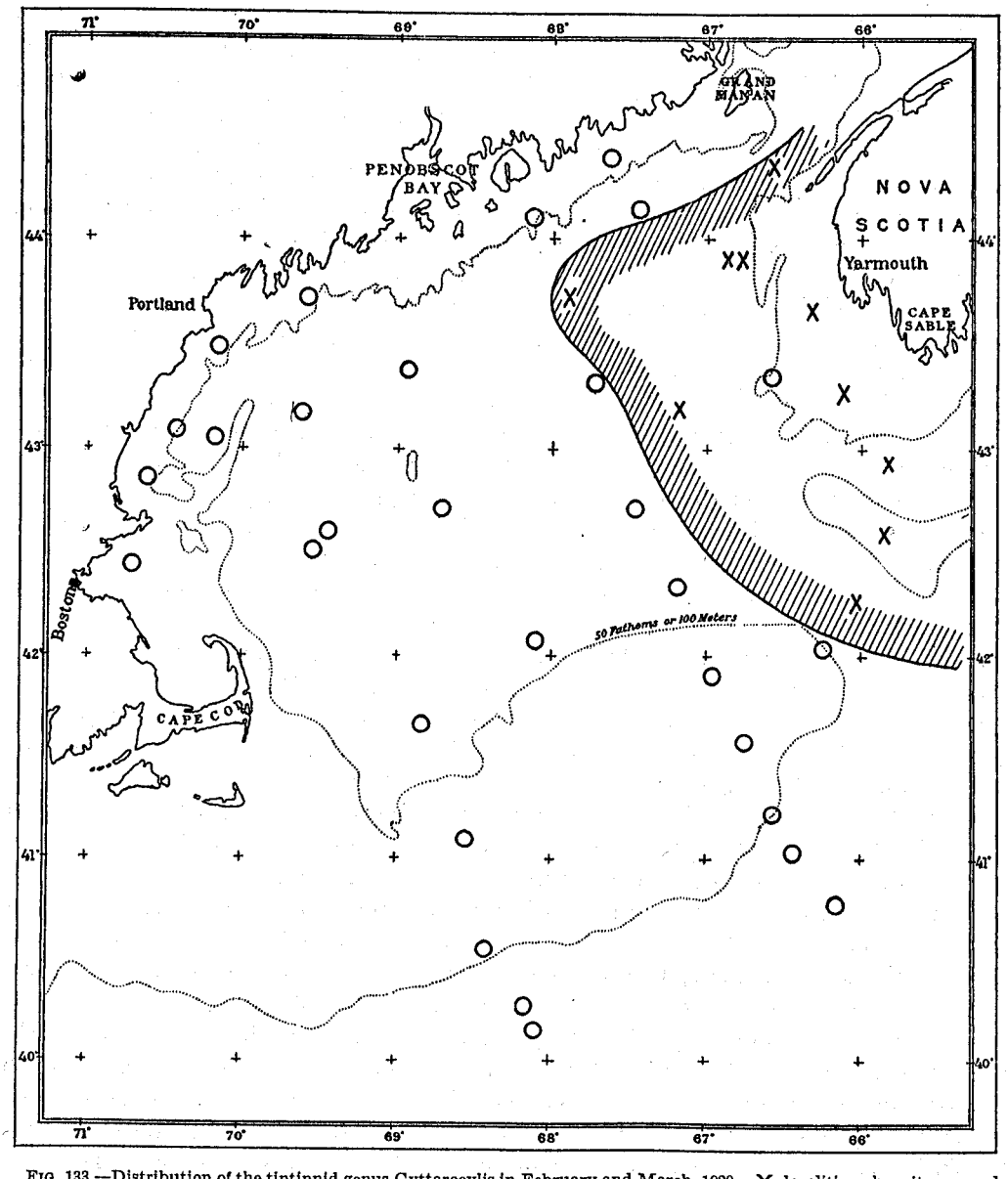


FIG. 133.—Distribution of the tintinnid genus Cyttarocylis in February and March, 1920. X, localities where it was, and O, where it was not found. The hatched curve marks its approximate western boundary at the time

on one form or another of the highly variable *Cyttarocylis denticulata*. This was notably the case for the rich haul off Cape Cod and for the towings off southern Nova Scotia in July and August, 1914, just mentioned, but the rich catch off Cape

Elizabeth (station 10319) was chiefly *C. serrata* (Brandt, 1906, Taf. 39, figs. 4 and 6). McMurrich (1917) records *C. ehrenbergi* and two species of Tintinopsis—*T. campanula* and *T. ventricosa*—from St. Andrews, while his unpublished plankton lists note *Cyttarocylis denticulata* and *C. subulata*.

According to Brandt (1910) the limits of *C. denticulata* in the North Sea area are chiefly determined by temperature, its upper optimum being about 12°. In a general way this is true also of the Gulf of Maine and of Nova Scotian waters, for it is more numerous in the cold Nova Scotian current than in the higher temperatures of the gulf, but the data are not sufficiently extensive to show whether its distribution within the gulf reflects the slight regional differences in temperature that prevail there.

## OTHER UNICELLULAR ORGANISMS

The reader must not assume that the foregoing notes exhaust the major groups of unicellular organisms in the Gulf of Maine. On the contrary, such important divisions as the coccolithophorids, the silicoflagellates, and the infurosia (apart from the tintinnids) have not been mentioned at all, not because they do not occur but because they have not been detected so far in our offshore hauls, or only on the rarest occasions. Infusoria, in particular, may be expected to prove of considerable ecologic importance when tow-net catches, preserved by methods suitable for these minute and very delicate organisms, are intensively studied. Such, at least, is the case in June in the Gulf of St. Lawrence, where the infusorian genera Mesodinium and Labœa occur in abundance, as they do also in the waters off Halifax in May. (Gran, 1919, p. 493.) The silicoflagellate genus Distephanus occurs at times in some numbers at St. Andrews. (McMurrich, 1917, p. 4.)

We have not detected Notiluca in any of the Gulf of Maine towings, though its wide distribution in general and its seasonal abundance in the Irish Sea and coastal regions of the North Sea region in particular, where it is one of the most frequent sources of phosphorescence (Ostenfeld, 1910; Herdman, Scott, and Dakin, 1910), point to its presence in the gulf as probable.

Globigerina is likewise to be expected in the gulf as an occasional immigrant from the ocean waters of the open Atlantic, but is never likely to prove of any importance in the Gulf of Maine plankton.

## NOTES ON THE BIOLOGY OF THE PHYTOPLANKTON

Perhaps no phenomenon in the natural economy of the gulf so arrests attention (certainly none is so spectacular) as the sudden appearance of enormous numbers of diatoms in early spring, and their equally sudden disappearance from most of its area after a brief flowering period. As precisely this same phenomenon takes place in north European waters, where biologists have long occupied themselves with the marine plankton, no wonder the possible factors, hydrographic and seasonal, or the physiology of the diatoms themselves, which first permit and then estop their almost inconceivably rapid multiplication and finally even prohibit their further existence, have been the subject of much study and discussion. Nevertheless, as Herdman (1920, p. 817) has recently declared, the factors governing this phenomenon still remain imperfectly understood.

The obstacle to the advance of knowledge along this line has not been any lack of plausible explanations; on the contrary, various changes take place in spring in the physical medium in which the plankton exists, any or all of which might, *à priori*, be assumed to control the life history of the planktonic plants. Such, for example, are the seasonal variations in the temperature of the water; in its salinity; in its density, viscosity, and vertical stability; in the activity of its vertical circulation; in its alkalinity; in the supply of dissolved foodstuffs; and in the strength of the sun; every one of which, directly or indirectly, affects the viability and reproduction of the phytoplankton, and which, in unfavorable combination, may make existence impossible for them.

It has been observed repeatedly, and in widely separated seas, that the vernal augmentation of the diatoms synchronizes with the first vernal warming of the water. But, as Moore, Prideaux, and Herdman (1915, p. 247) have emphasized, "it is to be remembered that the physical cause must have a latent period ahead of the biological effect." It may be stated as a general rule that the vernal flowerings of diatoms follow so closely after the commencement of vernal warming (if not antedating it) that the latter can not be the cause of the former. This is certainly the case in the waters between Cape Ann and the Isles of Shoals, where diatoms commence to multiply actively in March, the temperature still being at its winter minimum (p. 383), while in 1925 winter flowering of *Rhizosolenia alata* commenced in the falling temperature of December (p. 396). Furthermore, marine diatoms as a class have been found tolerant of such wide variations of temperature and of salinity, both over the geographic and seasonal ranges in nature, and in cultural experiments (Allen and Nelson, 1910; Fritz, 1921a), as to make it in the highest degree unlikely that slight changes in either of these environmental features, within the limits of both obtaining in the Gulf of Maine, are themselves of prime importance in the economy of these pelagic plants. But temperature and salinity in combination determine the viscosity, the density, and the vertical stability of the water, which in turn tend to control the activity of its vertical circulation and thus indirectly to favor or hinder the flotation and food supply of marine diatoms as the seasons change.

Herdman (1920) believes the increasing intensity of the sunlight is the chief stimulant for the spring flowering of diatoms, and certainly without sufficient sunlight the reproduction and even the continued existence of diatoms—for that matter, of all chlorophyllous plants—would become impossible. This may well be the case in the higher latitudes of northern Europe, likewise in Canadian waters, during the short winter days. And while terrestrial experience in the latitudes of the Gulf of Maine (40 to 45° N.) shows that the sun rises high enough in the sky for active photosynthesis at all seasons, the increasing percentage of hours of sunlight per day, and its greater intensity consequent on the increasing declination of the sun, no doubt help to make the spring a more favorable season for the flowering of diatoms than late autumn or winter. But this factor can not by itself explain the seasonal cycle of diatom flowerings as they actually occur, for if increasing light be a factor inducing their commencement it should equally favor their continuance throughout the summer, instead of the culmination and disappearance after a few weeks that characterizes most parts of the Gulf of Maine (p. 396).

On the whole, with successive observations and experiments it grows more and more probable from year to year that, given temperatures, salinities, and alkalinities (p. 486) in which diatoms can exist, with sunlight sufficient for active photosynthesis, their regional and seasonal abundance depends chiefly on the richness of the water in dissolved food substances, organic and inorganic, and to a less extent on the activity of vertical circulation of the water and its viscosity.[78]

The suddenness with which diatoms commence flowering in spring tends to corroborate this generalization, for if the gulf were abundantly supplied with nutrients the year round we might expect to find their numbers steadily augmenting throughout the coastal waters of the gulf during the late winter, as vertical circulation grows more and more active and as the sun rises higher and higher; but as a matter of fact (and this is true not only of the Gulf of Maine but of other northern coastal waters) the tremendous flowerings of diatoms so characteristic of early spring culminate almost between one week and the next.

The most reasonable explanation for this is that at least one of the nutritive substances on which they depend, whether it be nitrogen, phosphoric acid, silica, or some other, occurs in less than the minimum required for their active growth and reproduction during the winter and until the first days of spring, when the increasing outflow from the rivers, combined with an increasingly active vertical circulation of the sea water, raises the supply above this critical point, whereupon a rapid multiplication of diatoms at once ensues. Conversely, an exhaustion of one or other foodstuff is now generally accepted as the cause of the sudden disappearance of diatoms after their vernal flowering period. The diminishing viscosity, also, and the increasing vertical stability of the water, which characterize the advancing summer owing to the rising temperature, likewise militate against the continued multiplication of diatoms. The former renders flotation difficult, as explained below (p. 482), and the latter so effectively isolates the surface stratum of water (where diatoms find their optimum light conditions) from the underlying layers that replenishment with nutrients from below is effectively hindered.

Although our Gulf of Maine studies touch only the outer edge of this very complex subject, it is of such fundamental importance in the economy of the sea that a brief discussion here needs no apology.

Diatoms being producers, not consumers, it is, of course, from what Johnstone (1908, p. 212) has called the "ultimate foodstuffs in the sea" that they derive their nourishment, chief of which are carbonic acid, the nitrogen compounds, phosphoric acid, silica (because of their habit of secreting silicious skeletons), and various other mineral salts in minimal quantities; also oxygen (not, of course, a food substance but necessary for life). Except under very special circumstances it is hardly conceivable that the phytoplankton of the open sea ever suffers a shortage of oxygen or of the available sources of carbonic acid. But as all the other nutrients occur only in minute quantities in sea water we can readily understand that the supply of one or the other might fall temporarily below the minimal amount[79] required for diatom

[78] See Johnstone (1908), Herdman (1923), and Johnstone, Scott, and Chadwick (1924) for general discussions of the nutrition of the phytoplankton.

[79] For discussions of Liebig's "Law of the Minimum" in its relation to marine plants, see Johnstone, 1908, p. 234; Gran, 1912, p. 367.

growth, and in the long run probably the supply of nitrogenous compounds chiefly determines the regional richness and poverty of the phytoplankton as a whole.

Allen and Nelson's (1910) experiments on rearing marine diatoms corroborate this, for they found it necessary to increase the concentration of nitrates, and apparently also of phosphates, above that of normal sea water in order to produce active multiplication. Fritz's (1921a) work along this line is especially pertinent here, for she experimented at St. Andrews on the culture of planktonic marine diatoms of Gulf of Maine species with similar results, being unable to obtain any considerable and persistent growth without the addition to the normal sea water of the nutrient salts—nitrates and phosphoric acid—employed by Allen and Nelson. With these, however, she obtained flourishing cultures of *Thalassiosira nordenskioldi*, *Skeletonema costatum*, *Asterionella japonica*, *Nitschia closterium*, *Melosira hyperborea*, and various other planktonic species.

## NITROGEN

It has long been known that sea water absorbs nitrogen so readily from the air that the surface strata are usually saturated with this element, but it is still questionable whether any of the planktonic plants are able to utilize elemental nitrogen first hand. It has long been the commonly-accepted belief, also, supported by experiments on land, that no chlorophyllous plants can do so, unless, like the Leguminosæ, in symbiosis with nitrogen-fixing bacteria; but that all others—terrestrial or marine, unicellular or multicellular—are dependent on nitrogen compounds elaborated by some other means for their food supply of this essential element.

In 1920, however, Moore and Webster (1920) published the results of experiments which seemed to demonstrate that certain green unicellular algæ do possess the ability to obtain, and to fix by a process of photosynthesis, elemental nitrogen dissolved by the water from the air. A year later Moore, Whitley, and Webster (1921) carried out further experiments on a marine green alga, which they grew in measured volumes of sea water, finding that at the end of the experiment the amount of fixed nitrogen in plant and water combined exceeded the nitrite present at the beginning. From this they concluded that the excess must have come from the elemental nitrogen dissolved in the water, and so, in turn, from the air. These experiments, however, were not conclusive, no precaution having been taken to exclude the nitrogen-fixing bacteria which Reinke (1904) and Keding (1906) found on the fronds of several species of fixed algæ at Helgoland, and which, therefore, were probably present on the algal fronds used by Moore, Whitley, and Webster in their experiments, or to determine their presence or absence. And although Moore and his associates adduce several reasons why they think it improbable that the value of their experiments is detracted from by this "loophole" in technique, it remains an open question whether the increase in the amount of fixed nitrogen, which they demonstrated, did actually result from photosynthesis by the algal fronds experimented upon or from activity on the part of bacteria living symbiotic upon them.

So far as I am aware, the ability of marine phytoplankton to synthesize elemental nitrogen has not actually been tested by critical experiment directed to this definite end. But it has repeatedly been found that very much richer cultures of

planktonic diatoms may be grown with the aid of appropriate nutriants (including ammonium sulphate) than in normal sea water, and that exhausted cultures of diatoms may be temporarily revived by adding nitrogen in appropriate combination, which would hardly be the case were the diatoms able to avail themselves directly of the nitrogen gas dissolved in the water.[80] Therefore it may be assumed that diatoms, probably also peridinians, Phæocystis, Halosphæra, etc., require a supply of ready combined nitrogen for their existence.

The elemental nitrogen absorbed by the water from the air may serve as the source of this combined nitrogen through the medium of the bacteria just mentioned. These nitrogen-fixing bacteria have been found in the Baltic and in the North Sea, in bottom muds from many localities; also on the surfaces of a great variety of fixed algæ, including Fucus and Laminaria, and on the surfaces of planktonic organisms; likewise in the Indian Ocean (Keutner, 1905; Keding, 1906). Hence, they are probably cosmopolitan in such situations and may be expected to prove as widespread in the Gulf of Maine as they are in the North Sea region, though they have not been actually detected there as yet. The two genera, Clostridium and Azotobacter, have been found to exist under the most diverse physical conditions, and they may well prove of prime importance in the economy of life in the narrow coastwise belt where fixed algæ flourish, though this is still a matter of conjecture, as is the extent to which their activities depend on symbiosis with other bacteria or with algæ. But since they have never been detected free in the sea water it is not likely that their activities contribute much directly to the supply of nitrogen available for the use of planktonic plants on the high seas.

However this may be, normal sea water is extremely poor in nitrogen in combinations utilizable by plants—that is, as ammonia, nitrates, or nitrites—the chief sources for the latter in coastwise seas such as the Gulf of Maine being the drainage from the land and the decomposition of organic matter in the sea.

It has long been appreciated by biologists that northern rivers, especially those that flow from countries with heavy rainfall and much cultivated land and those that are polluted with organic wastes, do bring down to the sea vast amounts of this dissolved nitrogenous nourishment (Gran, 1915). It has been calculated from the nitrogen content of the Rhine (averaging 2 to 3 milligrams of nitrogen, in the form of dissolved compounds, per liter) that the North Sea receives annually not less than 390,000,000 kilograms (383,000 tons) of combined nitrogen in this way (Brandt, 1899, p. 230; Johnstone, 1908, p. 282).

The greater part of the watershed of the Gulf of Maine being timbered, not cultivated, and less densely settled than the countries bordering the North Sea, its river waters might be expected to prove less rich in nitrogen than the Rhine water; and the many analyses made by the United States Geological Survey prove such to be the case, with the rivers of Massachusetts richer in nitrogen than those of Maine. Thus the Charles River, a short distance above Boston, has been found to average about 0.879 part of nitrogen—as ammonia, nitrates, and nitrites—per million of water,[81] the Merrimac 0.524 part per million in its lower course above Haverhill, and

[80] Allen and Nelson (1910) give an extended discussion of this subject.
[81] Massachusetts Board of Health, 1890, examination of water supplies.

the Kennebec only about 0.3 part of combined nitrogen per million at Augusta (Whipple, 1907, p. 182). Perhaps 0.5 part per million would be a fair average for all the rivers emptying into the gulf—that is, only about one-fourth to one-fifth as rich as Rhine water. Nevertheless, this is a considerably higher concentration of total nitrogen than Raben (1905a and 1910) found in the sea water of the North Sea, where it ranged from 0.110 to 0.378 part per million, or in the Baltic (0.105 to 0.247 part per million). With a total annual runoff of not less than twenty-five hundred billion cubic feet of water from the rivers and streams that drain the watershed of the gulf, the latter must yearly receive at least 39,857 tons of nitrogen fixed in combinations readily assimilable by plants. This, roughly, is one-tenth the amount (383,000 tons) given by Johnstone (1908, p. 282) for the North Sea from Brandt's (1899) oft-quoted calculation of the nitrogen discharged by the Rhine. But the area of the Gulf of Maine, as inclosed by a line Cape Cod–Cape Sable, is only about one-fifth that of the North Sea, hence its river waters contribute at least half as much of nitrogen compounds yearly per unit of sea area as do those of the North Sea, and very likely more than half, for the other rivers that drain into the North Sea may not carry as heavy a load of nitrogen as does the Rhine.

Whipple's (1907) analyses of the water of the Kennebec, which may be taken as typical of the rivers tributary to the gulf, may not prove a definite seasonal periodicity in the concentration of dissolved total nitrogen, the range being from 0.24 to 0.49 part per million of water for the months of January, March, April, May, June, and August; but the highest concentrations (0.487 and 0.327) were in March and April, just when the total outflow is swelling with the spring freshets. Therefore it is safe to assume that the land drainage that empties into the gulf is at least as rich in nitrogen in spring, when the discharge from the rivers is at its maximum, as it is during the rest of the year, if not actually richer, as the analyses suggest. With the concentration of dissolved nitrogen compounds probably at least twice as high in river water as in the sea water of the gulf, the freshening of the latter, which is caused in spring by river freshets, is probably accompanied by a considerable increase in the concentration of nitrogen in the coastal zone over the values obtaining there in winter, with the alteration greatest near the mouths of the larger rivers and along the zones where their discharges have the greatest effect on salinity.

Although the decomposition of dead animals and plants in the sea does not actually add anything to the store of nitrogen preexisting in the water, simply transforming it from one form to another, it must constantly be making available for the use of the phytoplankton large amounts of this foodstuff that was previously bound up in other organic forms [82]—that is, in the bodies of animals and in attached plants, such as eelgrass (Zostera) and the larger algæ; and great though the amount of nitrogenous fertilizer brought down to the Gulf of Maine by its affluent rivers is, this source may rival it.

As every seaside farmer knows, eelgrass (Zostera) rots much more slowly than do the various algæ such as the "rock weeds" (Fucaceæ) and "kelps" (Laminariæ)

[82] Johnstone (1908) gives an interesting chapter on the circulation of nitrogen.

and the many smaller forms, but even for Zostera time brings progressive decomposition. After it has disintegrated to a fine dustlike state, further oxidization probably takes place more rapidly, particularly when it is suspended in the upper, more illuminated water layers. Is it not reasonable, then, to think of such organic particles or aggregates of particles as foci around which diatoms can multiply, being nourished by the nitrogenous substances as these constantly go into solution, just as the weeds in our gardens thrive around the particles of manure or of nitrogenous fertilizers that are similarly disintegrating or dissolving in the soil? At any rate, whether or not this particular picture be correct, a vast supply of organic matter is derived from the Zostera, the constituents of which must eventually join the general nutritive store of the sea water in which it decays and from which it was taken in the first instance. Even such of it as passes through the digestive tracts of bottom-dwelling mollusks must also travel the same path in the end, either as excreta or by the final death and decay of the endless chain of animals that feed one on another. What is true of Zostera is equally true of the more rapidly decaying marine algæ.

Qualitatively, at least, all this applies as well to the Gulf of Maine as it does to the other side of the North Atlantic, Zostera, with the "rock weeds," "kelps," etc., being abundant, with the general conditions of temperature, etc., under which they live, die, and decay, much the same. And since Zostera forms dense fields in the sandy and muddy bottoms of sheltered bays, estuaries, etc., all around the coast from Cape Cod to Nova Scotia, with beds of "rock weeds" (Fucaceæ), Laminariæ, etc., along the rocky or stony shores where it fails, the organic débris produced by the annual decay of submerged marine vegetation along the coast, spermophyle and algal, must reach very large proportions.

The decay of the dead bodies of the members of the animal communities that thrive so abundantly in the gulf, both on the bottom and planktonic, are also constantly making nitrogenous compounds available in the first instance as detritus, finally to find their way into solution. The importance of the rain of dead bodies of planktonic organisms, which is constantly descending through the water, as providing pastures for animals living on the bottom below, has long been realized. Some are devoured by other animals en route; others, like the medusæ and ctenophores, may entirely decompose and go into solution as they sink; but it is probable that in moderate depths, such as those of the Gulf of Maine, fragments at least of most of them reach the bottom before they entirely disintegrate. Naturally a larger amount of plant detritus accumulates on bottom in shoal water near land than out at sea because nearer the source of supply, and animal débris may also be expected to be most abundant in moderate depths. Think, for instance, of the product of the death rate in an extensive mussel (Mytilus) bed. But the following analyses prove that there is some nitrogenous débris (derived from plants and animals combined) everywhere in the uppermost layer of mud, silt, or sand on the bottom of the gulf, in deep water as well as in shoal.

*Analyses of nitrogen (as $N_2$) in sea sediments from the Gulf of Maine and vicinity, performed by the chemical laboratory, United States Geological Survey*

| Station | Locality | Depth in meters | Per cent $N_2$ |
|---|---|---|---|
| 10288 | Latitude 48° 28′, longitude 67° 30′ | 227 | 0.09 |
| 10291 | Latitude 43° 24′, longitude 66° 22′ | 64 | .12 |
| 10292 | Latitude 43° 19′, longitude 64° 59′ | 157 | .11 |
| 10294 | Latitude 42° 36′, longitude 64° 27′ | 176 | .06 |
| 10295 | Latitude 42° 22′, longitude 64° 16′ | 500+ | .24 |
| 10301 | Latitude 44° 31′, longitude 67° 24′ | 73 | .01 |
| 10513 | Latitude 43° 47′, longitude 69° 08′ | 80 | .13 |
| 10518 | Latitude 43° 07′, longitude 69° 19′ | 194 | .24 |
| 10522 | Latitude 43° 00′, longitude 69° 35′ | 157 | .32 |
| 10523 | Latitude 42° 58′, longitude 69° 55′ | 219 | .32 |
| 10525 | Latitude 43° 04′, longitude 70° 23′ | 110 | .20 |
| 10526 | Latitude 43° 05′, longitude 70° 33′ | 44 | .19 |
| 10530 | Latitude 43° 38′, longitude 69° 46′ | 77 | .12 |
| 10534 | Latitude 43° 27′, longitude 69° 42′ | 137 | .17 |
| 10540 | Latitude 43° 03′, longitude 68° 51′ | 185 | .19 |
| 10541 | Latitude 42° 00′, longitude 68° 20′ | 201 | .27 |
| 10548 | Latitude 43° 30′, longitude 68° 38′ | 122 | .19 |
| 10550 | Latitude 43° 13′, longitude 68° 30′ | 198 | .19 |
| 10551 | Latitude 43° 09′, longitude 68° 05′ | 192 | .07 |
| 10552 | Latitude 43° 18′, longitude 67° 11′ | 201 | .11 |
| 10553 | Latitude 43° 09′, longitude 66° 53′ | 186 | .19 |
| 10556 | Latitude 42° 57′, longitude 66° 42′ | 218 | .05 |
| 10575 | Latitude 44° 06′, longitude 67° 04′ | 117 | .13 |
| 10577 | Latitude 44° 20′, longitude 67° 26′ | 110 | .16 |
| 10595 | Latitude 43° 58′, longitude 68° 16′ | 101 | .13 |
| 10608 | Latitude 41° 58′, longitude 69° 40′ | 174 | .13 |
| 10617 | Latitude 42° 04′, longitude 69° 57′ | 64 | .09 |
| 10623 | Latitude 42° 14′, longitude 70° 15′ | 24 | .17 |
| 20064 | Latitude 42° 20′, longitude 67° 13′ | 320 | .19 |

Owing to technically unsatisfactory preservation of the specimens, these determinations can be regarded only as approximations of the amounts of nitrogen actually present in the muds; but recognizing this possible source of error, the average is about 0.16 per cent of nitrogen (as $N_2$), for the whole series (otherwise expressed, about 3.2 pounds per ton of mud or sand).

As long as this store of nitrogenous detritus remains mingled with the mineral deposits that cover the sea floor, it remains unavailable for the use of the planktonic vegetation, though it supports many mud-eating animals that live on the bottom. It must be constantly going into solution, however, as the breaking down by decomposition proceeds, a process hastened in regions of strong tides where vertical currents keep much of this flocculent material in suspension, as is proved by the considerable amounts of fine organic débris often taken in the tow nets. Its availability for the support of diatoms and of the other planktonic plants thus depends largely on the state of circulation of the water, a question discussed below (p. 479).

The gradual impoverishment of the animal plankton, which takes place from autumn on, with the dying of the large medusæ, copepods, and other groups, has been commented on (pp. 47, 88). Its natural result is to cause a more rapid accumulation of animal débris during the cold half of the year than in summer. Generally the death rate among the animals living on bottom along the littoral zone is also higher in winter than in summer. Everyone who frequents the shores of the gulf knows that this is true of the algæ, vast quantities of rockweed and kelp being torn adrift from the rocks by the autumnal gales and piled up along the beaches, where they are soon ground up

into fine fragments. The largest amounts of eelgrass (Zostera) leaves are also thrown off around the shores of the gulf during the autumn and early winter; but these are so tough and decay so slowly that great accumulations of their fragments are still to be found the following spring, especially in the deeper channels that cut the mud flats where fields of this plant flourish, and it may be several years before they are reduced to the state of fine silt. Thus, the amount of nitrogen in solution in the sea water tends to increase during the winter, while conversely the denitrifying bacteria (which are known to exist in the sea) are less active at low than at high temperatures.

Rain and snow falling on the surface of the gulf likewise add nitrogenous compounds to its waters, for they wash out ammonia from the air and nitric acid formed during electrical discharges. But the amount of nitrogen dissolved in rain is much less in temperate than in tropical climates, Muntz and Marcano's (1889 and 1891) analyses showing larger amounts (an average of 2.23 milligrams nitric acid and 1.55 milligrams ammonia per liter) in the rain water at Carracas, Venezuela, than have been found in Continental Europe or in England. No nitrogen analyses have been made of the rain water that falls on the Gulf of Maine, or, so far as I can learn, for any neighboring part of North America, but probably it does not differ much from European analyses—that is, is in the neighborhood of 0.2 milligram nitric acid and 0.5 to 0.9 of ammonia per liter.

## SILICA

The obvious dependence of diatoms on silica (which is present in only very minute quantities in sea water) for the construction of their shells has naturally tended to focus attention on the fluctuations in concentration of that substance as probably governing the abundance of marine diatoms, and several recent authors, among them Michael (1921), have definitely accepted it as the chief determinant.

Diatoms require much more silica than nitrogen, the disparity between these two substances being much greater in the dry matter of these plants than in the sea water in which they live. Evidently it would be impossible for diatoms to form their silicious frustules without a sufficient supply of silica; in fact such a failure, with resultant abnormal forms, has actually been recorded by Allen and Nelson (1910) for experimental cultures, while these were undergoing rapid multiplication.

*Sources for dissolved silica.*—We might naturally expect to find the land drainage from an area as largely composed of felspathic rocks and of glacial débris as is the watershed of the Gulf of Maine, much richer in dissolved silica than the sea water, an expectation confirmed by several analyses of the waters of several New England rivers and springs made by the United States Geological Survey, as well as for river waters in other parts of the world. Thus, according to Fuller (1905, p. 53), 12 representative springs in various parts of the State of Maine carry from 5.1 to 15.1 parts of silica (as $SiO_2$) per million, the average for all 12 being about 10 parts per million, which is about five times as much as the sea water off Gloucester at the season of its highest concentration (p. 476). Spring waters, of course, undergo various and rapid modifications on their way first to the rivers and then to the sea, a river being "the average of all its tributaries plus rain and ground water, and many rivers show also the effects of contamination from towns and factories" (Clark, 1916, p. 64). Nevertheless, Clark's (1916, p. 71) analyses of the water of the Androscoggin a few miles above tide water [83]

[83] Average of 38 analyses of weekly samples taken between Apr. 25, 1905, and Jan. 16, 1906.

show as much as nine parts silica (as $SiO_2$) per million. Androscoggin water is, therefore, almost as rich in silica as the spring water average just quoted (Clark's exact figures are $SiO_2$, 18.63 per cent of total solids, salinity 48.3 per million). According to one analysis the upper waters of the Merrimac are even richer in silica than this ($SiO_2$, about 31 parts per million), but since the Merrimac flows for many miles through an alluvial valley in its lower course, and at the same time receives several important affluents from swampy areas, it probably reaches the sea with a much smaller percentage of silica in its water.

If we can take the Androscoggin as fairly typical of the rivers of northern New England (including the St. John River, of which no analyses are available), which is justified by the nature of its watershed, it appears that, on the whole, the river water emptying into the Gulf of Maine is 7 to 8 times as rich in dissolved silica ($SiO_2$) as our analyses off Gloucester suggest as a fair average for the latter. A discrepancy of this sort obtains between the silica contents of river and sea water in temperate zones generally, and its effects are probably accentuated in the Gulf of Maine, just as the effect of land drainage is in reducing surface salinity by the concentration of the run-off from a large watershed into a comparatively small and topographically circumscribed area of sea. It would therefore be reasonable to expect the waters of the Gulf of Maine to average high in silica when sufficient analyses are made to plot the distribution of silica in boreal seas generally.

In addition to the silica brought down by the rivers in the dissolved state, probably much larger amounts are carried to the sea, suspended in the form of the finely divided clay which is derived from the disintegration of felspars, etc. Though most of this clay is precipitated to the bottom on mixture with the salt water, part of it is carried to great distances. Murray and Irvine (1892, p. 240) suspected from their cultural experiments "that the pelagic silicious organisms might, in part at least, obtain the silica for their frustules and skeletons" from this clayey matter. So far as I know these experiments have been neither confirmed nor refuted, nor is it clear whether they were sufficiently precise to eliminate other possible causes for the abundant growth of diatoms which ensued on the introduction of clay into the artificial culture solution. But we must reckon with the possibility that diatoms not only make use of the dissolved silica but also of the insoluble silicates, given vertical circulation strong enough to keep the latter in suspension in the water.

A third possible source of silica is the slow solution of the rocks that form part of the coast line of the Gulf, and of its submarine boulders, sands, and clays. Silicious deposits of this sort have commonly been regarded as so nearly insoluble in sea water as to be negligible biologically; but as Clark (1916, p. 132) points out (geologists generally recognize this), sea water does attack and in the end dissolve the most refractory silicates, even if very slowly. In fact, Joly (1901) found that sea water dissolves more silica ($SiO_2$) from felspar than does distilled water.[84] But there are two reasons for hesitancy in applying Joly's generalizations to conditions as they occur in nature. First, I am unable to judge from his brief account whether his analyses took due account of the small amount of dissolved silica which we must

[84] Earlier tests by Thoulet (1889) gave the opposite result.

suppose to have been present originally in the sea water employed in his tests, and second, because distilled water exercises much less solvent action than do the land waters with their load of dissolved organic compounds, humus acids, and $Co_2$, which actually do the work of erosion on their way to the rivers and so to the sea; but, however slowly rock silicates are degraded in the sea, they are so degraded in the end. Indeed, all minerals, given time, finally succumb to the combined action of water, oxygen, and carbonic acid. Where a constant and rapid interchange of water between the bottom and the upper layers is kept up by vertical circulation (water, too, of low alkalinity—that is, of comparatively high carbonic acid tension—as is the case on Georges Bank (p. 481) and in the Bay of Fundy) degradation of silicates will be more rapid than in the deeps, where, as Murray (1912, p. 187) points out, "the soluble by-products are removed and the supply of oxygen and carbonic acid maintained by diffusion only."

Furthermore, we must bear in mind that in the case of the degree of concentration of silica we are dealing with solutions so attenuated that although the destructive action of sea water on felspathic rock fragments is almost inconceivably slow, it may be sufficient under hydrographic conditions as favorable as Georges Bank offers to yield the very small extra amount of silica needed to favor the active growth and multiplication of diatoms when added to what is in all sea water. Finally, the frustules of dead diatoms are themselves a potential store of this element and in one of its less insoluble forms.

It is still to be proved that there is not always a sufficient supply of silica at all times and in all parts of the sea for the growth and multiplication of diatoms. But stress has often been laid on the apparent parallelism between the seasonal fluctuations in the concentration of dissolved silica which Raben (1905) reported for the waters of the North Sea and of the Baltic (Murray and Irvine's earlier analyses are open to criticism) and the ebb and flow of the diatoms. Indeed, the correspondence between the two sets of phenomena, as it appears on Johnstone's diagram (1908, fig. 30), is striking enough. Subsequent analyses made by Raben himself during the years 1904 to 1912 (Raben, 1905a to 1914), both for the central and eastern North Sea and for the western part of the Baltic, show that the seasonal fluctuations in the amount of silica are less regular than his earlier work suggested. But he again found maxima in February and November over the periods of years covered by the tests, the silica ($SiO_2$) content varying in the Baltic from 0.53 to 1.76 milligrams per liter in February, to 0.40 to 0.93 in May, 0.20 to 1.49 in August, and 0.93 to 1.36 in November, averaging as follows:

*Average silica ($SiO_2$) content in the western Baltic, 1902 to 1912*

| Month | Silica, milligrams per liter | Number of analyses | Month | Silica, milligrams per liter | Number of analyses |
|---|---|---|---|---|---|
| February | 0.97 | 19 | June | 0.80 | 2 |
| March | .83 | 5 | August | .86 | 14 |
| April | .65 | 4 | November | 1.17 | 23 |
| May | .69 | 17 | | | |

Diatoms are at their maxima in this part of the sea in spring. Hence, the general correspondence between the silica curve and the fluctuations of the diatoms is at least suggestive. Furthermore, only a very slight difference in the concentration of silica dissolved in the sea water may be needed to control the multiplication of diatoms—perhaps less than one part in two million of water.

To test whether a similar parallel between seasonal concentration of dissolved silica and abundance of diatoms would be found in the Gulf of Maine, samples of sea water of about 8 liters each were collected monthly off Gloucester from December 28, 1920, to October 26, 1921, and shipped in 2-gallon tinned-iron cans to the chemical laboratory of the United States Geological Survey for analysis. The determinations for silica were made by Dr. R. C. Wells, who has described his methods (Wells, 1922), the results being as follows:

*Soluble silica in sea water collected at the surface about 1 mile south of Eastern Point Light, Gloucester, Mass.*

| Date of collection | Silica as $SiO_2$ in milligrams per liter of water=parts per million | Date of collection | Silica as $SiO_2$ in milligrams per liter of water=parts per million |
|---|---|---|---|
| Dec. 28, 1920 | 1.5 | June 27, 1921 | [1] 1.9 |
| Jan. 26, 1921 | 2.5 | | 1.9 |
| Mar. 2, 1921 | 2.9 | July 27, 1921 | .6 |
| Mar. 25, 1921 | 1.4 | Aug. 26, 1921 | .3 |
| Apr. 25, 1921 | .3 | Oct. 26, 1921 | [2] .4 |
| May 26, 1921 | .4 | | .7 |

[1] Average, 1.4. [2] Average, 0.55.

These are the first analyses for silica for sea water off the North American coast. Unfortunately, the samples of water were not large enough to allow duplicate determinations except in two instances.[85] As the diagram (fig. 134) illustrates, the seasonal fluctuations proved much wider than Raben's work would have suggested, with a pronounced maximum early in March, perhaps a second maximum in June and July, and something like six or seven times as much silica per liter at the beginning of March as in May or in autumn. That is to say, in the particular year in question (1921) the sea water near Gloucester was richest in silica a week or two prior to the time when we have usually found diatoms commencing to flower actively, became rapidly impoverished during the month when we have found diatoms most plentiful there in other springs, and poorest in silica at about the time the rich diatom flowerings come to a close. During June the supply of silica accumulated somewhat, and correspondingly we have twice found diatoms flowering in the bay late in summer or early in autumn (September in the year 1915, August in 1922; pp. 394 and 391). With the seasonal fluctuations so notable for diatoms and fairly demonstrated for the concentration of silica, with the maxima for the former

[85] Doctor Wells writes me that although the iron of several of the containers was somewhat rusted, in most cases careful analysis of the sediment showed practically no silica; and by analysis the iron of the cans was found to contain not more than 0.0002 gram silica per gram, so that measurable contamination of such large volumes of water by that agency is ruled out of consideration.

preceding those of the latter, and with the dependence of flowerings of diatoms on an adequate supply of silica obvious, the parallelism between the curves for this substance and for abundance of diatoms can not reasonably be regarded as accidental.

## PHOSPHORIC ACID

Recent analyses of seasonal fluctuations in the amount of phosphoric acid in north European seas make it probable that exhaustion of the supply of this essential foodstuff operates, widespread, to check the vernal flowerings of diatoms. Phosphoric acid ($P_2O_5$) exists in such weak solution in sea water (usually less than one part per million), and its analysis is attended with such difficulty that none of the earlier determinations can be depended on; but recent tests[86] have shown a definite seasonal periodicity in the silica content of the English Channel, the North Sea, and the Baltic. Atkins's (1923a and 1925a) data for the neighborhood of Plymouth (espe-

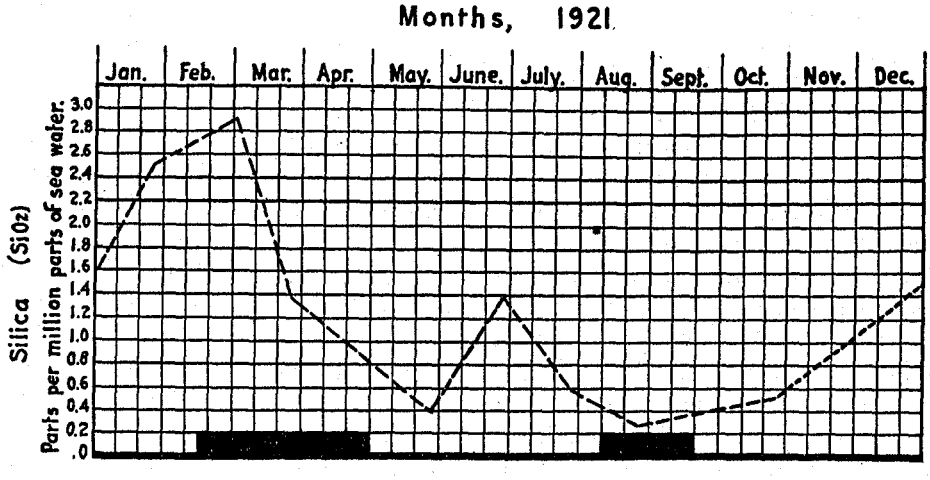


FIG. 134.—The broken curve shows the concentration of dissolved silica (as $SiO_2$) near Gloucester, monthly, for the year 1921, from determinations by Dr. R. C. Wells (see p. 476). The solid black line indicates the flowering seasons of diatoms for that neighborhood

cially significant, as they extend over two years) show maximum values in winter and minimal in summer, when the water may be almost phosphate free. Atkins's (1925a, p. 718) conclusion that "where illumination is adequate the phytoplankton increases until the phosphate is almost absolutely used up" is supported not only by the parallelism between the increase in phosphoric acid in northern seas in winter, followed by its depletion in late spring, and the vernal flowerings of diatoms, but by experimental evidence, for he had earlier (1923) found that in a culture of the diatom *Nitschia closterium* a great increase in the number of diatoms reduced the phosphoric acid from 2.38 parts per million (milligrams to the liter) to 0.006.[87]

A supply of phosphoric acid being essential for plant growth, it is obvious enough that whenever and wherever this substance is entirely used up the lack of it

[86] In review of these see Mathews (1916) and Atkins (1923a and 1925)

[87] In one of Moore and Webster's (1920) experiments on photosynthesis on a unicellular fresh-water alga a lack of phosphate was demonstrated as the growth-limiting factor.

must, as Atkins points out, limit the abundance of the phytoplankton. He has made interesting calculations of the amounts of diatoms that could be produced, supposing all the phosphate in the water to be consumed. The facts so far garnered, however, do not warrant the assumption that a poverty in phosphorus can safely be invoked as the universal cause for the eclipse of the vernal flowerings of diatoms when this event takes place. As we have seen, a parallelism of the same sort has been established with fair probability between the amount of silica in the water and the abundance of diatoms. There is also good reason to believe that at times and over large areas of sea the supply of available nitrogen falls below the minimum requisite for their active reproduction. The strong probability that different groups of planktonic plants, and even different species within the major groups, differ widely in their nutritive requirement, makes the question complex.

I have no first-hand information to offer on the richness of the Gulf of Maine water in phosphoric acid, but the fact that the vernal swarmings of diatoms are succeeded by peridinians and not by other diatoms over most of the area of the gulf is sufficient evidence that water that is no longer fit to support rich flowerings of the latter, through the exhaustion of some substance essential to their growth, still offers a favorable environment for the former.

Thus it does not seem likely that the spring diatom maxima in Massachusetts Bay and in the southwestern part of the gulf generally as nearly exhaust the phosphates as Atkins found to happen in the English Channel. But if diatoms require a richer supply of phosphates than peridinians do (as they certainly require a more abundant supply of silica) the reduction in the available supply of this nutrient resulting from their consumption of it may terminate the flowerings of diatoms, though still leaving the water rich enough in dissolved phosphates to support an abundance of peridinians. It is true that Brandt (1905, p. 11) and others following him have suggested that peridinians may need more phosphorus than diatoms, not less, but nothing whatever is definitely known as to their requirements.

The desirability of analyses of Gulf of Maine water for phosphoric acid at different times of year is obvious, and further speculation on the dependence of the local phytoplankton on fluctuations in the supply of this nutrient is best postponed until such are undertaken.

In addition to the major foodstuffs which I have mentioned, planktonic plants, like terrestrial plants, require a small but available supply of various other substances—iron, sulphur, sodium, etc. Nothing whatever is definitely known as to their exact requirements in this respect, but recent experiments on the cultivation of diatoms have shown that some species require substances which others can do without. In the case of *Thalassiosira gravida*, E. J. Allen (1914) was unable to obtain good cultures in artificial sea water to which he added the same nutrient solution that had produced abundant growth in natural sea water until a small percentage of the latter was added to the artificial medium, when excellent cultures ensued. Provided this small amount—1 per cent or so—of natural sea water was added, the constituents of the artificial sea water (which formed all but this trifling proportion of the culture medium) could be varied within wide limits, as could its total salinity, without either hindering or apparently helping the growth of the diatoms. Thus this particular genus appar-

ently requires "some specific substance present in minute quantity in the natural sea water" (E. J. Allen, 1914, p. 439), but not in the artificial.

Fritz (1921a), experimenting in the culture of diatoms at St. Andrews, New Brunswick, found that *Melosira hyperborea* not only made considerable growth in artificial sea water but continued to multiply rapidly in cultures in natural sea water long after *Thalassiosira nordenskioldi*, *Chætoceras debile*, and *Skeletonema costatum* became exhausted. Her conclusion that the persistence of Melosira is permitted by its independence of some substances which the other forms required but soon exhausted seems justified.

Suggestive, also, in this connection is Crawshay's (1915) observation that the excretory products of the copepod *Calanus finmarchicus* (apparently not, however, of Pseudocalanus or Acartia) exert a strong fertilizing action on the diatom genus Nitschia; but no such effect followed E. J. Allen's (1914, p. 429) introduction of the crustacean genus Hemimysis, with its fæces, into artificial sea water, which proved as barren for diatom growth with as without them.

Nathansohn (1906) has suggested that the supply of carbonic acid ($CO_2$) may temporarily fall below the minimum required for active growth of the phytoplankton, a possibility also accepted by Gran (1912, p. 380); and Moore's calculation [88] that 20,000 to 30,000 tons of carbon are annually converted from inorganic to organic form per cubic mile of water in the Irish Sea emphasizes the vast amount which the flowerings of diatoms and peridinians utilize. More recent experimentation on the dynamics of photosynthesis [89] have shown that when the total available $CO_2$ has been withdrawn from the bicarbonates present in sea water the latter becomes fatally alkaline, and since sea water has never been found in this state or even approximating it, although many determinations of alkalinity have been made, it is safe to conclude that the growth of marine phytoplankton is never prevented by a shortage of carbon dioxide.

The facts outlined above show that the coastal waters of the Gulf of Maine are probably more fertile for diatoms in spring than at any other time of year with respect to dissolved silica; likewise in nitrogen, one of the other nutrients on which this particular group of planktonic plants chiefly depends. The density and state of vertical circulation of the water also influence their abundance, both by governing the availability of the phosphoric acid and compounds of nitrogen that go into solution on the bottom of the sea and by influencing the flotation of the diatoms themselves.

The influence which the state of circulation of the water exerts on the seasonal abundance of diatoms seems first to have been fully appreciated by Whipple (1905, p. 103) for fresh water, for which it is now accepted generally. Briefly it is as follows: During periods of stagnation (that is, when there is no vertical circulation) the bottom waters of lakes are the seat of active decomposition of organic matter, with consequent increase of ammonia and solution of inorganic substances. When vertical circulation recommences this "foul" water is brought to the surface, where,

[88] Quoted from Herdman (1920 and 1923).
[89] Especially Osterhout and Haas (1918); Moore, Prideaux, and Herdman (1915); Moore, Whitley, and Webster (1921).

under further oxidization, compounds favorable to the growth of diatoms result. At the same time the vertical currents bring diatoms up to the surface from the bottom, where they or their spores had previously been resting, prevented from growth by darkness and lack of available food substances. Once near the surface, they multiply rapidly under favorable surroundings, and this multiplication continues either until the available supply of nutrient substances is exhausted or until a cessation of the vertical currents allows them to settle once more below the fertile and illuminated stratum, when they lie over until the next period of vertical circulation.

In the same way the state of stability of the water, joined to the effects of the river freshets, influences the distribution and availability of the food substances on which diatoms depend for their nutrition in coastal seas such as the Gulf of Maine. As Nathansohn (1906) pointed out, wherever there are upwelling currents these may be expected to bring a rich supply of nitrogenous compounds up to the surface from the deeps, where they accumulate from the decomposition of the rain of dead plankton. In the Gulf of Maine local upwellings are a characteristic event along the western and probably along the northern coasts in spring, following offshore winds (Bigelow, 1914a, p. 394). But here and in shoal boreal seas generally the active vertical mixing by tides, by dominant currents, and by winds, which takes place whenever or wherever the water possesses little vertical stability, is no doubt more effective in dispersing accumulations of dissolved nutritive compounds through the upper strata of water than are the more definite upwellings, because more widespread, given an accumulation of organic detritus on the bottom.

The analyses of nitrogen in samples of mud and sand (p. 472) prove this last requisite fulfilled for the area of the Gulf of Maine as a whole; probably most abundantly so around the coastal zone, where submarine vegetation (Zostera and algæ) and animals (bottom dwellers as well as planktonic) die and decay in vast quantity. Atkins (1923 and 1925) has also emphasized the importance of vertical circulation in making available to the phytoplankton of the upper illuminated layers the dissolved phosphates that accumulate in the deeper strata. As Gran (1912, p. 379) has pointed out, it is in areas where the summer and winter temperatures of the surface differ most that vertical circulation is most active during the brief period (or periods) when vertical stability is lost (a period generally coinciding with the lowest surface temperature), and our first winter's work proved that the Gulf of Maine is a typical example of this.

The physical aspect of this subject has been touched upon in earlier papers (Bigelow, 1914a and 1917) and will be discussed in the third part of the present report.[90] It will therefore suffice to note here that the whole coastal zone of the Gulf and the water over its offshore banks, down to a depth of at least 100 meters, is in such an active state of vertical mixing at the end of the winter and during the first days of spring (when the temperature is lowest for the year and just before the river freshets lower the surface salinity appreciably) that it often carries sand in suspension,[91] not to speak of light flocculent material.

[90] Section 2 of Part II, Vol. XL, Bulletin of the Bureau of Fisheries.

[91] In 1920 we had instances of this on Georges Bank in February (station 20047) and on German Bank on Apr. 15 (station 20163).

In the western coastal zone, south of Cape Elizabeth, and in the basin generally, the vernal period of vertical mixing is brief, its activity lessening as soon as the combined effect of solar warming and of the freshening of the surface increases the vertical stability of the water. This becomes very stable indeed by the early summer with very little interchange taking place between the upper and deeper strata from that time until into the autumn. But strong tidal currents keep the water in the northeastern corner of the gulf in a state of more active vertical circulation throughout the year, especially in the Bay of Fundy, along western Nova Scotia, and locally on Georges Bank. In the Grand Manan Channel, an extreme example, the water is kept practically uniform in temperature from surface to bottom, even in midsummer.

Planktonic diatoms, with their silicious frustules and without power of locomotion, tend to sink unless kept afloat mechanically by some movement of the water. Although sinking is more or less hindered by their spines, slime threads, disclike outlines, etc.,[92] they are more liable to sink than other members of the phytoplankton are, as Gran (1915, p. 136) has emphasized.

The mechanical influence of the state of circulation of the water on the flotation of diatoms or on small objects of any sort is obvious. Indeed, particles as heavy as sand may be kept in suspension by active vertical currents, as just remarked; and from what has just been said it is evident that diatoms are more apt to remain in suspension in the coastal waters of the Gulf of Maine from midwinter on through spring, when the water is actively mixing, than in summer. The flotation of diatoms or of any of the unicellular planktonic organisms is likewise made more easy in winter and early spring than in summer by the more viscous condition of the water during the cold season. The importance of viscosity in this respect, first appreciated by Ostwald (1903), is now so generally recognized (Steuer, 1910; Gran, 1912; Murray and Hjort, 1912) that no general discussion of it is called for here.[93] It is in waters such as those of the Gulf of Maine, where a cold winter alternates with a warm summer in the sea as well as in the air, that seasonal differences in this respect are greatest, because the viscosity of the water depends almost wholly on its temperature within the range of salinities there obtaining (say 27 to 34 per mille). The following table is compiled, in a slightly modified form, from Krummel (1907, p. 282), Murray and Hjort (1912, p. 690), and Murray (1913, p. 102).

*Viscosity for sea water of 30 to 33 per mille salinity, 100 being that of distilled water at 0° temperature*

| Temperature in degrees centigrade | Viscosity | Temperature in degrees centigrade | Viscosity |
|---|---|---|---|
| 0 | 104.5–105.2 | 5 | 89.1–89 |
| 1 | 100.4–101.1 | 10 | 77.2–77.8 |
| 2 | 97.3–98 | 15 | 67.5–68.2 |
| 3 | 94.3–95 | 20 | 59.9–60.5 |

[92] For a summary of these arrangements for flotation see Steuer, 1910, p. 193.

[93] As a homely and extreme illustration of the effect of differences in viscosity in fluids familiar to every biologist, consider how much more rapidly a round cover glass, resting on its flat surface (which we may conceive as representing a Coscinodiscus), will sink in water than in ordinary xylol-balsam, fluids hardly differing in specific gravity but of which the latter is much the more viscous.

With the temperature of the upper strata in the coastal waters of the Gulf only about 1 to 0.5° at its annual minimum when the vernal flowerings of diatoms commence, but rising to upwards of 18° off Massachusetts Bay and even to 20° locally in the center of the gulf in August, the viscosity decreases, say, by 40 per cent (from about 100 to about 60) during the spring and early summer. Consequently, other things being equal, a diatom would sink four-fifths faster in midsummer than during the first days of spring. Other things are not equal, however, because the specific gravity of the water as well as its viscosity decreases with the rising temperature and with diminishing salinity of spring. Thus, the surface stratum is not only a thinner fluid but a lighter one absolutely in summer than in winter, which makes for a still greater disparity between the tendency of diatoms to sink in the cold and in the warm seasons.

It would, perhaps, be safe to say that differences in specific gravity of the water and in its viscosity would necessitate twice as active vertical circulation to hold any given object in suspension in summer as in early spring. As we have seen, however, (p. 481), the reverse actually obtains, the active vertical mixing characteristic of spring giving place to a condition of comparative vertical stagnation in midsummer, consequent on the increasing vertical stability of the water, which must increasingly hinder the flotation of diatoms in the gulf, just as happens in the fresh-water lakes described by Whipple (1905). Thus the seasonal cycle of viscosity and of vertical circulation combined tends to put a period to the seasonal multiplication of the species of diatoms which are characteristic of spring by increasing their tendency to sink.

In the preceding pages I have tried to show that on theoretic grounds the gulf, taken as a whole, offers its most favorable environment for planktonic diatoms in spring, because of the following combination of circumstances: The supply of two of the nutrients on which it is probable that diatoms chiefly depend—nitrogen and silica—is then greatest. (European analyses suggest that this also applies to phosphoric acid.) The circulation of the water then tends to bring up a supply of nitrogen compounds and of dissolved phosphates most actively from below, the high viscosity of the water then most favors the flotation of diatoms, and the increasing strength of the sunlight from late winter on increasingly favors the processes of photosynthesis. It is probable that for abundant flowerings of diatoms all these requirements must be satisfied. Conversely, fluctuations in the amount of any one of the essential foodstuffs may govern the amounts of diatoms actually present at any given time or place, and may even terminate the flowerings if it fall below the requisite minimum.

The parallelism that has actually been shown to exist between the fluctuations in the concentration of silica in the sea water of Massachusetts Bay and of the diatoms there (p. 476, fig. 134) makes this our most suggestive illustration. Without the accumulation of this substance (which takes place during the winter when there are few diatoms to make use of it) the tremendously productive flowerings which we have encountered in spring probably could not take place, any more than they could unless there were enough nitrogen in available form to nourish them. But after the flowerings have abounded for a few weeks in this particular location they so reduce the supply of silica (as the analyses show) by converting it into an unavailable

form (that is, their own shells) that the water becomes unable to support their active multiplication.

It is obvious that the water of the coastal zone north of Cape Ann, along the coast of Maine, and in the Bay of Fundy must continue fertile for diatoms until much later in the year, as is proven by the rich flowerings which take place there late in the spring and in early summer (p. 396). On theoretic grounds this regional difference may have any or all of several causes. First, and probably most important, is the discharge from the rivers, richer in nitrogen, phosphorus, and silica than the sea water with which it mixes. The importance of river waters as carriers of dissolved nutrients is so great that the regions immediately off river mouths might be expected to be richest in diatoms. Though this is not strictly the case in the Gulf of Maine, fuller knowledge may show a closer correspondence between the outpourings from the rivers and the vernal diatom flowerings than is now apparent. Certain facts point in this direction, especially the general parallelism between the season of spring freshets and melting snow, on the one hand, and the date of appearance of the diatom flowerings off different parts of the coast, on the other. Thus, generally speaking, it is off the mouths of the most southerly group of large rivers—Merrimac, Piscataquis, and Saco—between Cape Elizabeth and Cape Ann, where the flood waters from the land are felt earliest in the spring, that the diatoms flower earliest in great numbers. There is no important influx of river water into the gulf south of this, and the expansion of the diatom flowerings around Cape Ann into Massachusetts Bay corresponds roughly with the probable expansion of the "spring current" of land water to the southward past the cape.

The large rivers east of Cape Elizabeth—Kennebec, Penobscot, Machias, St. Croix, and St. John's—come into flood later in the season; correspondingly, the augmentation of diatoms commences later in the season along this part of the coast than farther west and south.

As the outflow from the rivers diminishes in late spring and summer, the sea water might be expected to remain richer in silica, phosphorus, and nitrogen near their mouths than elsewhere—i. e., close along the stretch of coast between Cape Elizabeth and Nova Scotia, which includes all the localities where we have actually found notably rich diatom flowerings in summer (p. 392). In line with this is the fact that Fritz (1921a) did not find it necessary to include silica among the nutrients which she added to sea water at the mouth of the St. Croix River in order to obtain abundant growth of several genera of diatoms there.

The viscosity is likewise more favorable for the growth of planktonic diatoms in the northeastern part of the gulf than in the southwestern in summer, in inverse ratio to the local differences in temperature, the Bay of Fundy at 10 to 11°, for example, offering a much more favorable medium for the flotation of diatoms than Massachusetts Bay at 16 to 18° in the proportions given in the viscosity table (p. 481). A similar regional difference exists, with respect to the vertical circulation of the water, during the warm months of the year, this being least active in the southwestern part of the gulf where the tidal currents are weakest, and most active east of Mount Desert, to culminate in complete and constant stirring of the water from surface to

bottom throughout the season in the Grand Manan Channel and locally in the Bay of Fundy.

These several factors unite to make the coastal zone east of Penobscot Bay on the whole a more favorable environment for diatoms in summer than any other part of the gulf except Georges Bank, to be discussed later (p. 485). Since this theoretic generalization corresponds with the quantitative distribution of diatoms as actually observed during the warm months, the factors just mentioned are probably the chief ones which explain the persistence of rich flowerings of diatoms in abundance in the Mount Desert region and in Passamaquoddy Bay throughout the summer, contrasted with their exhaustion in the Massachusetts Bay region by early May. I have not been able to trace the dependence of particular flowerings on physical or chemical conditions in the sea water more closely than this.

Our failure to find diatoms in as great abundance between Mount Desert Island and Grand Manan as the flowerings farther west, on the one hand, or those reported by Fritz (1921) at St. Andrews at the mouth of the St. Croix River, on the other, is puzzling, for this section of the coastal zone not only receives a considerable influx of land water from several streams that may be expected to be rich in dissolved foodstuffs, but there is a dominant outflow along it from the Bay of Fundy.

No part of the gulf becomes uninhabitable for diatoms even when the water becomes warmest and most stable and flotation most difficult. On the contrary, certain species then reach their maximum development, as an example of which the summer flowerings of Asterionella and Skeletonema will serve (pp. 431, 448). The latter, as it occurs in Massachusetts Bay, is especially interesting because the dates when an abundance of Skeletonema has been recorded in 1915 and 1922 (early autumn and late summer, respectively; p. 476) follow so closely the rise in the concentration of silica recorded for late June in 1921 (fig. 134) as to suggest that it is the accumulation of silica taking place during the late spring and early summer (when there are few diatoms in that region) which makes the water there able to support the autumnal flowerings of Skeletonema.

The general scheme of circulation in the gulf (with the water from the rivers tending to swing westward and to hug the coast line during most of the year, as shown by the distribution of salinity) is a sufficient explanation for the fact that the vernal flowerings of diatoms of its inner parts appear first close in to the land and attain a greater abundance and endure longer there than over the deep basin. The contrast in this respect between the coastal zone and the offshore banks, on the one hand, and the central deeps of the gulf on the other, simply reproduces on a small scale that between coastal or neritic waters and more oceanic regions in general. The gradual expansion of the diatom flowerings offshore from the land out over the central part of the gulf, where it does not reach its maximum until early May (p. 388), follows the offshore dispersion of the spring freshets of land water with their load of nitrogen, phosphorous, and silica.

It is in just such areas as the open basin of the Gulf of Maine, where the transition from a state of free vertical circulation in early spring is sudden to one of very pronounced vertical stability in summer, when the supply of nitrogen and of phosphates from the deeps is thereby prevented, and where the silica content of the

water is probably low except for a brief period in spring while the rivers are in flood, that the vernal flowerings of diatoms are briefest and vanish most completely after their culmination.

The case is quite otherwise on Georges Bank, where one diatom community or another flourishes from late winter to midsummer, but where these flowerings are local by contrast to the extensive vernal flowerings in the inner part of the gulf.

The distance of the bank out from the land and the general distribution of salinity in the gulf forbid the possibility that the nutrients on which its diatoms depend are contributed directly by river water, while hydrography in general equally rules out any possible updraught of nutrients from the ocean deeps, this not being an area of upwelling. Neither can we suppose that the general surface outflow from the gulf reaches the bank especially rich in dissolved foodstuffs, for it is only for a brief period in the spring that the basin of the gulf to the north supports an abundant diatom flora.

Probably the rich animal population of the sea floor of the bank makes the bank itself a richer source for nitrogen than its comparative barrenness in fixed plant growth would suggest. The destruction of plankton that takes place along the meeting zone of cool and warm waters just off its southern face also affords a rich potential food supply for pelagic plants as well as animals, though to what extent the products of this decomposition actually reach the shallows of the bank is a question. With the comparatively active vertical circulation that prevails locally on the bank even in midsummer, tending to sweep any organic débris from the bottom up to the upper layers, whether in suspension or in solution, the bottom no doubt contributes a greater store of assimilable nitrogenous compounds to the overlying sea water than in the deeper parts of the gulf to the north. This applies also to phosphates going into solution from the dead bodies of animals decomposing on the sea floor. Furthermore, the activity of vertical circulation on the bank, combined with low surface temperatures of summer dependent thereon, makes its waters a favorable environment physically for the flotation of pelagic plants, and these factors combined may well account for the summer flowerings there. There is also the interesting possibility that small amounts of silica go into solution from the felspathic sands, pebbles, and gravel that floor the bank (p. 475).

The precise causes of the periodic rise and fall of the peridinian flora are even more obscure than those that determine the diatom flowerings which they replace in summer and autumn, partly because, being less spectacular, they have attracted less attention, and partly because the peridinians as a whole are less obviously dependent upon any one nutrient substance than are the diatoms on a sufficiency of silica. And as I have pointed out (p. 478), the suggestion that the abundance of peridinians depends upon the available supply of phosphates is not borne out by the seasonal succession of this group and of diatoms compared with recent analyses for the phosphate content of the water. Nor is it by any means certain that the seasonal fluctuations of the peridinians mirror the fluctuations in the supply of any one food substance in the water as closely as the diatom flowerings are supposed to do. Since the group as a whole is more thermaphile than most of the diatoms characteristic of the Gulf of Maine, with the three most abundant species of Ceratium following

a regular seasonal succession there, temperature is undoubtedly an important factor in their economy.

Recent studies [94] have brought out the possibility that flowerings of pelagic plants may become self-poisoned under certain circumstances when they are most productive by increasing the alkalinity of the water as they draw $CO_2$ from the dissolved bicarbonates through the process of photosynthesis, thus increasing the proportionate amount of carbonates and making the solution more alkaline. Moore, Whitley, and Webster (1921) have shown that this change probably does exercise a profound biologic effect in inclosed pools, first killing off the animals (which are much more sensitive to high alkalinity than the plants are) and finally the plants themselves. A slight rise in alkalinity has been found to accompany the vernal multiplication of diatoms, etc., in the Irish Sea (Moore, Prideaux, and Herdman, 1915) from Ph 8.1 to 8.16 in December to Ph 8.2 to 8.4 in spring and summer; likewise from Ph 8.14 in the English Channel off Plymouth in December to Ph 8.27 in May (Atkins, 1923). But none of the determinations of alkalinity that have been made anywhere in the open sea have approached the figure fatal to plant cells (Ph about 9) [95]; and it seems certain that this never happens in the Gulf of Maine (which is one of the less alkaline of seas), a considerable number of tests by Mayer (1922) and at our spring, summer, and winter stations for the years 1920 to 1923 giving a maximum alkalinity of Ph 8.1. In short, it is hardly conceivable that the life or multiplication of diatoms or peridinians is ever hindered in the open gulf by a too alkaline state of the water.

It is also possible that the continued existence of exceptionally rich flowerings of diatoms may become self-limited by lack of oxygen, the dissolved supply of this element being used up, so to speak, in the oxidation of the dead plants, just as the decay of organic matter may reduce the supply of oxygen too low to support animal life in water contaminated by sewage. Whether this ever actually takes place in the open sea is yet to be learned, but it is not likely to be other than an exceptional event and one limited to very special inclosed inlets, probably never occurring in waters subject to as free circulation as those of the Gulf of Maine.

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[94] See especially Moore, Prideaux, and Herdman (1915); Osterhaut and Haas (1918); and Moore, Whitley, and Webster (1921).

[95] Atkins (1923) states that he was able to maintain a pure culture of the diatom *Nitschia closterium* in water as alkaline as Ph 9.4.

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