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

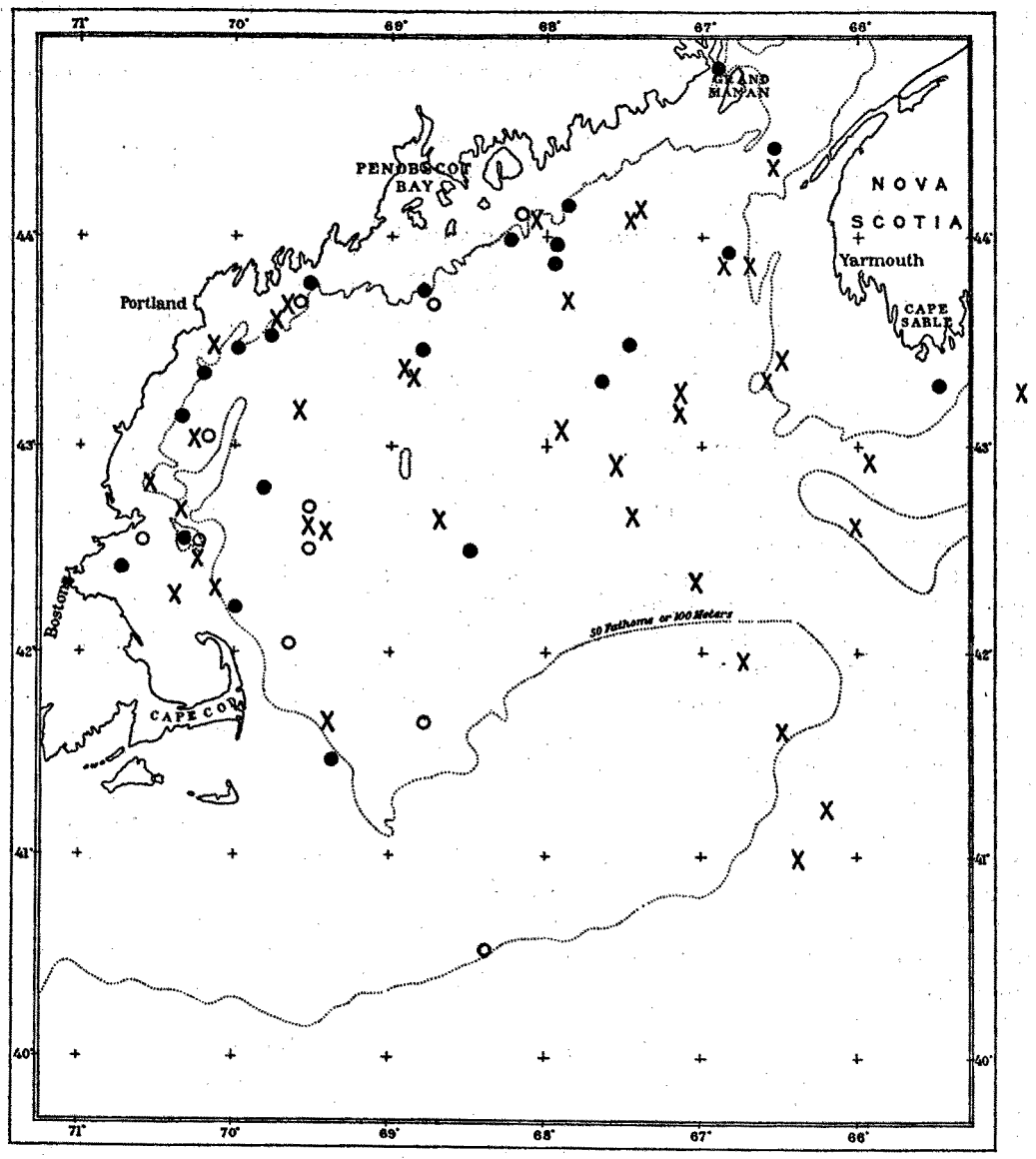

FIG. 45.—Occurrence of the naked pteropod *Clione limacina*. ●, locality records for June, July, and August; ○, the winter months; X, March, April, and May

(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

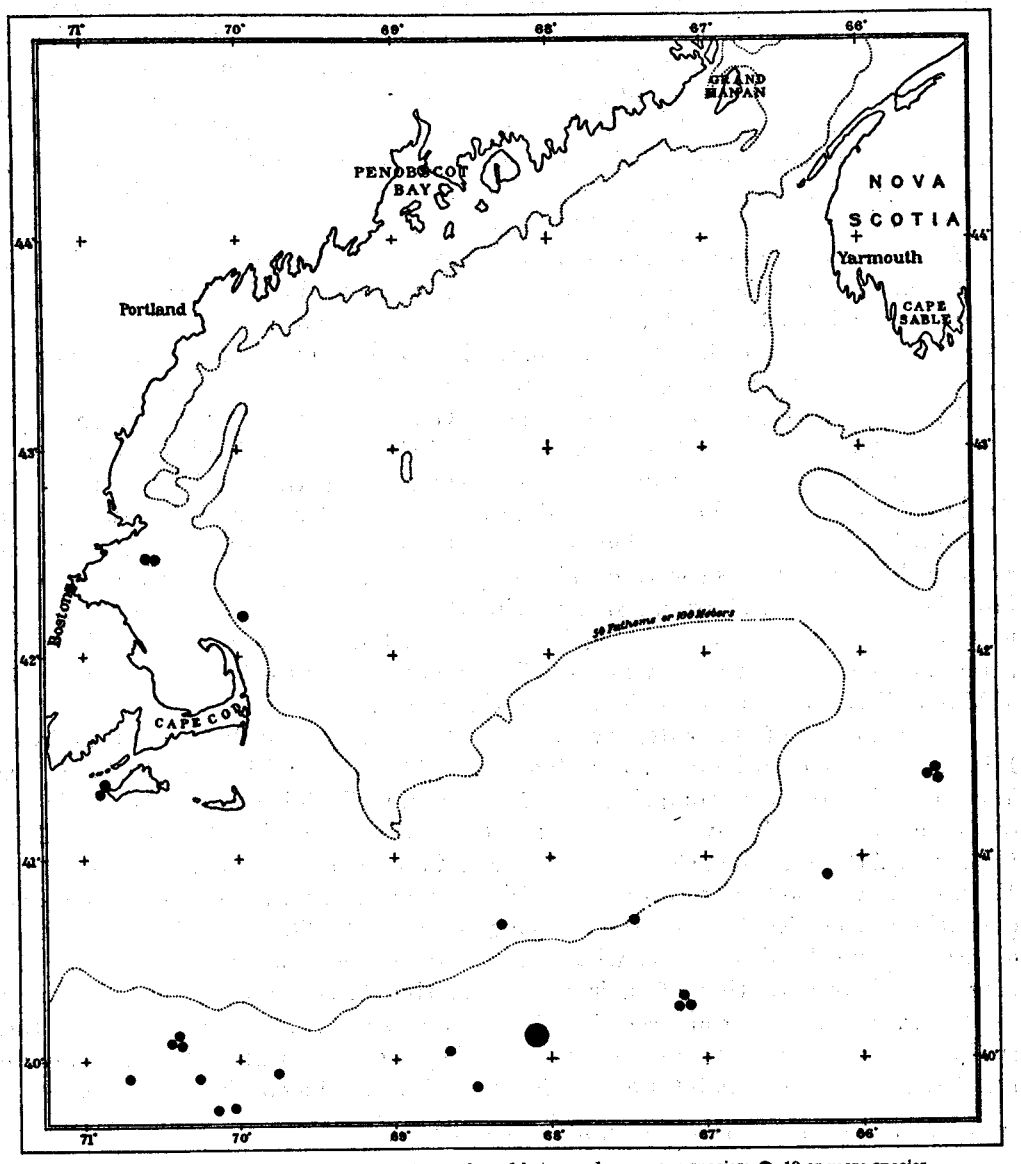

FIG. 46.—Locality records for oceanic pteropods and heteropods. •, one species; ●, 10 or more species

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	286	20081	140–0	206
	225–0		20087	200–0	255
10307	230–0	245	20112	200–0	290
20055	180–140	230	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

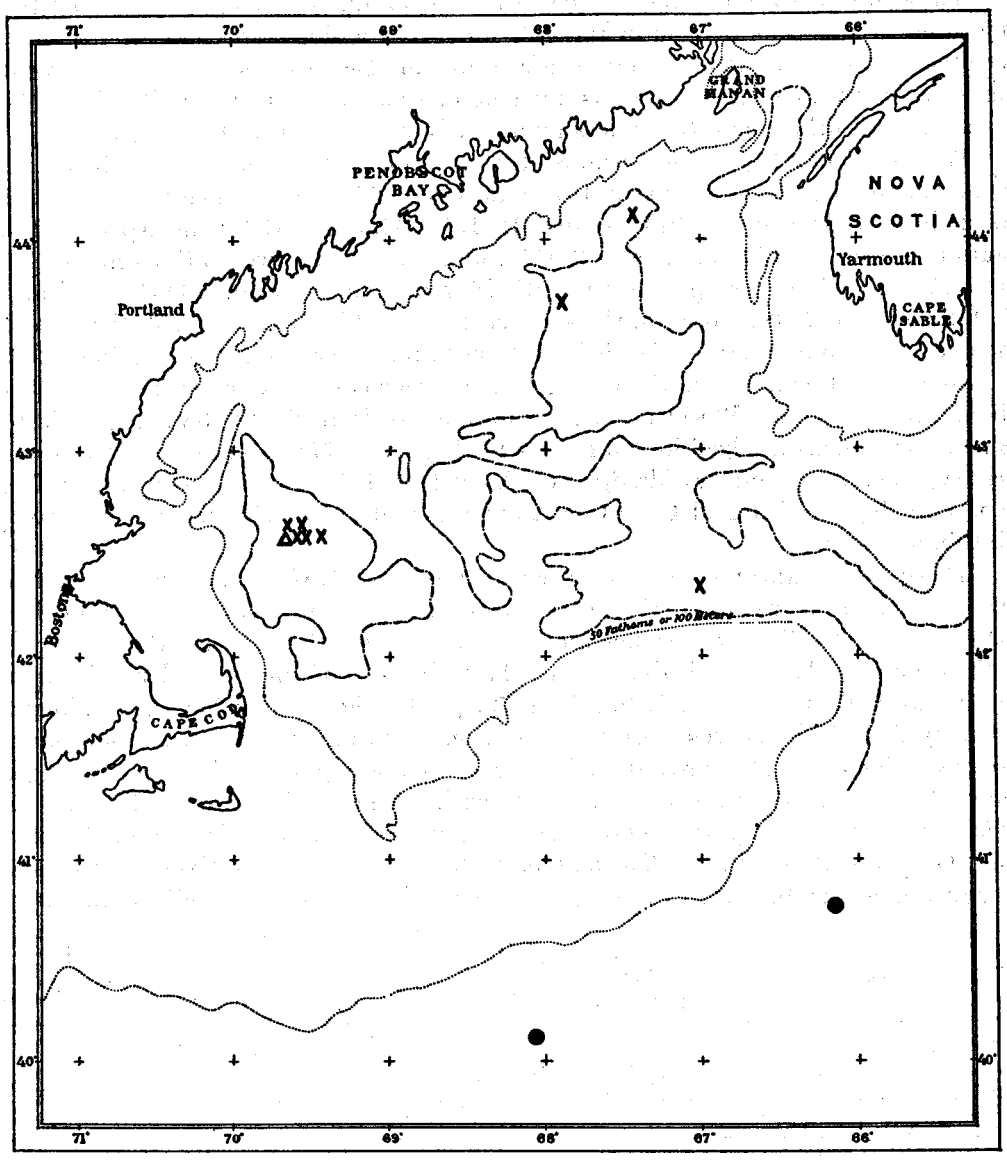

FIG. 47.—Locality records for the decapodous shrimp Pasiphæa. X, *P. multidentata:* ●, *P. tarda:* △, S. I. Smith's record.
(See p. 131)

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.

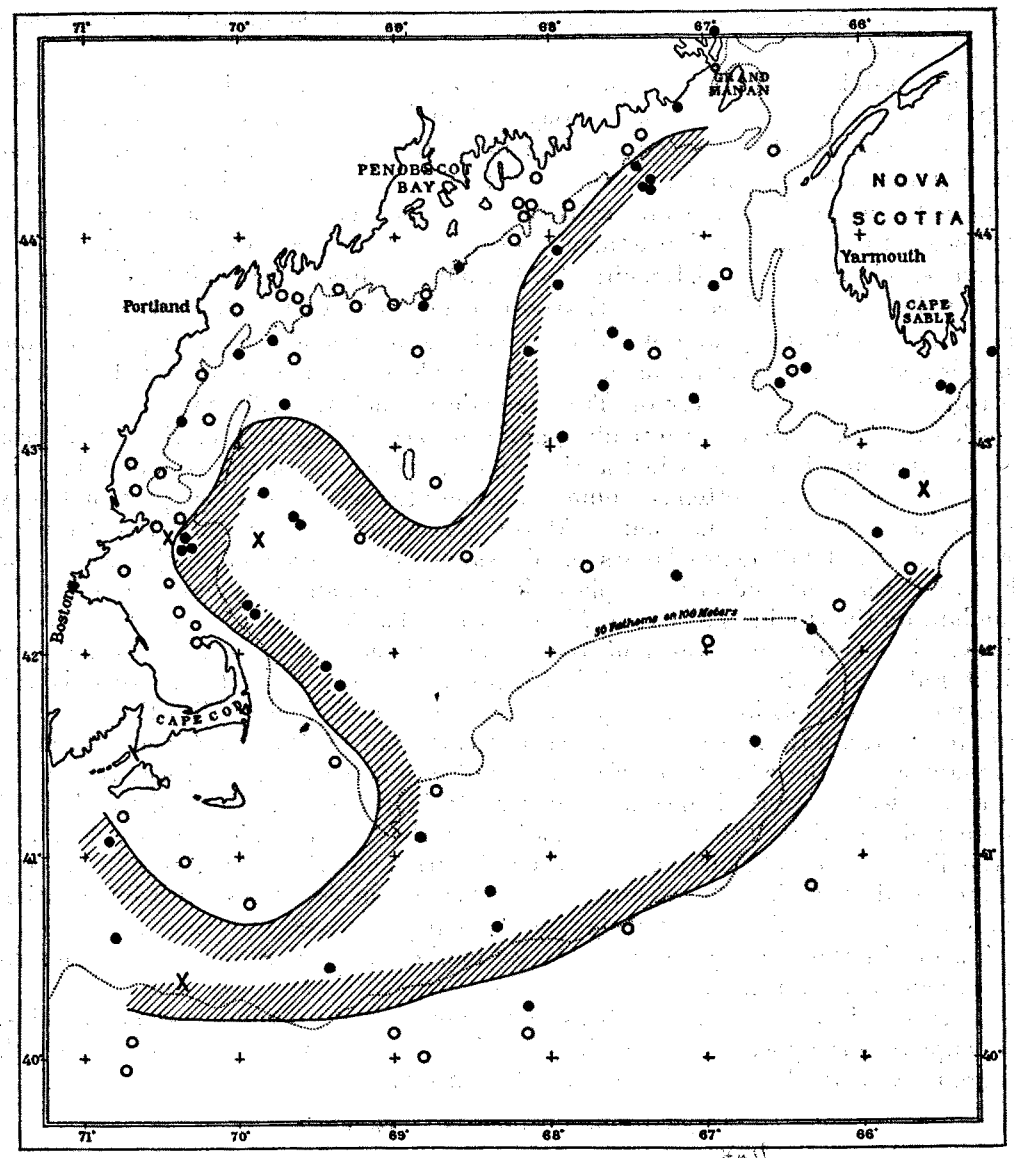

FIG. 48.—Occurrence of the euphausiid shrimp, *Thysanoessa inermis*, for June, July, and August. ●, occurred; ○, not taken; X, records by Hansen (1915). The hatched curve incloses the area where it has occurred at 50 per cent of the stations

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

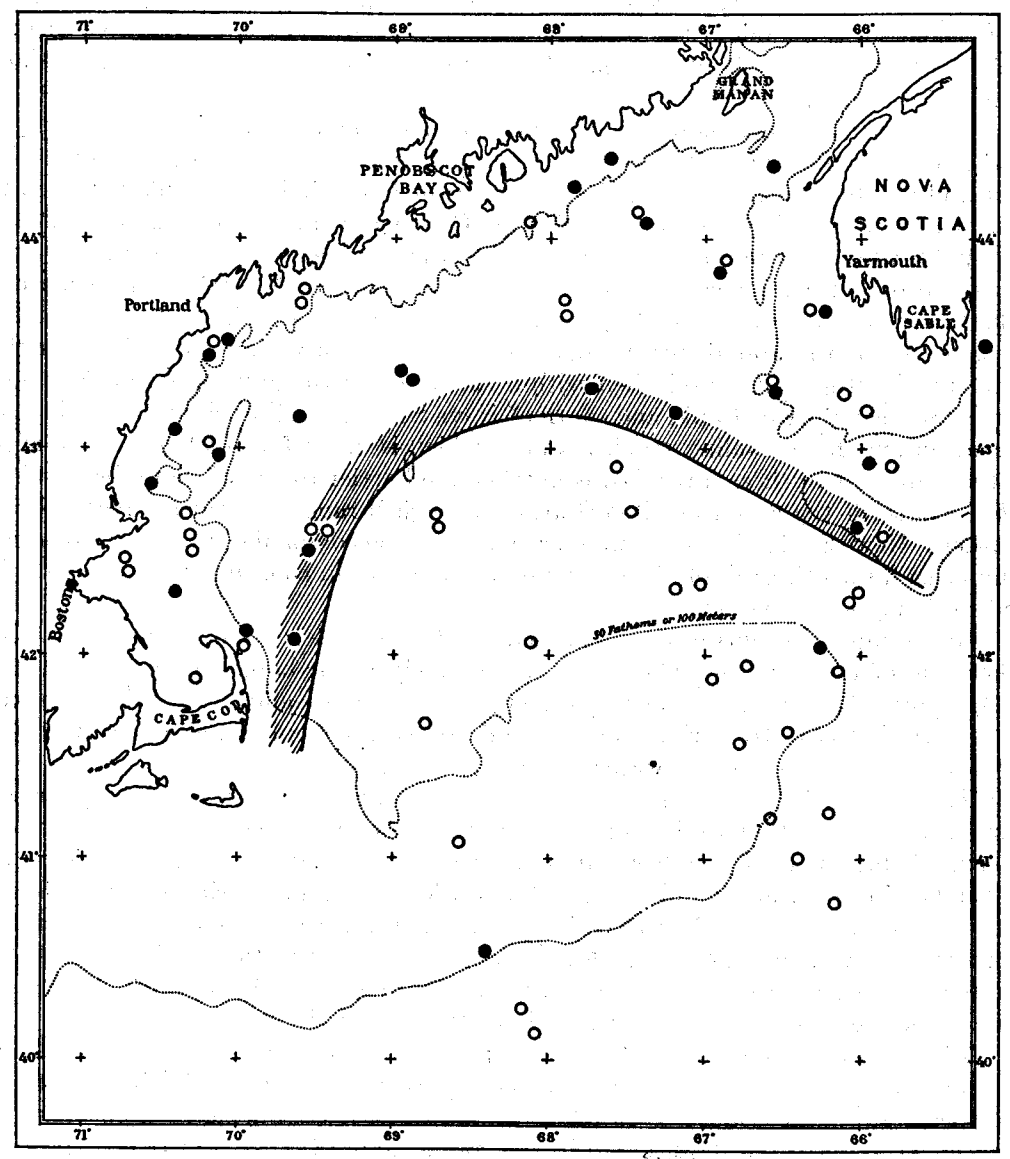

FIG. 49.—Occurrence of the euphausiid shrimp, *Thysanoessa inermis*, February to April, 1920. ●, occurred; ○, none taken. The hatched curve incloses the area where it occurred in about 50 per cent of the stations for March and April

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-

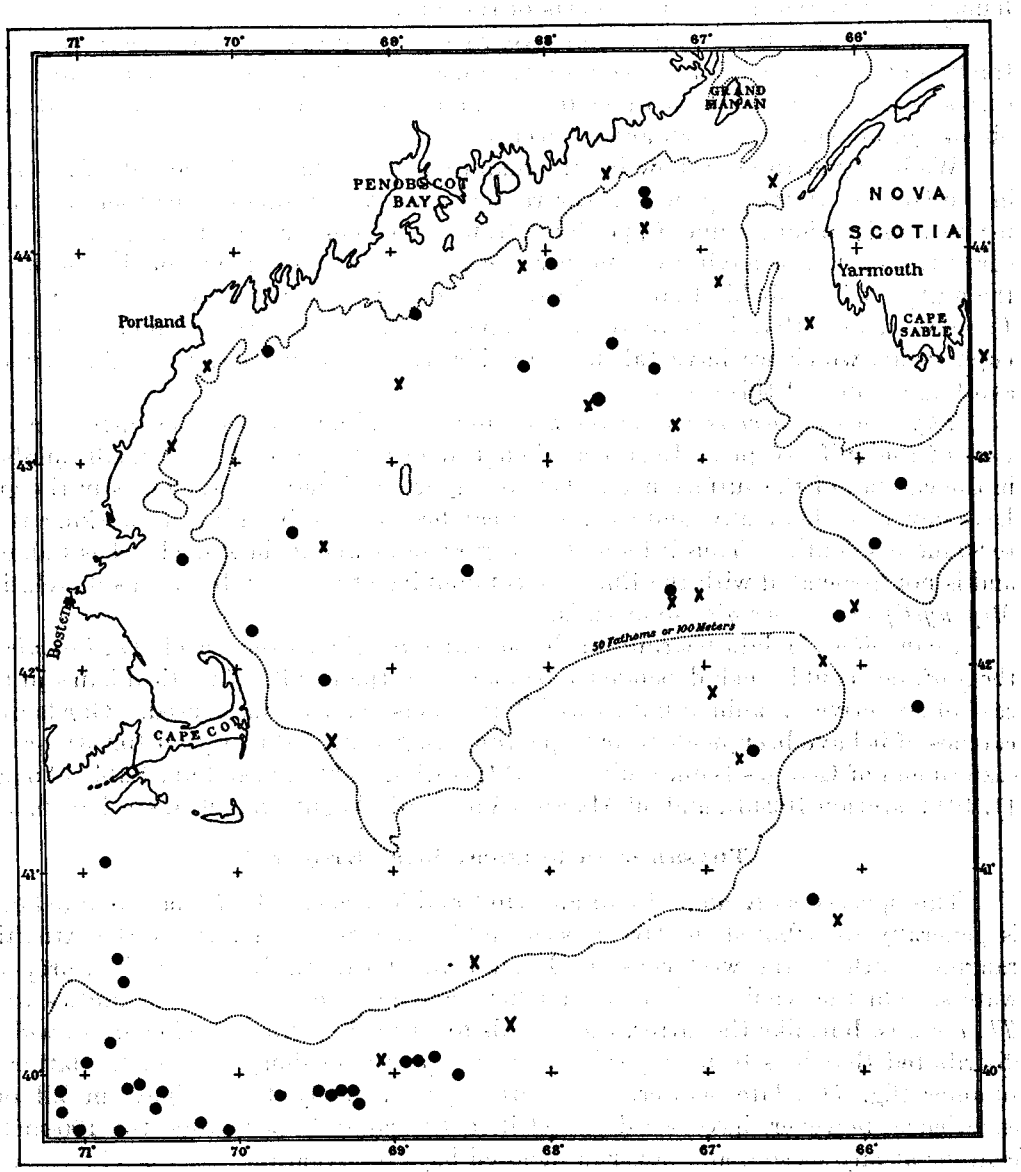

FIG. 50.—Occurrence of the euphausiid shrimp *Thysanoëssa longicaudata*. ×, locality records, February to May, 1920; ●, July to September, including Hansen's (1915) records

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.

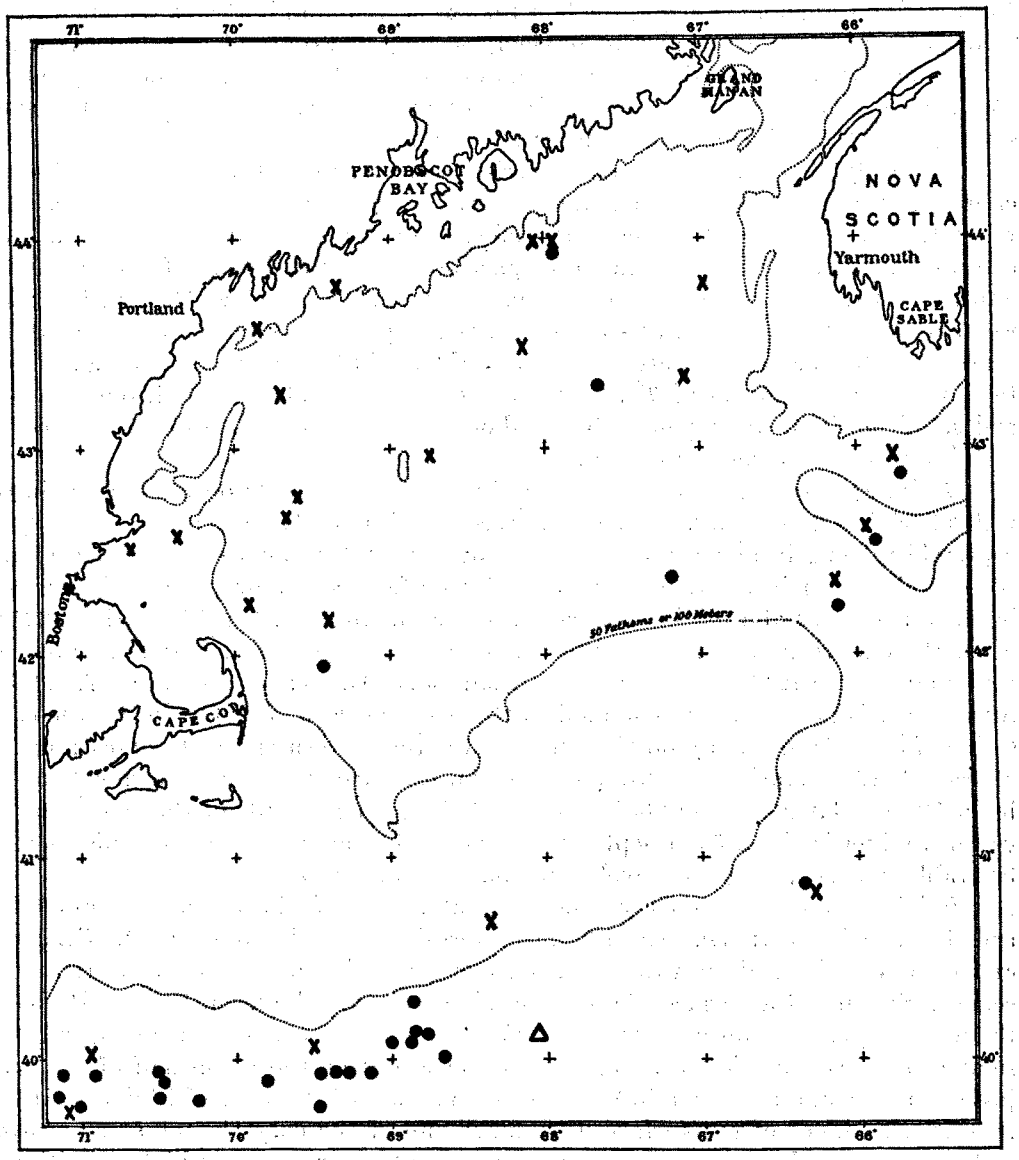

FIG. 51.—Occurrence of the euphausiid shrimps *Nematoscelis megalops* and *Thysanoessa gregaria*. ●, locality records for Nematoscelis, July to September, including Hansen's (1915); △, locality records for Nematoscelis, February to May, 1920; ×, locality records for *Thysanoessa gregaria*

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

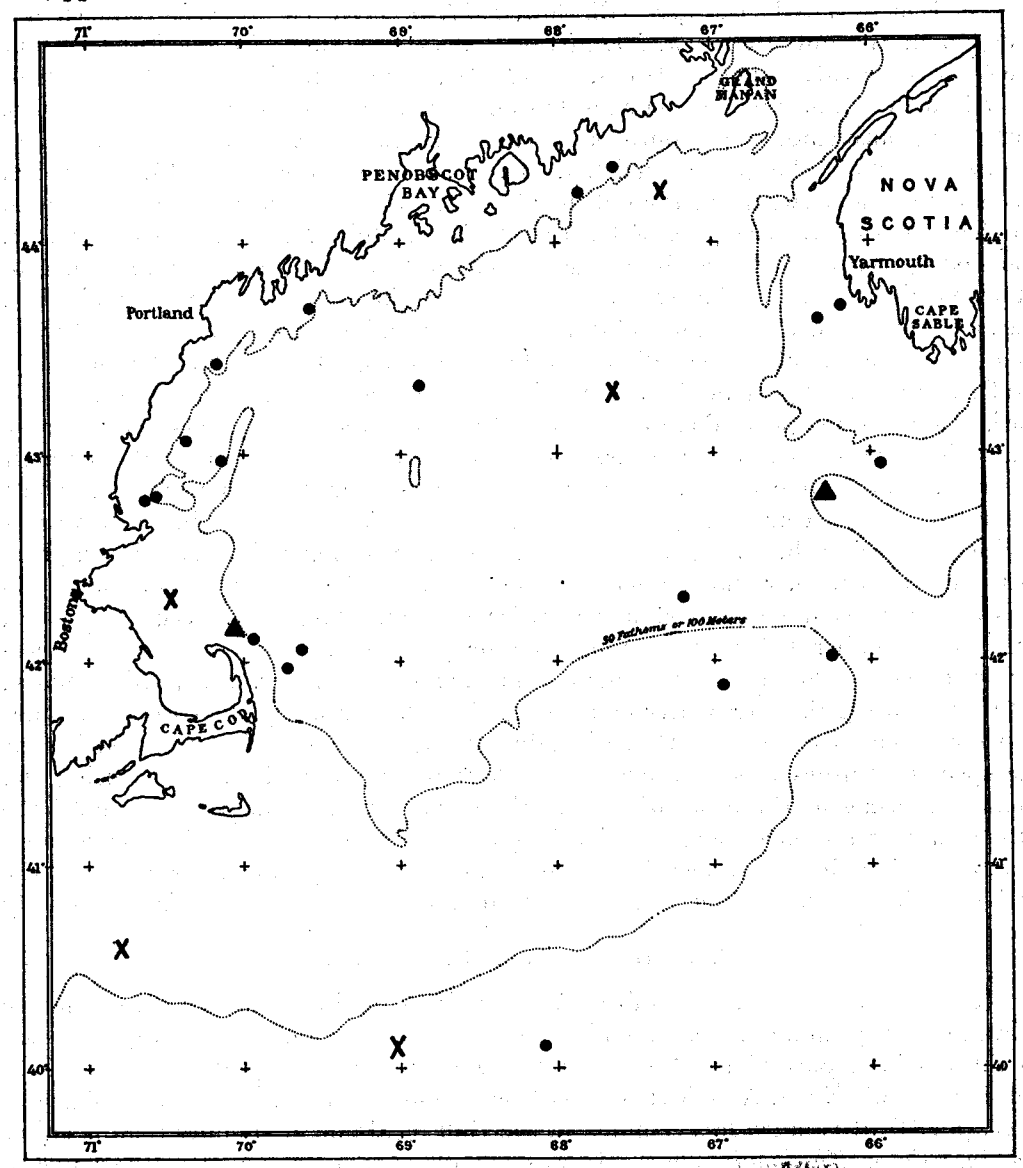

FIG. 52.—Occurrence of the euphausiid shrimp *Thysanoessa raschii*. ●, locality records, February to May, 1915, 1920, and 1921; X, August, 1912 to 1916; ▲, August records by Hansen (1915)

(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. 183. 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

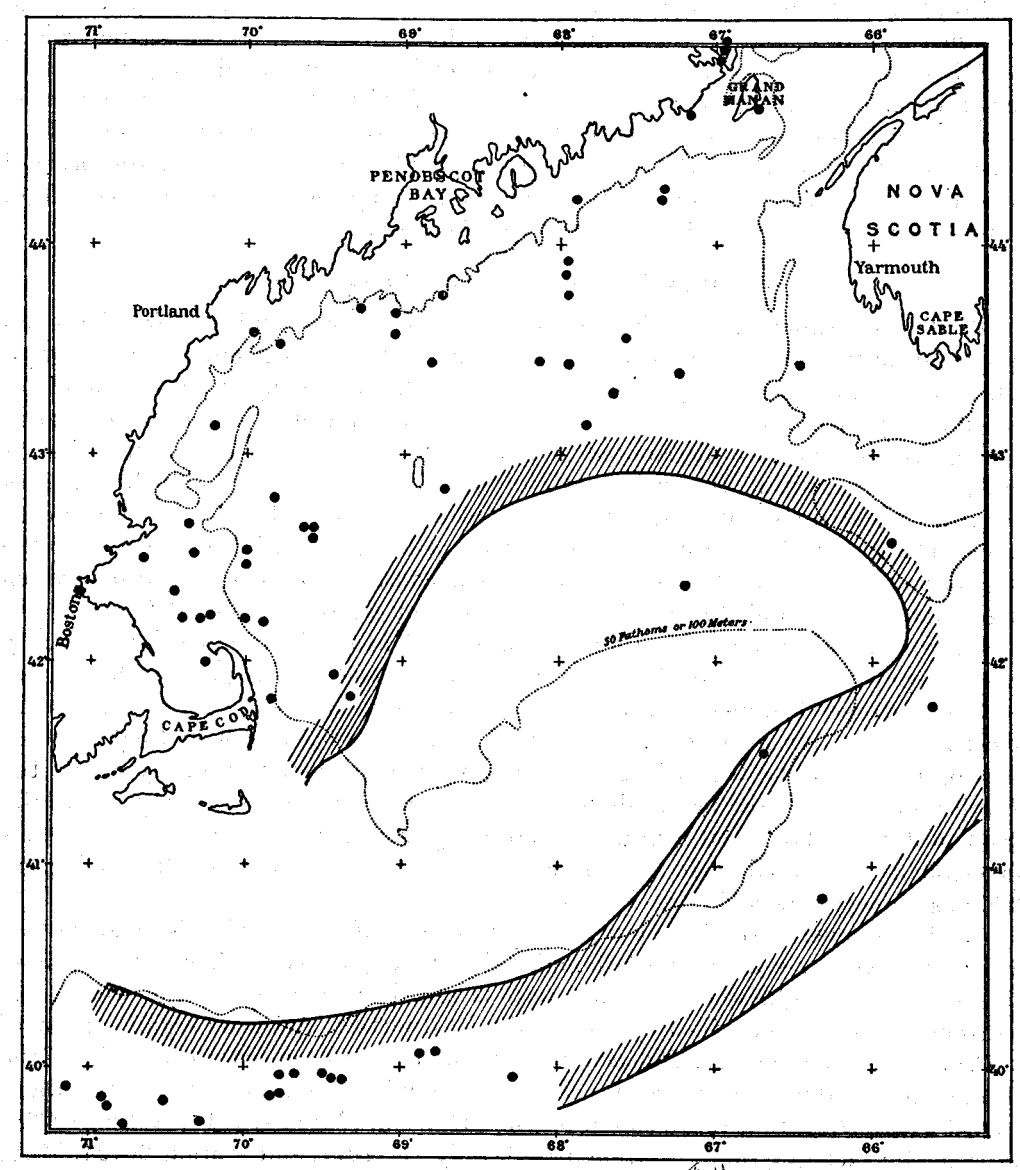

FIG. 53.—Occurrence of the euphausiid shrimp *Meganyctiphanes norvegica*, July to September 15. ●, locality records. The hatched curve incloses the area of regular occurrence in summer and early autumn

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-

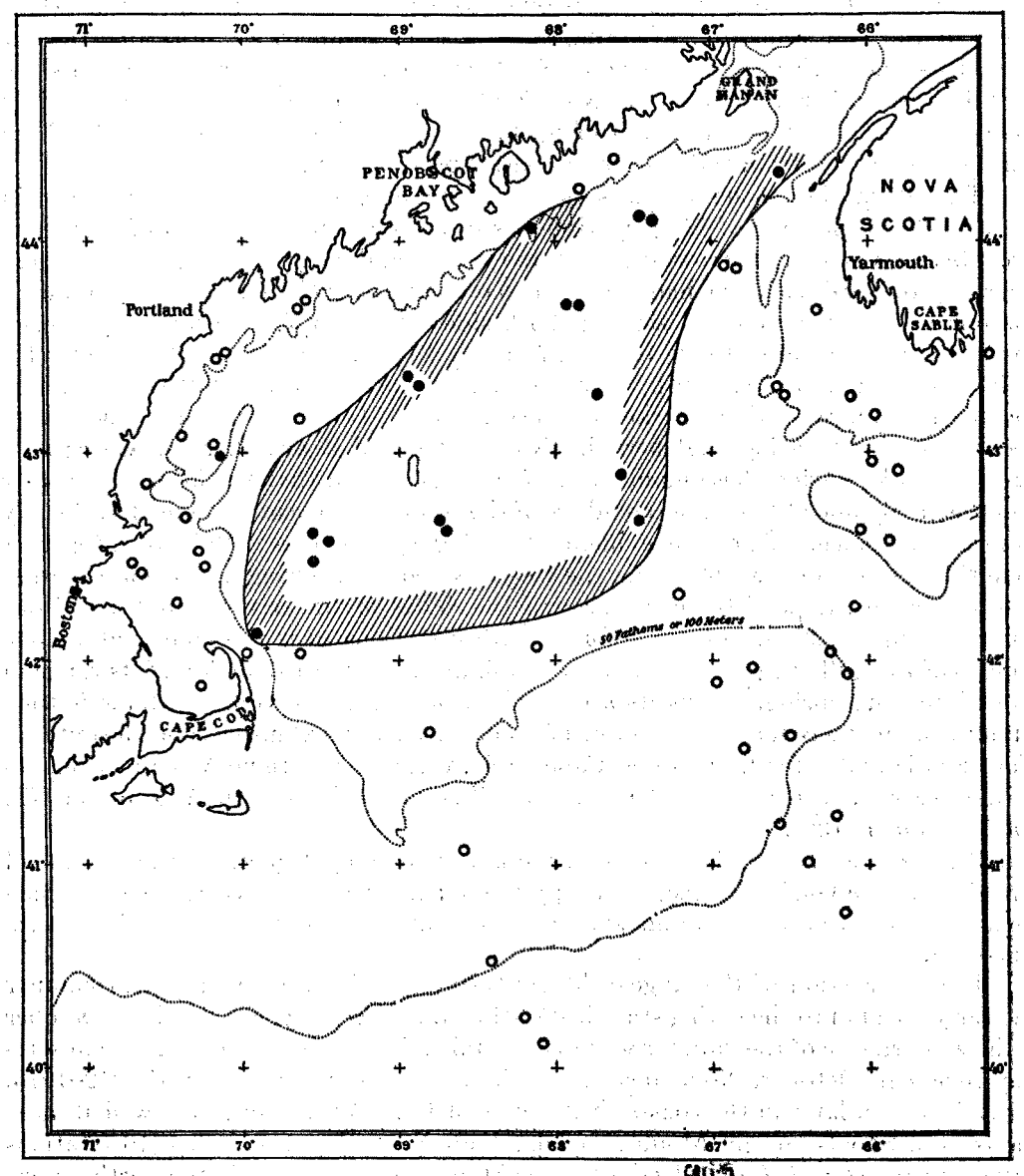

FIG. 54.—Occurrence of the euphausiid shrimp *Meganyctiphanes norvegica*, February to April, 1920. ●, locality records; ○, not taken. The hatched curve incloses the area where it occurs regularly in early spring

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.

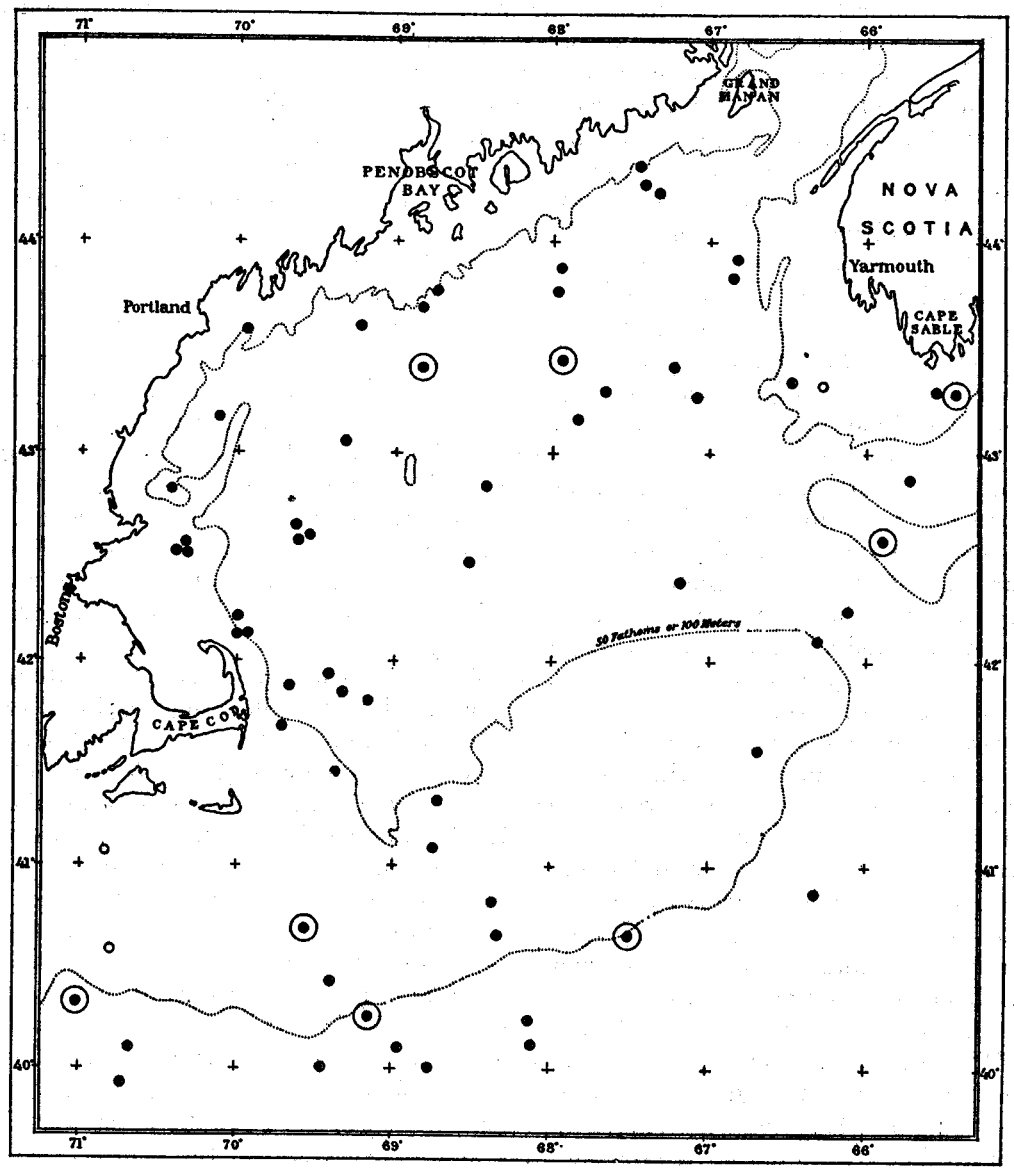

FIG. 55.—Occurrence of the amphipod genus Euthemisto, July, August, and the first week of September. ●, locality records for *E. compressa*; ○, locality records for *E. bispinosa*; ⊙, locality records for both species together. The large symbols are for the more notable swarms

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.

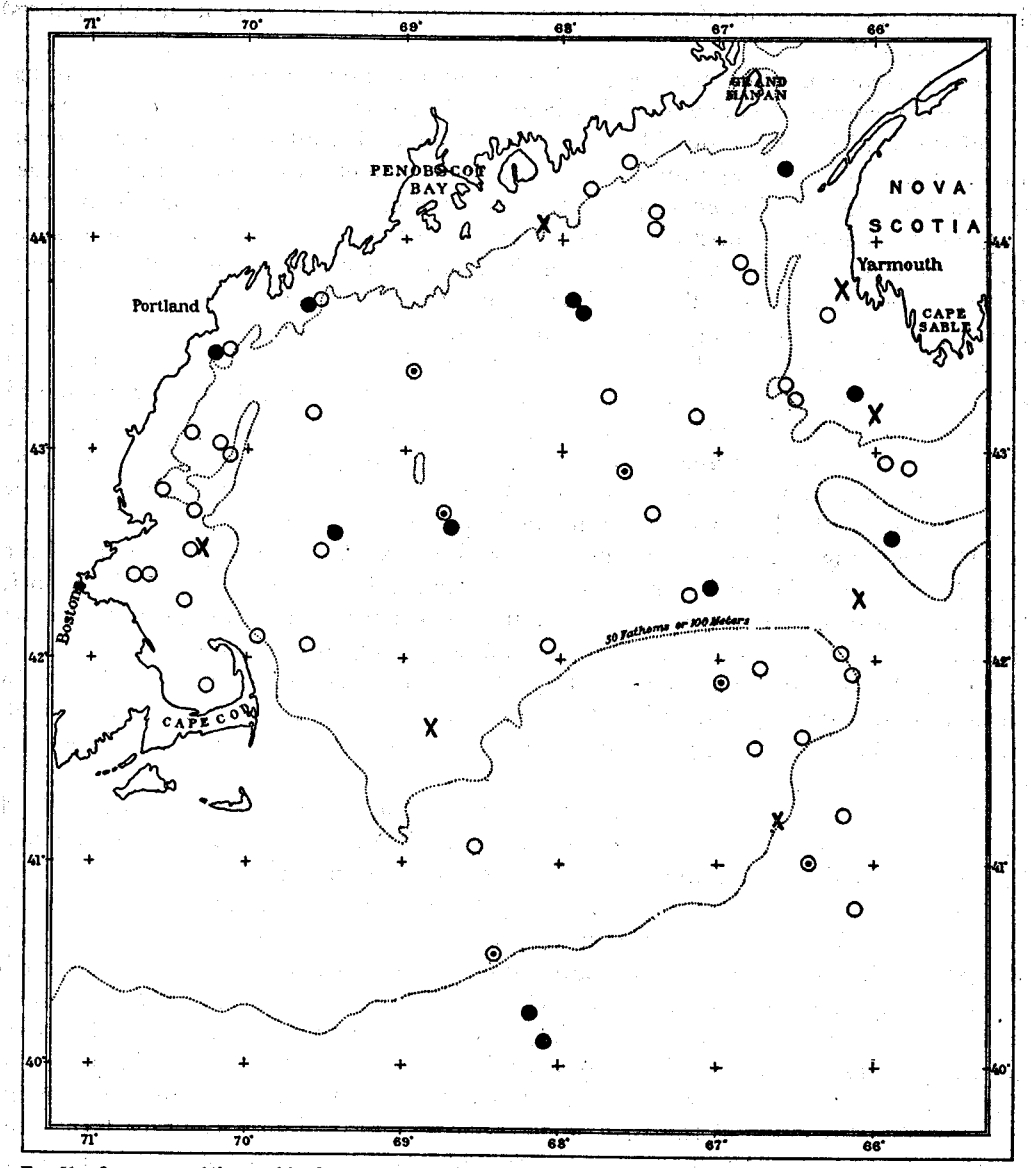

FIG. 56.—Occurrence of the amphipod genus Euthemisto from February to April, 1920. ●, locality records for *Euthemisto compressa:* ⊙, locality records for *E. compressa* and *E. bispinosa;* ○, stations where neither occurred; X, locality records for larvæ too young for identification as the one species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

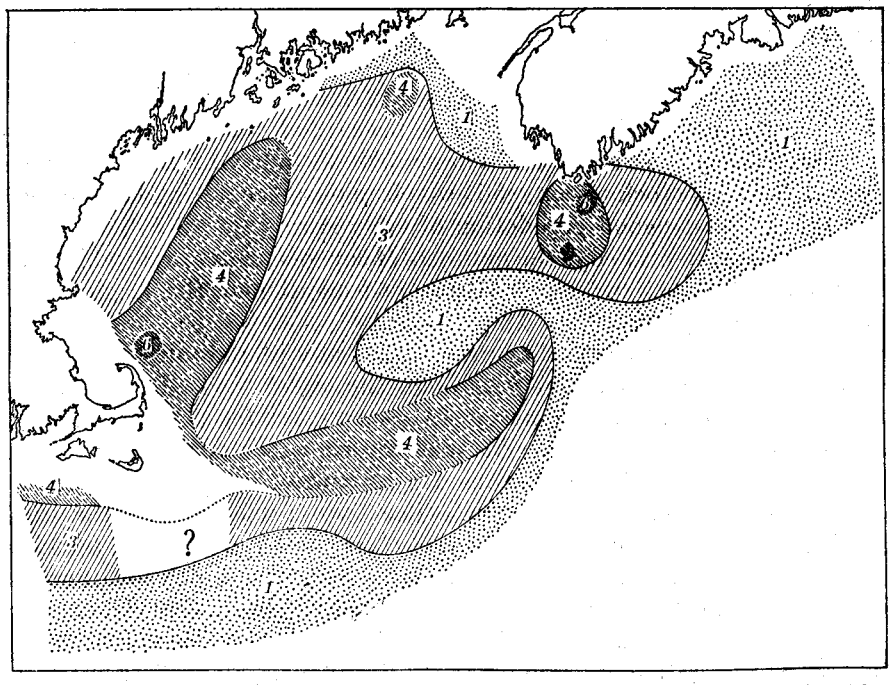

FIG. 57.—Number of copepods per square meter of sea area, July and August, 1914, as calculated from the catches of the vertical hauls. 1, scanty (less than 20,000); 2, intermediate (20,000 to 70,000); 4, rich (70,000 to 150,000); 6, very rich (150,000 or more). Reproduced from Bigelow, 1917, fig. 94.

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

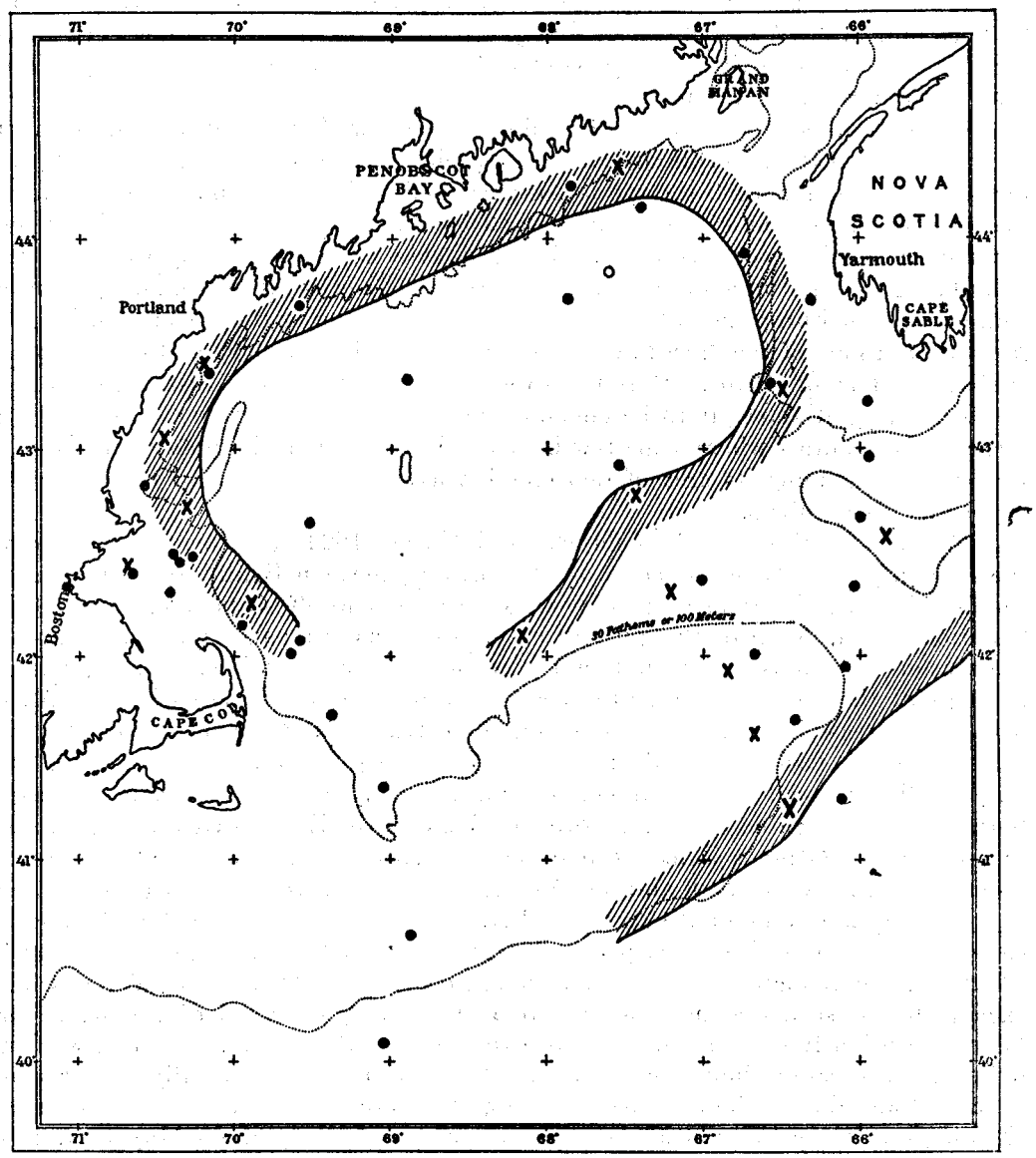

FIG. 58.—Occurrence of the copepod *Acartia clausi* during the spring of 1920. X, locality records for February and March; ●, locality records for April and May. The hatched curve incloses the area where it occurred in March

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