It is to be noted that this has been observed in the shoal water of the banks as well as in deep water. *A. clausi* has seldom been found plentiful enough in the Gulf of Maine to suggest that it is ever important there as a food supply for larger ani-

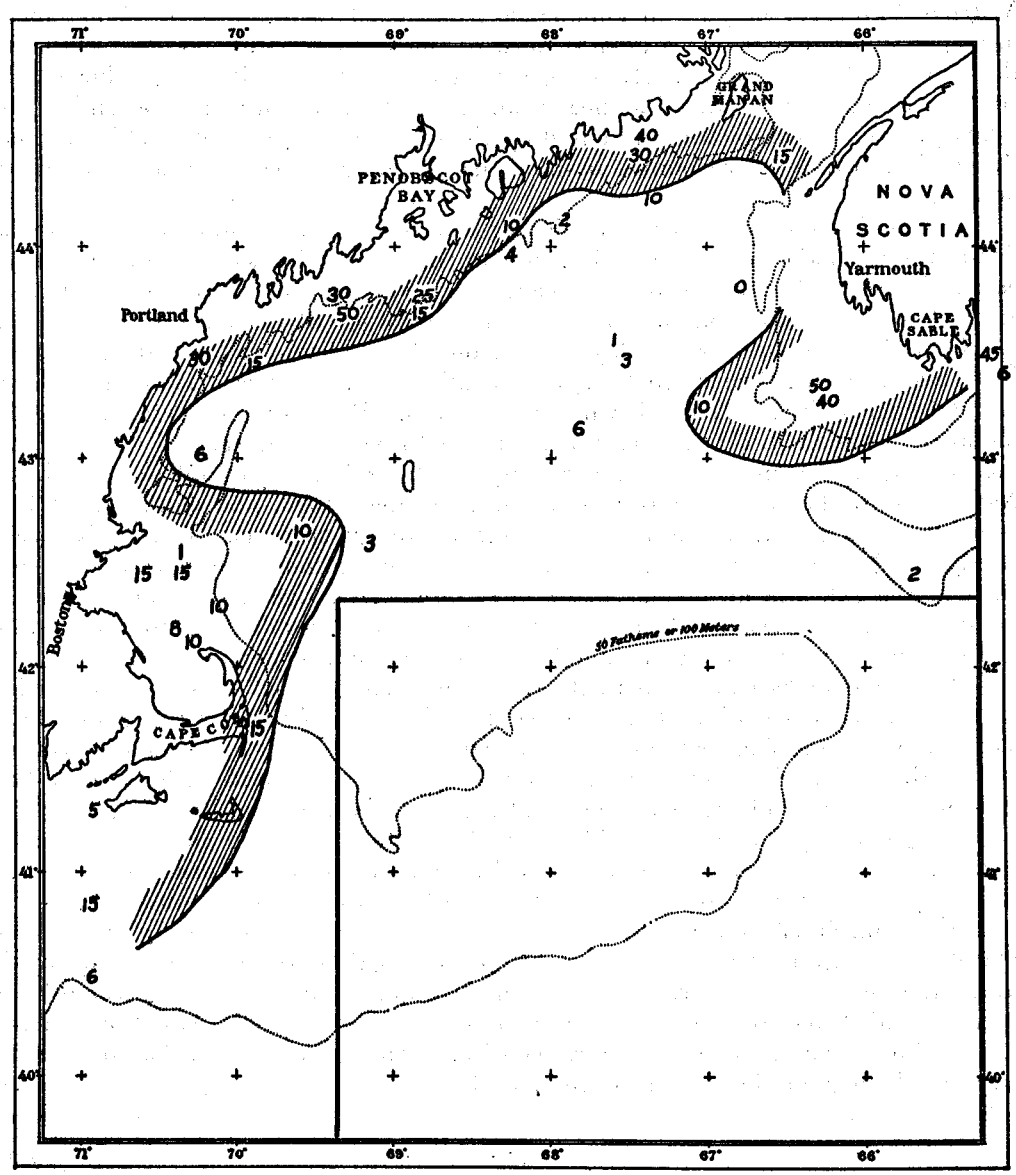

FIG. 59.—Percentages of the copepod *Acartia clausi* in the total catches of copepods of all kinds in the vertical hauls from June to October, 1915. The hatched curve incloses the area where it usually constitutes more than 10 per cent of the copepods in summer

mals. This is likewise true of it, as a rule, in north European seas, though it has been recorded there among the stomach contents of various fishes; but as Farran (1903, 1910, and 1911) reports it as taken throughout the year on the mackerel-

fishery grounds off Ireland, most commonly in autumn, it may prove a more important ingredient in the food of the European mackerel than it is ever likely to be off the seaboard of eastern North America.

Acartia longiremis Lilljeborg

This species is of minor importance in the Gulf of Maine but is recorded sufficiently often to deserve brief mention. In the Atlantic *A. longiremis* ranges from the polar basin on the north, where it has been taken at many localities both on the European side and along the Arctic coast of Canada (Willey, 1921), to the Mediterranean on the one side and southward to Chesapeake Bay on the other. It is also reported from the Gulf of Suez. Its distribution, in general, has recently been charted by Steuer (1923).

It has usually been described as more or less neritic, though less so than *A. clausi*. According to Farran (1910 and 1911) it is mainly a littoral form in the more southern parts of its range, though often found in the open sea off Norway. Herdman, Thompson, and Scott (1898) record it regularly in the Gulf of St. Lawrence, out to the Straits of Belle Isle, and again between longitude 31° 40′ W. and the British coastal waters, but not at all in the intervening zone. It was not found at Woods Hole either by Wheeler (1901) or by Sharpe (1911), nor was it found in Rhode Island waters by Williams (1906 and 1907) or off New Jersey by Fowler (1912). Probably, however, it is to be expected all along southern New England, for Fish (1925) found it at Woods Hole from January to May, while Dr. C. B. Wilson contributes the statement that it occurs in and about Chesapeake Bay, though less abundantly than *A. clausi*.

The only previous records for *A. longiremis* in the Gulf of Maine are as follows: Station 10020 (about 4 per cent of the copepods), Gloucester Harbor, and 6 miles off Cape Porpoise (2 per cent of the copepods) during the summer of 1912; station 10251, off Cape Elizabeth, August 14, 1914 (especially interesting because upwards of 90 per cent of the hundreds of copepods taken in the surface net were adults and juveniles of *A. longiremis*) [93]; and Passamaquoddy Bay, January 16, 1920, when *A. longiremis* (adult and young) constituted 13 per cent of the copepods taken (Willey, 1921).

During the cruises of 1915 and 1920 this species proved much less plentiful and less generally distributed in the gulf than *A. clausi*, its status in the gulf differing widely from year to year. In 1920 it was not detected at all in February. In March (fig. 60) it occurred at 38 per cent of the stations, confined to four distinct regions: (1) the coastal zone from Cape Cod to Cape Elizabeth, (2) the eastern part of Georges Bank and the deep water to the north, (3) Browns Bank, and (4) the shallows off western Nova Scotia out to German Bank. In every case the number of specimens taken was trifling, the highest frequency in the vertical hauls being only 95 per square meter of sea surface. The scarcity of this species during March appears also from its percentage in the total copepod catch (0–30 per cent; average 2½ per cent).

[93] Identified by Dr. C. O. Esterly.

During April it became so scarce in the Massachusetts Bay region and over the northwestern part of the gulf generally that it did not appear there in the catches of the vertical nets, although the surface tows picked up a few at the localities marked

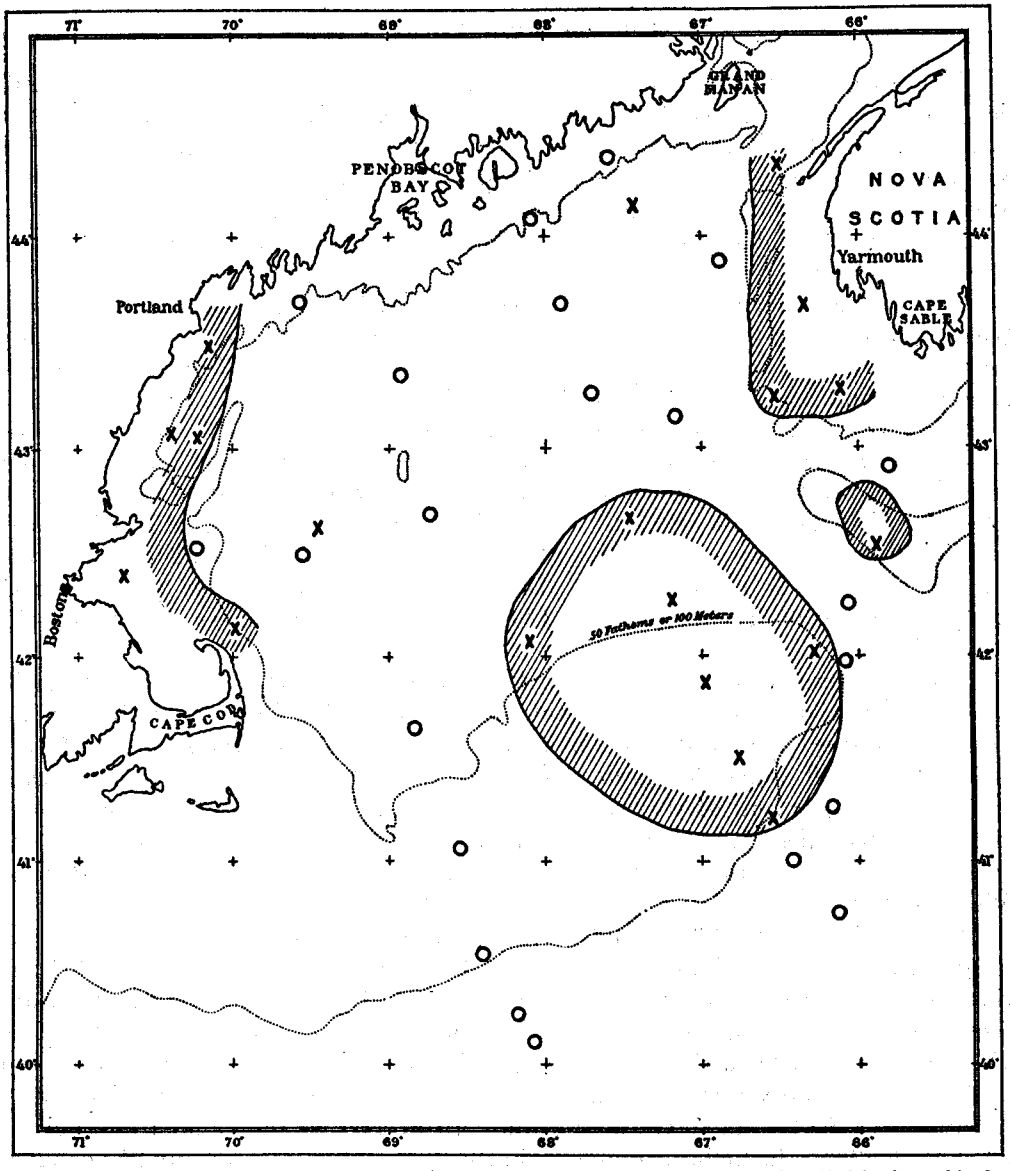

FIG. 60.—Occurrence of the copepod *Acartia longiremis*, February to April, 1920, surface and vertical hauls combined. X, present; ○, not found. The hatched curve incloses the areas where it occurred at every station

on the chart (fig. 61); but, by contrast, it had spread generally over the whole eastern side of the gulf, with a rather definite line of demarcation between the areas where it did and did not occur in sufficient number for the vertical net to take it (fig. 61), but

not to the deep water off the southeastern slope of Georges Bank. The numerical frequency of *A. longiremis* likewise rose by April to a maximum of 2,800 per square meter off Cape Cod, 1,300 per square meter in the northern channel, and 863 per square

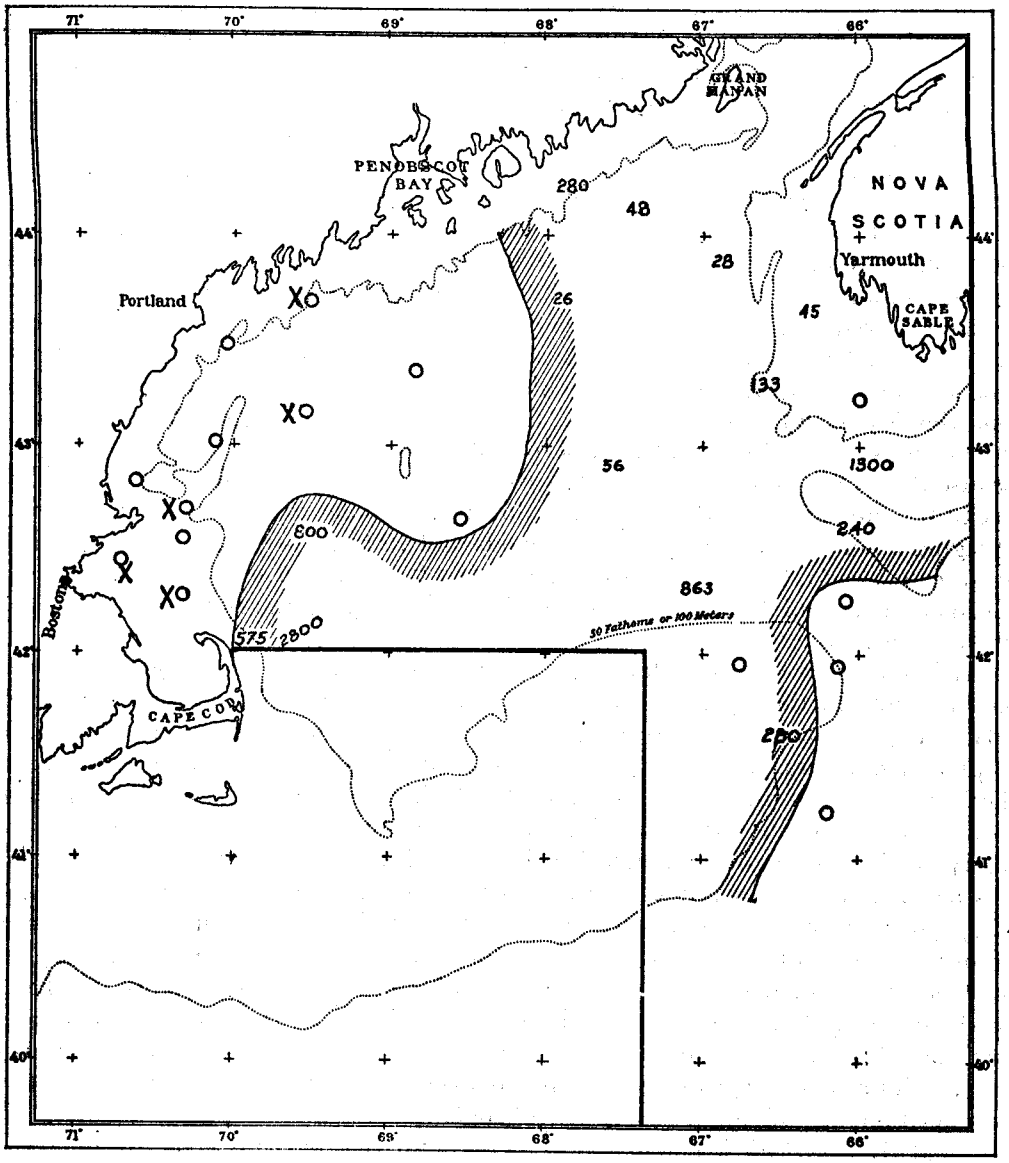

FIG. 61.—Numbers of the copepod *Acartia longiremis* per square meter of sea area, April, 1920, as calculated from the vertical hauls. ○, none in vertical haul; X, taken in surface haul. The hatched curve incloses the area where it was plentiful enough to be taken regularly in the verticals

meter north of Georges Bank, though on the average it was still only about 2½ per cent of the total copepods (0–14 per cent). In 1920 it reappeared in Massachusetts Bay in May, when it occurred at all the stations there and along the line from Cape

Cod out across the western end of Georges Bank, with frequencies of from less than 10 to nearly 3,000 specimens per square meter, averaging 3½ per cent of the copepods taken in these vertical hauls. In the year 1915 it was not detected anywhere in the gulf in May or during the first three weeks of June, though vertical hauls were made at 20 stations during that period, but on June 26 (station 20099) it was taken at the rate of 430 per square meter in the western basin, and it figures in the lists (p. 298) for two August stations. In September it occurred in all the vertical hauls in the coastal zone from Cape Cod northward and eastward toward the mouth of the Bay of Fundy, as well as on German Bank (80 per cent of all the stations for the month), averaging 4,490 per square meter where the vertical net took it.

During the first half of October, 1915, it continued universal along the coastal zone from off Cape Cod to the neighborhood of Mount Desert Island (six stations), varying in abundance from 1,140 to 14,225 per square meter (average about 5,600). It also occurred in two out of three vertical hauls over the shelf south of Marthas Vineyard on the 22d (stations 10332 and 10333), frequencies of about 6,000 and 4,000 square meters. By the last week of the month it seems that it had vanished from the Massachusetts Bay region, for not a single specimen was detected at four stations there; but this can not be interpreted as a regular seasonal change, because it was taken at all the stations within 15 to 20 miles of land, from off Cape Cod to the mouth of the Bay of Fundy during December, 1920, and January, 1921, averaging about 5.5 per cent of the copepods and 10 to 15 per cent of the extremely sparse community at the mouth of Massachusetts Bay and off the Isles of Shoals (stations 10489 and 10493), though not found at any of the four stations farther out in the basin.

It is not clear from the data just outlined whether *A. longiremis* has two seasonal maxima in the gulf, one in late spring, another (much more pronounced) in early autumn, separated by a period of a month or more during which it nearly or quite disappears, as the records for the two years 1915 and 1920 suggest; or whether it followed different seasonal cycles during the two years, multiplying from April on in 1920, but not appearing at all until June in 1915. In either case it clearly attains its maximum abundance in the gulf during the warm half of the year. It is never more than a minor factor in the plankton except when all other species of copepods are very scarce, and never occurs in numbers that would be called large for other more important copepods, 14,265 per square meter being the highest frequency yet recorded for it east or north of Nantucket. *A. longiremis*, like *A. clausi*, contracts its range to the shoaler waters of the gulf during the cold half of the year, including the offshore banks as well as the coastal zone. When its numbers increase, its area of occurrence spreads out over the deep basin of the gulf, but we have not taken it outside the continental edge.

That *A. longiremis* is endemic in the gulf is proved by the presence of numerous juveniles, together with adults, at the one August station already mentioned (p. 177). This, however, does not forbid the possibility that its numbers are recruited by immigration as well as by local propagation. On the average, *A. longiremis* was relatively more important in the catches at the surface than in the vertical hauls in March and April, though not in May, as appears in the following table of its percentage in 1920, counting only the stations at which it occurred:

Time	Surface hauls	Vertical hauls
	Per cent	*Per cent*
March	14.5	6
April	11	5
May	3	4

In several instances the greater percentage on the surface was the result of a definite concentration there, proved by the capture of hundreds of specimens in the surface net at several stations where *A. longiremis* was so scarce deeper down that the vertical net missed it altogether—for instance, off the Isles of Shoals on March 5 (station 20061); off the northern edge of Georges Bank, March 11 (station 20063); on its eastern edge and southern slope, April 16 (stations 20108 and 20109); and, notably, on March 23, off Yarmouth, Nova Scotia (station 20083), where the richest surface catch of all was made (711 specimens). At a rather larger number of localities the yield of the vertical nets was considerable, where few or none were taken on the surface, as shown in the following table:

Locality	Date	Hour	Station	Number per square meter in vertical hauls	Number taken in surface hauls
Near Mount Desert	Apr. 12, 1920	1 p. m	20099	280	0
Northern Channel	Apr. 15, 1920	10 p. m	20105	1,300	53
Browns Bank	Apr. 16, 1920	1 a. m	20106	240	2
Deep water north of Georges Bank	Apr. 17, 1920	7 a. m	20112	863	0
Western basin	Apr. 18, 1920	4 a. m	20115	800	0
Off Cape Cod	May 16, 1920	11 p. m	20125	470	0
Southwest part of basin	May 17, 1920	8 a. m	20127	1,437	27

The most that can be said from this is that at times *A. longiremis* tends to gather at the surface, both in spring and in midsummer, but that on other occasions it keeps at least a few fathoms down. The hauls here listed give no evidence of diurnal migrations, for the richer surface catches were more often between 9 a. m. and 5 p. m. than at night, and, on the other hand, several of the hauls in which it most predominated in deeper levels were between sunset and sunrise.

A. longiremis has been found over a very wide range of salinity, being common in water as brackish as 6.72 per mille in the Baltic and as salt as 35.32 per mille in the English Channel. In the Gulf of Maine it occurs well within these limits. It is likewise eurythermal over a wide range of temperature, being present in the gulf indifferently in water as warm as 16° and as cold as 0.3° to 2°. The physical limits within which it reproduces locally have not been determined, but the presence of juveniles in August (p. 177) proves that reproduction takes place successfully in summer temperatures, probably upwards of 10 to 12°.

Acartia tonsa Dana

This species was originally described from Port Jackson, Australia, and was reported by Giesbrecht (1892) from the west coast of South America, and from the Malayan Archipelago by Cleve (1901). On the one side of the North American

continent it occurs in numbers at San Diego, Calif., in the bays, but rather infrequently outside (Esterly, 1905). On the other, it is reported from the Gulf coast of Louisiana (Foster, 1904), and is a dominant copepod in sheltered inlets and brackish ponds at Woods Hole. It is abundant, also, in the open water in that neighborhood, and recorded from the Gulf Stream off Marthas Vineyard (Wheeler, 1901; Sharpe, 1911). Cape Cod seems the northerly boundary to its presence in numbers, for although Wheeler (1901) reports it from Plymouth Harbor on the southern shore of Massachusetts Bay (this is the only gulf of Maine record), none of the *Grampus*, *Albatross*, or *Halcyon* gatherings in the gulf have contained it. McMurrich did not detect it at St. Andrews, nor has it been found in Canadian waters farther east or north.

Aetidius armatus Brady

Dr. C. B. Wilson contributes the following on the faunistic status of *Ae. armatus:*

This species is quite cosmopolitan and has a wide distribution throughout the northern Atlantic, Pacific, and Indian Oceans. It is widely distributed in the northern fauna, but nowhere occurs in any numbers. Farran (1910) has reported it as a characteristic inhabitant of the lower layers of the northeast Atlantic off the coast of Ireland and Scotland. Carl With (1915), in his report on the copepods of the Danish Ingolf expedition, said that it was found in deep water, probably as a member of the Atlantic fauna, in the Iceland-Faroe channel, Denmark, and Davis Straits. It has also been taken in the North Sea and in several of the Norwegian fjords, and was included in the list published by Esterly (1905) of copepods found in the San Diego region off the coast of southern California.

In the summer of 1915 the Canadian fisheries expedition took it in small numbers in the deep oceanic triangle off the mouth of the Laurentian channel, between the Scotian and Newfoundland Banks (two stations), and outside the continental edge off Cape Sable (Willey, 1919).

It has not been recorded previously from the Gulf of Maine, but the spring, summer, and autumn cruises of 1915 and of 1920 yielded odd specimens of it at eight stations—one for March, three for April, two for May, one for August, and one for October. It has not been reported at Woods Hole.

Although this species is evidently only a rare stray in the Gulf of Maine (at most it amounted to 1 per cent of the copepods, with a maximum frequency of 87 individuals per square meter of sea area) the locations of the captures are of interest, all being either in the peripheral belt of the gulf, with a preponderance in its eastern side, or over the continental edge. A distribution of this sort (fig. 62), which parallels the dominant counterclockwise eddy of the gulf, indicates that the species is an immigrant in the gulf from the open Atlantic and not endemic there. The fact that all but one of the records within the gulf were in hauls shallower than 100 meters suggests that it enters in the upper layers and across Browns Bank, not along the bottom of the eastern channel; but it tends to keep at some little depth, for it was not detected in any of the surface hauls from February to May, 1920, even at the stations where it occurred in the verticals.

Anomalocera pattersoni Brady

This beautiful bluish green or Prussian blue calanoid is generally distributed over the North Atlantic between latitudes 36 and 67° N., in the Mediterranean and in the North Sea and English Channel (Giesbrecht, 1892; Brady, 1878–1880; T. Scott,

1911). It seems not to enter the Baltic, probably being barred therefrom by low salinity. It is recorded from the Indian Ocean, doubtfully from the Pacific (Giesbrecht and Schmeil, 1898), and from the Black Sea (van Breemen, 1908). Off the

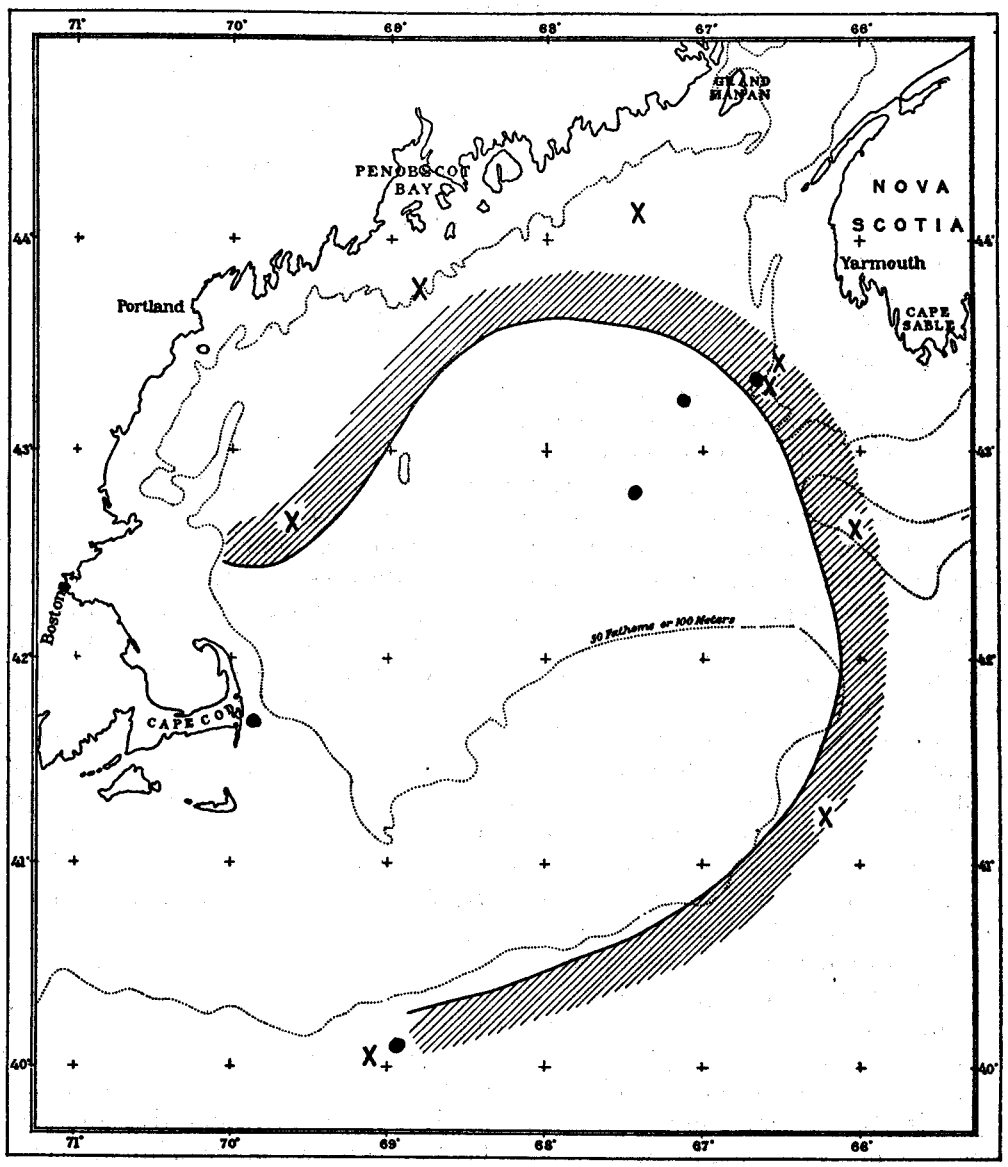

FIG. 62.—Occurrence of the copepods *Æetidius armatus* and *Candacia armata*. X, locality records for *Æetidius armatus*: ●, locality records for *Candacia armata*. The hatched curve incloses the zone where tropical-oceanic species occur most frequently

North American seaboard it has been reported from the Gulf of St. Lawrence (T. Scott, 1905; Herdman, Thompson, and Scott, 1898; and Willey, 1919); off Halifax and Shelburne, Nova Scotia (Willey, 1919); at many localities in the Gulf of Maine;

at Woods Hole and in the Gulf Stream off Marthas Vineyard (Wheeler, 1901); and likewise at several stations on the continental shelf and along the continental edge between Woods Hole and Chesapeake Bay (Bigelow, 1915 and 1922).

Because of its large size and brilliant color this is the most conspicuous of all Gulf of Maine, copepods, but is usually so scarce there that horizontal hauls must be depended upon to outline its distribution, the verticals being apt to miss it. Up to the present, time has not permitted search for it in the mass of copepods taken in the deep horizontals for the period February to May, 1920, but it did not occur at all in the surface hauls for those months (table, p. 303), and only three times and in minimal amounts (1 per cent of the catch) in the verticals, suggesting that although these captures prove its presence in the gulf in spring it is then very scarce. This is corroborated by the fact that in July it has been detected at only two of the forty-odd stations for which the copepod catches of the horizontal nets were examined by Doctor Esterly or by me (p. 10)—one of them in Massachusetts Bay and the other a few miles north of Cape Ann—but Anomalocera must either multiply in the gulf or invade it during midsummer, for it has occurred at fully 50 per cent of our stations for August and at localities generally distributed over the whole inner and northern part of the gulf north of a line Cape Cod–Cape Sable. Although no tows were made on Georges Bank in August during the period 1912 to 1921, Dr. W. C. Kendall, in his field notes (p. 12), records "green copepods" (which, from his description, can only have been Anomalocera) from enough of the surface tows on the northwestern part of the Bank and thence to Cape Cod and off Marthas Vineyard, in the last week of August, 1896 (fig. 63), to show that this copepod is as generally distributed over the offshore grounds during that month as it is in the inner parts of the gulf. The seasonal history of Anomalocera is the same in the Gulf of St. Lawrence, where the Canadian fisheries expedition did not find it at all in May or June, but widely distributed (though nowhere plentiful) in August. Similarly, it appeared in the last week of July off Halifax, where it was wanting in May (Willey, 1919).

Judging from the year 1915, Anomalocera practically vanishes from the gulf after the end of August, for it was taken in only two of the horizontal tows at the 12 September stations (on the 1st and 6th, stations 10308 and 10314), and did not appear in a collection of copepods made at St. Andrews by Dr. A. G. Huntsman on the 15th (Willey, 1919, p. 220). We have only one record of it in the gulf in October,[94] none for November, one for December (see table, p. 304), none for January, February, or until March (see table, p. 305).

Thus, Anomalocera certainly persists in the gulf throughout the greater part of the year; and it is probable that a few survive over the coldest period, though it has not actually been taken within our limits at that time. From September until July it is always very scarce, but it has a brief period of comparative abundance during the month of August, when it may become so nearly universal in all parts of the open gulf that surface tows usually pick up at least one or two. It is such a noticeable object in the catch that its presence is almost certain to be recognized. It is equally a summer copepod at Woods Hole (Fish, 1925, fig. 46).

[94] Vertical haul off Penobscot Bay, Oct. 9, 1915, station 10329.

Anomalocera is likewise least plentiful in the North Sea region generally in February, but from year to year may reach its maximum there at any time from May to November (T. Scott, 1911). Recognition of the brevity of its period of maxi-

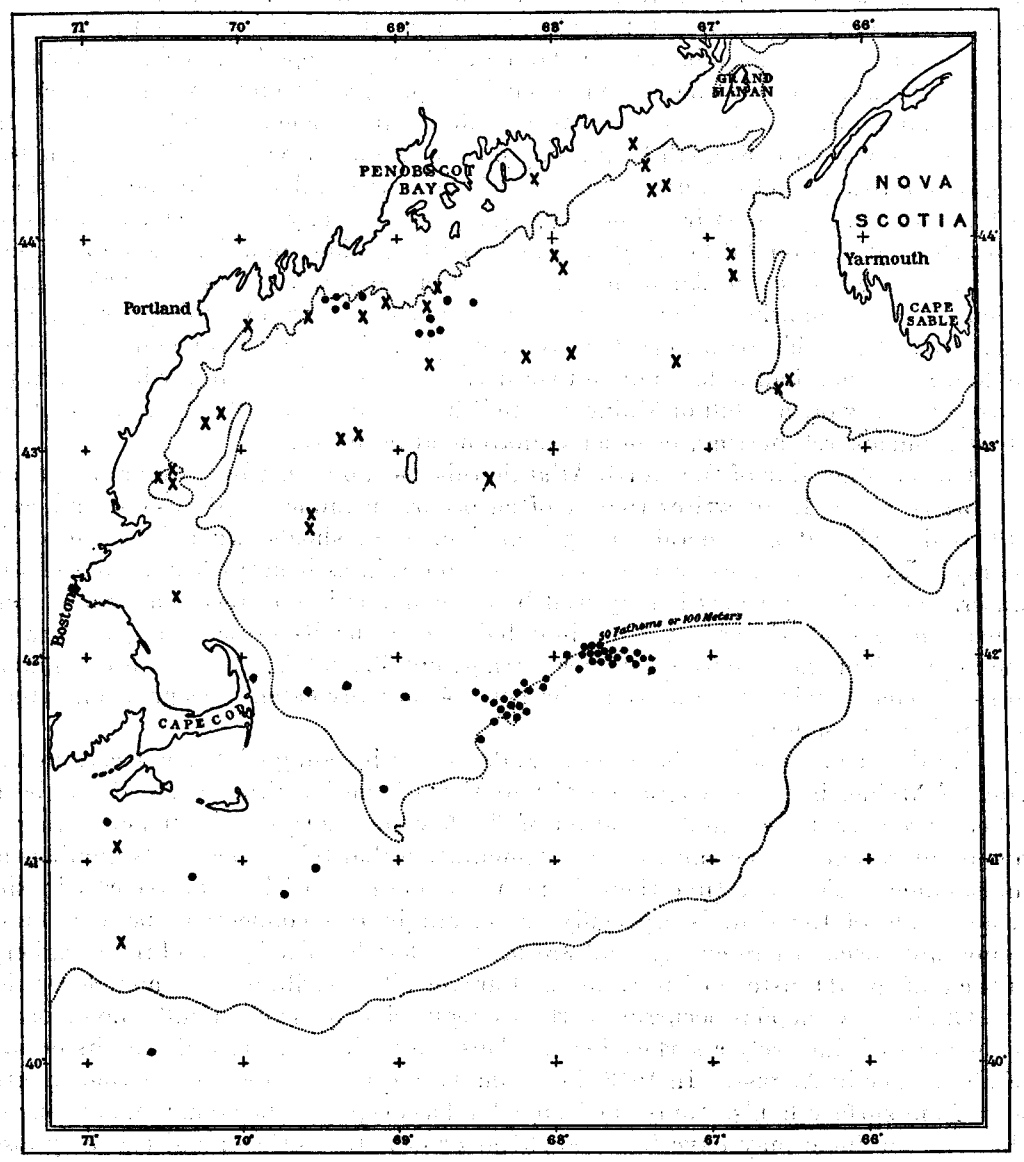

FIG. 63.—Occurrence of the blue copepod *Anomalocera pattersoni* in August. ×, locality records for August, 1912 to 1914; ●, locality records for August, 1896 (from Dr. W. C. Kendall's field notes)

mum abundance (now sufficiently established as usual if not invariable) forces me to correct a previous statement that it markedly diminished in the Gulf of Maine from 1913 to 1915 (Bigelow, 1917, p. 292). Its more frequent occurrence in the

towings of 1912, 1913, and 1914 than in those of 1915 may simply have been a seasonal phenomenon associated with the fact that in the first three years the *Grampus* cruised in August, when Anomalocera is at its maximum, whereas in 1915 most of the towing was done either before July or from September on, when this copepod is scarce, with only five towing stations for August, at two of which it occurred.

Anomalocera is peculiar among Gulf of Maine copepods in being seldom, if ever, abundant even at the season when it is practically omnipresent, the catch usually amounting to less than 50 to 60 individuals (Bigelow, 1915, p. 288). In tow after tow Doctor Kendall found only one or two or "a very few." Sixty is the largest number actually counted for any of the horizontal hauls in the gulf since 1912, and 550 the greatest frequency per square meter in any of the verticals (Massachusetts Bay, station 20120, May 4, 1920). Drifting along in a dory on a day when the water is glassy calm, Anomalocera may often be seen right in the surface film, when, as Sars remarked (1903, p. 141), its movements are exceedingly rapid and energetic. On such occasions I have usually noticed one here and one there, seldom more than half a dozen or so together. Evidently it can never be important in the economy of the Gulf of Maine, where it has not been reported from the dietary of either mackerel, herring, or other plankton-eating fishes.

On the other side of the North Atlantic this copepod must be far more plentiful, for Brady (1878–1880) writes that it often occurs in immense profusion, and Sars (1903) describes it as generally congregated in great shoals, when its presence is betrayed by a disturbance of the surface like fine rain as it keeps leaping out of the water. On such occasions it may well be of economic importance, and Norwegian fishermen, who have christened it "blue bait," consider its presence a good sign of the approach of the schools of summer herring; but T. Scott's (1911) failure to find it in fish stomachs raises the question whether it is actually eaten to as great an extent as has been supposed.

No direct observations have been made on the breeding of Anomalocera in the Gulf of Maine, but the geographic distribution of the localities where it has been taken argues that local multiplication of the few that survive winter and spring—not immigration—is the cause of the augmentation that takes place in its numbers in midsummer. The fact that there is no preponderance of locality records in the eastern side of the Gulf is especially significant in this connection, because most immigrants occur there chiefly, and are more or less localized around the periphery of the gulf (p. 51) instead of as evenly and universally distributed as Anomalocera is.

Of all the Copepods occurring with any regularity in the open gulf Anomalocera is the most distinctively a surface form. This is especially the case during its period of abundance in August. In 1913, for example, most of the records for that month were from surface hauls, "only one from a haul as deep as 40 fathoms; and of course, that one specimen may have been caught at or near the surface; and this may also be true of the few specimens yielded by hauls from 20, 25, and 30 fathoms in the Gulf of Maine" (Bigelow, 1915, p. 295).

This tendency to keep close to the surface was well illustrated in August, 1914, at the following stations, in spite of the fact that the mouth area of the surface net was much less than that of the nets towed deep.

Anomalocera	Station and depth in meters								
	10245		10246			10254			
	0	100–0	0	50–0	150–0	0	25–0	75–0	225–0
Number of specimens in sample	1	0	6	0	0	10	0	0	0
Percentage of total copepods in sample	33	0	12	0	0	2½	0	0	0

There is no positive evidence that Anomalocera ever sinks more than a few meters in the Gulf of Maine in summer, and most of the Gulf of St. Lawrence records listed by Willey (1919) are likewise from the surface or from trivial depths. In winter and spring it seems to live slightly deeper, for it was not taken in any of the surface hauls from November, 1912, to April, 1913, or February to May, 1920; but it descends to only a moderate depth—probably to escape the most severe winter chilling—the vertical records for December, March, and April all being from hauls shoaler than 75 meters.

Anomalocera is similarly an inhabitant of the upper strata of water in north European seas. Sars (1903) always found it swimming close to the surface off the west and south coasts of Norway, and T. Scott (1911) describes it as most generally met with at or near the surface, very rarely in deep water, though he gives its vertical range as extending down to 700 meters.

This copepod occurs only in water of tolerably high salinity, and its preference for the surface makes it easy to establish the precise conditions under which it is living at any given station. In the Gulf of St. Lawrence it occurred regularly in water as little saline as about 30 per mille (Willey, 1919; Bjerkan, 1919). In the Gulf of Maine most of the records are from salinities of 31.55 to 33.06 per mille, and south and west of Cape Cod it occurs in water salter than 35 per mille, which is a usual salinity for it in the eastern North Atlantic. It is certainly able to survive a wide range of temperature, but in the Gulf of Maine it is most abundant when the surface water in which it lives is warmer than 10°, which may prove about the lower limit for its successful reproduction. Temperatures as high as 21° to 25°, even, seem not unfavorable for it.

Anomalocera is an inhabitant of the open sea, never yet recorded from harbors or from estuarine situations except when brought in by heavy winds or by surface currents, as occurs at times in Norway (Sars, 1903) and at Woods Hole (Wheeler, 1901). In its relationship to the North American littoral it may be described as intermediate between neritic and oceanic, maintaining itself in the Gulf of Maine and in the Atlantic basin alike.

Asterocheres bœcki (Brady)

Doctor Wilson contributes the following note on this copepod, which is only accidental in the plankton:

This species occurred in the form of two partially mutilated specimens taken in one of the surface tows early in March, 1920. As far as could be determined, these specimens were identical with those described by Brady in his monograph on British Copepoda as *Artotragus bœcki*, but

Brady, as he himself admitted in his later writings, confused the two genera, Artotragus and Asterocheres, and should have assigned his species to the latter instead of the former. Most of the species of this genus are parasitic upon, or commensal with, some invertebrate animal, but Brady gave no information upon this point. Scott, in his "Catalogue of the Crustacea of the River Forth," reported obtaining this species in the water passages of sponges (*Chalina oculata*) growing on the walls of a pier. It was later recorded by Norman and Brady from a tidal pool on the coast of England, and it was added that this was probably a truly commensal or parasitic species, accidentally found in a free condition. This readily explains why more specimens were not found in the present collections, and it is significant that these two came from close to the coast of Maine south of Portland [station 20059].

Calanus finmarchicus (Gunnerus)[95]

General distribution.—Farran (1910, p. 83), whose words I can not better, has described the distribution of *Calanus finmarchicus* as "centered in the North Atlantic. It has also been recorded from the South Atlantic off Cape Colony, the west coast of South and North America,[96] the Mediterranean, the Adriatic, and the Polar Ocean." Following the North Atlantic around from east to west, we find it occurring in dense though limited swarms off the mouth of the English Channel (Farran, 1910); on the south and west coasts of Ireland, where Farran (1903) found it the most abundant and economically important of the copepods; and on the west coast of Scotland (T. Scott, 1898, p. 182). Many authors have described the extraordinary abundance of this species in Norwegian seas. Gran (1902), Paulsen (1906), and Damas (1905), in particular, comment on the shoals of it between Norway, Iceland, and Greenland. The Ingolf expedition (With, 1915) had it at many localities off west and east Greenland. Sars (1900, p. 35) describes it as "by far the commonest of all the Copepoda in the north polar basin explored by the *Fram* expedition, forming, indeed, in all the samples the great bulk of the contents." Cleve (1900) remarked its abundance in the Labrador current. Herdman, Thompson, and Scott (1898) record it from practically every tow netting across the North Atlantic from Liverpool to the Straits of Belle Isle—largest in the Labrador current—and Farran (1910, p. 83) speaks of it as "in great abundance along the coast of North America in the path of the Labrador current, forming, in the summer months, a rich belt, which, off Newfoundland, is at least 500 miles wide." Corroborating this, the international ice patrol has taken great masses of it on the Grand Banks; Willey (1919) found it the commonest copepod between Nova Scotia and the Newfoundland Banks, in the Gulf of St. Lawrence, and along the outer coast of Nova Scotia.

It dominates the plankton of the Gulf of Maine at all seasons, as will shortly be described, and outside the immediate coastal zone is usually plentiful and often the dominant copepod over the continental shelf off southern New England to longitude about 72° W.; that is, abreast of Long Island, New York (Bigelow, 1915). South of this its occurrence along the seaboard of the United States becomes more seasonal and less regular. It is to be expected in abundance over the shelf between the latitudes of New York and Chesapeake Bay during the cold half of the year and into early summer, Rathbun (1889) having found it characterizing the plankton at many

[95] According to With (1915) the relationship of *C. helgolandicus* Sars to *C. finmarchicus* is still in doubt, but Dr. C. B. Wilson writes "Whatever may be the outcome, it seems reasonably certain that all the specimens from the Gulf of Maine are *finmarchicus*."

[96] Esterly (1905, p. 126) describes it as the commonest copepod about San Diego, Calif., and as often very predominant.

localities in this zone during April and May of 1887, while Fowler (1912) reports it in great abundance along the New Jersey coast in June, 1911, and early July, 1912. In cool summers, such as that of 1916, it continues extremely plentiful along the zone of lowest temperature on the shelf, narrowing to the southward to abreast the mouth of Chesapeake Bay until the end of summer and becoming much less plentiful in autumn, as I have described in a previous report (Bigelow, 1922), but in warm years—e. g., 1913—it practically vanishes south of New York by July (Bigelow, 1915, p, 269). So far as known, the latitude of Chesapeake Bay may be set as the southern limit to its occurrence off the east coast of the United States in numbers sufficient to color the plankton at any season. Westward and southward from abreast of Cape Sable the zone of abundance for *Calanus finmarchicus* is bounded offshore by the high temperatures and salinities of the "Gulf Stream," a boundary which fluctuates in location from season to season but which is never far outside the edge of the continent.

Regional distribution in the Gulf of Maine.—In the gulf *Calanus finmarchicus* is decidedly more oceanic than neritic (p. 35), but exists to some extent in estuarine situations as well as offshore. I can offer little first-hand information as to its occurrence in inclosed waters, most of our stations having been located out at sea, but it has appeared in abundance in Gloucester Harbor (p. 194), and we have likewise taken it in abundance in the harbors of Kittery, Portland (Bigelow, 1914, p. 117), Eastport, Provincetown, and in Casco Bay. Doctor McMurrich, in his manuscript list, records it regularly at St. Andrews, often in abundance, during the winter of 1915–16, from November through April, but only occasionally during the later spring, summer, or early autumn. Willey (1921) found it in abundance in the mouth of the St. Croix River during the winter of 1916–17, but decidedly rare in the winter and spring of 1919 and 1920. If these observations in the St. Andrews region apply equally to other parts of the shore line of the gulf, *Calanus finmarchicus* is to be classed as a winter copepod in estuarine waters, where it has never been found in the swarms in which it often occurs in the open sea. Williams (1906) similarly found it an abundant winter visitor to Narragansett Bay, and Fish (1925) found it in winter and early summer at Woods Hole.

Outside the estuaries and inside the continental edge, *Calanus finmarchicus* is universal in the Gulf of Maine, both in deep water and over the shoal banks, but it is consistently less abundant in the coastal zone northward and eastward from Cape Ann along Maine and Nova Scotia than off Massachusetts Bay and in the basin in general. Although the distinction between regions fertile and poor in Calanus is apparently least marked in early spring, when the species as a whole is least plentiful in the gulf, the chart for February and March, 1920 (fig. 64) shows no frequencies as great as 3,000 per square meter anywhere in the peripheral belt inside the 100-meter contour between Cape Ann and Cape Sable, with the whole of Georges Bank equally barren except for the transitory swarm of Calanus which we encountered over and off its southeastern slope on March 12, 1920, as I have described (p. 168). On the other hand, all but one of the vertical hauls in the basin and in the channels (eastern and northern) yielded more than 1,500 *Calanus finmarchicus* per square meter, and most of the hauls more than 5,000, with a maximum of 33,700 in the western basin.

In April of that year Calanus was more evenly distributed, with the coastal belt supporting about as many per square meter as the basin, but with three circumscribed centers of abundance—(1) from Cape Cod out over the western basin (sta-

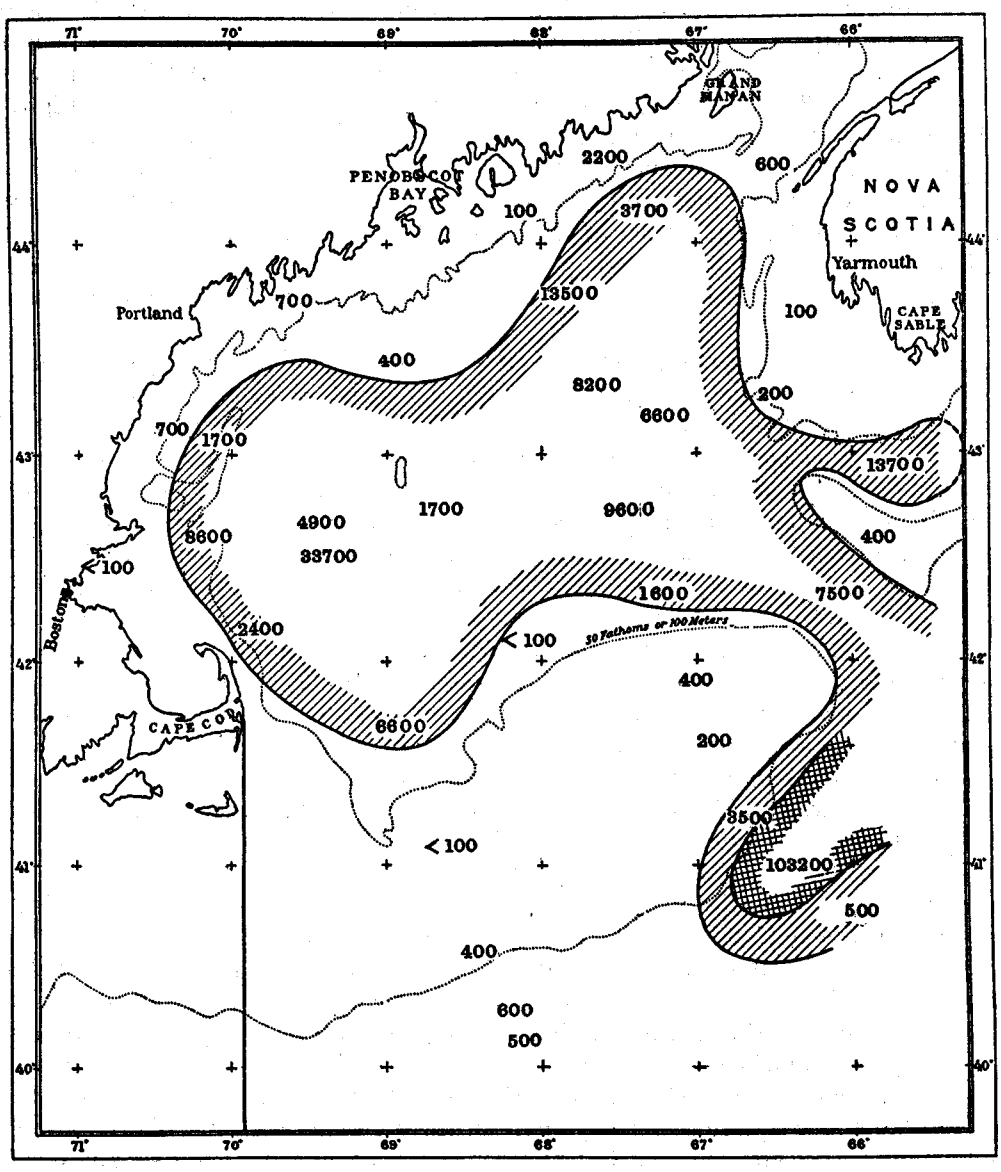

FIG. 64.—Numbers of the copepod *Calanus finmarchicus* per square meter of sea area, February and March, 1920, as calculated fron the vertical hauls. The single hatched curve incloses the area where there were usually upward of 1,000; the double hatched curve upwards of 100,000

tions 20114, 20115, 20116, and 20117), (2) in the northern channel (station 20105), and (3) on the eastern peak of Georges Bank (station 20108)—reminiscent of the local March swarm. From April on reproduction of Calanus takes place so much

more rapidly in the basin and off Massachusetts Bay than along the coasts of Maine and off western Nova Scotia that by May and June (fig. 65) we have found a marked contrast between the rich Calanus population of the former and the sparse catches of the tow net in the latter, a distinction persisting in our experience throughout the summer and into September, except that on August 11, 1914 (station 10243) there was a notable shoal of this copepod close in to Cape Sable.

We have no data on the numbers of Calanus existing in the offshore parts of the gulf later in the autumn, but in October, 1915, this copepod was far more numerous along Cape Cod, in Massachusetts Bay, and between Cape Ann and Cape

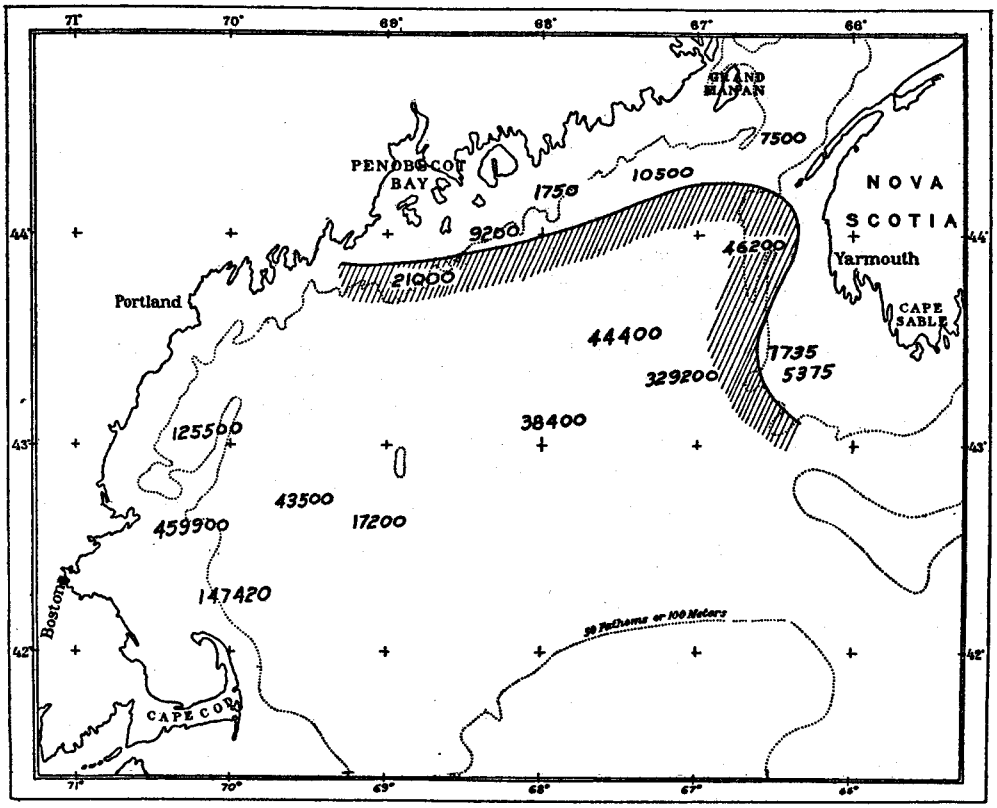

FIG. 65.—Numbers of the copepod *Calanus finmarchicus* per square meter of sea area, May and June, 1915. The hatched curve incloses the area where there were regularly more than 15,000

Elizabeth (23,000 to 122,000 per square meter) than from abreast Penobscot Bay eastward (7,700 to 14,700 per square meter)—that is, the southwestern part of the gulf was then much more prolific of Calanus than the northeastern, and probably as much so as any part of the basin, judging from the large numbers per square meter off Cape Cod (102,500) and at one station in Massachusetts Bay (122,200).

In the parts of the gulf visited by the *Halcyon* during December, 1920, and January, 1921, *Calanus finmarchicus* was most abundant in the western basin on the one side and in the Fundy deep on the other, and least so in the northeastern

part of the basin, but the data are not sufficient to show whether or not it was more plentiful in the offshore parts of the gulf than near land, as is so constantly and characteristically the case in summer (p. 189).

Our several sections across Georges Bank have shown that in summer the offshore boundary to abundant *Calanus finmarchicus*—indeed, to an abundance of copepods of all kinds—abreast the Gulf of Maine is but a few miles outside the continental edge (p. 21). Even on July 23 and 24 in the cold summer of 1916, when Calanus was reasonably plentiful over the southwestern part of Georges Bank generally, it was represented by only an occasional specimen a few miles outside the 100-meter contour, where the general aspect of the plankton was more oceanic (station 10352).

During the cold half of the year Calanus spreads somewhat farther offshore. It may even be extremely plentiful along the southeastern slope of Georges Bank in early spring (p. 189), and on May 17, 1920, it was about as numerous at the outermost station off the western end of the bank (17,000 per square meter at station 20129) as in over the latter or in the neighboring part of the basin of the gulf to the north, but it is probable that very few Calanus exist at any season more than a few miles outside the 1,000-meter contour west of the longitude of Cape Sable.

The regional distribution of Calanus is so irregular, with particular swarms often so soon dissipated, and the relative abundance of the species in different regions is in a state of such constant change, that it is not safe to postulate a typical rule for it from its quantitative distribution at any given time; but sufficient data have now been accumulated over a period of years to show (*a*) that *Calanus finmarchicus* is far more plentiful in the open waters of the gulf than in estuarine situations or among the islands, and usually most plentiful some miles offshore; (*b*) that the coastal belt inside the 100-meter contour, from Cape Ann northward and eastward to the mouth of the Bay of Fundy, is a zone of comparative scarcity for it, as contrasted with the Massachusetts Bay region, the basin as a whole, or the northern parts of Georges Bank; and (*c*) that the chief center of abundance is in the southwestern part of the gulf, along Cape Cod, off Massachusetts Bay, in the neighboring parts of the basin, and as far northward as the region of the Isles of Shoals. The eastern basin, the northern channel, and the neighborhood of Cape Sable are secondary centers, where Calanus is occasionally extremely plentiful, but we have never taken it in frequencies as great as 100,000 per square meter anywhere else within the gulf (fig. 66).

In 1920 the stock of *C. finmarchicus* increased slightly throughout the coastal zone generally between Cape Cod and Mount Desert from March to April, raising the average numbers per square meter for this region from about 1,800 to about 5,000.[97] At the head of Massachusetts Bay, off Boston Harbor, there were something like four hundred times as many Calanus on April 6 (station 20089, 1,250 per square meter) as on March 5 (station 20062, only 3 *C. finmarchicus* per square meter). On the other hand, the *Albatross* found fewer Calanus in the eastern basin of the gulf generally in April (average about 2,540 per square meter) than in March (aver-

[97] Eight stations for March and 11 for April.

age 7,320 per square meter), though the difference is perhaps not great enough to be significant in the case of a planktonic animal so usually occurring in swarms or streaks which the net may chance either to hit or to miss.

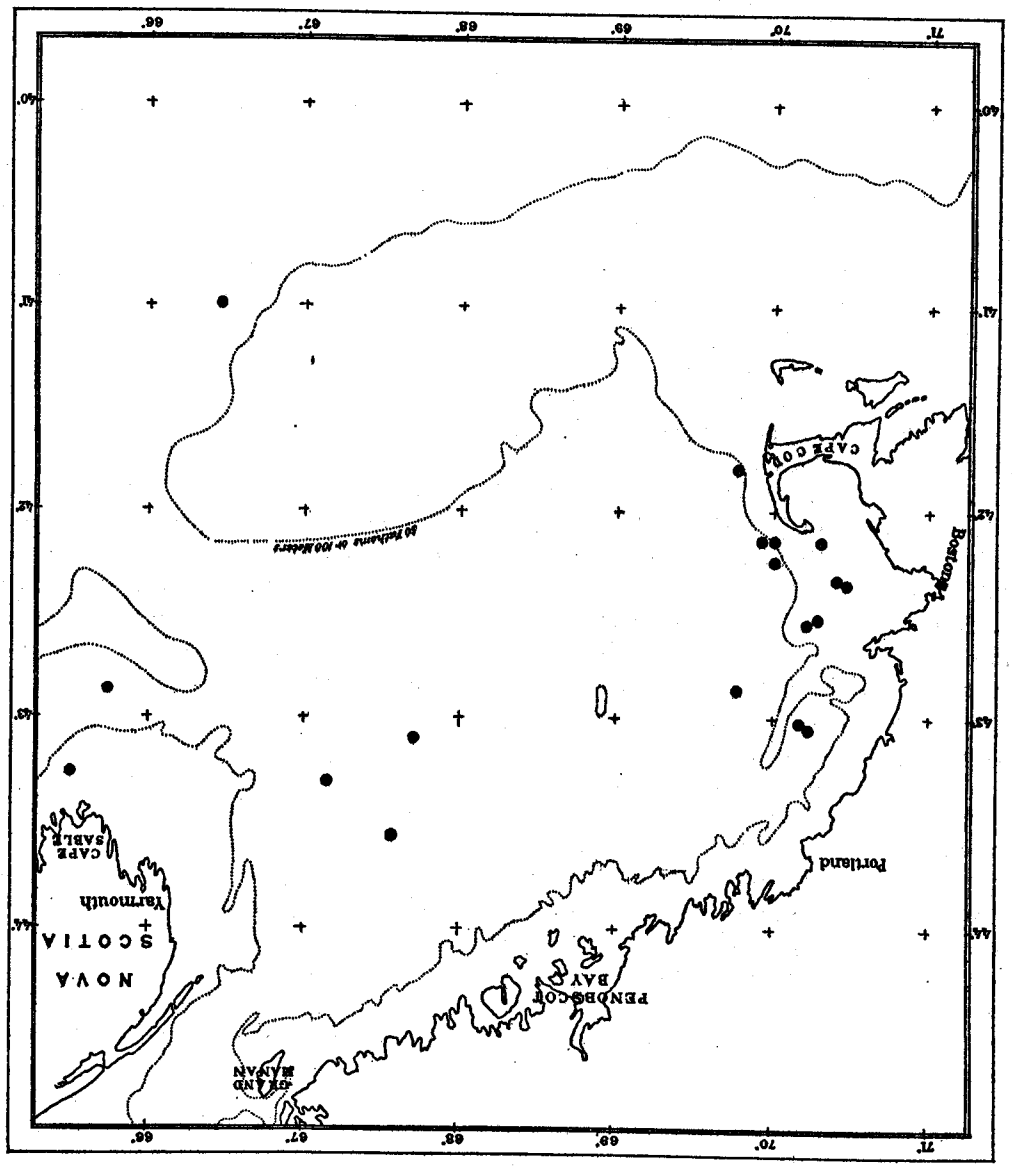

FIG. 66.—Localities where the vertical hauls have taken more than 100,000 *Calanus finmarchicus* per square meter of sea area, all years and seasons, including July stations for 1916, where an assumed percentage of 70 per cent Calanus in the vertical hauls indicated more than 100,000 per square meter

The dissipation of the swarm existing off the southeastern slope of Georges Bank in March has been noted (p. 190). Over the eastern end of the bank *Calanus finmarchicus* increased eight to ten fold from March 12 to April 16, by the evidence

of the vertical hauls, and three-fold on Browns, but decreased by about that same proportion in the eastern channel, a change probably too small to be significant. In the western basin the average number of *C. finmarchicus* at all the stations was practically the same in April (about 13,000 per square meter) as in February and March (about 12,000), but an equalization of the species had taken place.

The augmentation of the stock of *C. finmarchicus* that takes place during the later spring is the most notable event in the seasonal history of the animal plankton of the gulf. In 1920 this multiplication of Calanus began in the Massachusetts Bay-Cape Cod region by the middle of April, as I have just pointed out (p. 41), and by the first week in May it had progressed sufficiently to raise the numbers per square meter to an average of 19,000 for all the stations from near Cape Ann out across the western end of Georges Bank.

In 1913 no notable increase of Calanus was observed in Massachusetts Bay until the first week in May; this was first evidenced in Gloucester Harbor, where on the 3d Welsh found the water "reddened for areas of about a square yard, several yards apart, with what proved to be swarms of copepod nauplii and young copepods. And on the 17th, hauls off Magnolia, Mass., yielded great numbers of small copepods, chiefly *C. finmarchicus.*" (Bigelow, 1914a, p. 407.)

In the spring of 1915 the vernal augmentation of Calanus either commenced earlier in the season than in 1913 or 1920, or proceeded more rapidly, for on May 4 the vertical net took it at the rate of 459,900 per square meter off Gloucester (station 10266), this being the greatest number ever counted in the gulf. It was only slightly less numerous in the eastern basin off German Bank on the 6th, and the average number per square meter for a belt right across from the Massachusetts Bay region in the west to German Bank and Lurcher Shoal in the east was about 150,000. It is probable that the multiplication of Calanus does not proceed so rapidly in the northern parts of the gulf, though it may commence there as early as mid-April (p. 41), the June counts off Penobscot Bay and eastward [98] ranging from only 7,500 to 21,000 per square meter for 1915. Probably a fairer concept of the late spring status of the species, both numerically and regionally, would result from the union of the May with the June counts despite the disparity in date, which gives an average of about 96,000 per square meter for the whole gulf north of a line Cape Cod-Cape Sable, or about 63,000 if the vertical hauls for May, 1920, be included. Although this calculation may very well be 100 per cent out of the way, due to faults inherent in the process of estimation and to the paucity of stations, at least it shows that the stock is many times as great in late spring and early summer as it is in winter or during March and April.

It is not possible to follow the seasonal fluctuations of *C. finmarchicus* at close intervals through the summer for want of sufficient data for late June and July, nor have the percentages in which the species occurred been determined for the vertical hauls for August, 1912 or 1914. This was done for the vertical hauls for August, 1913 (Bigelow, 1915, p. 286), and for most of the horizontal hauls at various depths for stations for 1912 and 1914, when the total numbers of copepods were calculated from verticals. With Calanus so greatly preponderating over all other copepods

[98] No vertical hauls were made in this part of the gulf in May.

combined, this will at least give an idea of the general status of the species. The average numbers of *Calanus finmarchicus* per square meter for all parts of the gulf combined have been as follows: July and August, 1912, about 45,000; August, 1913, about 28,000; July and August, 1914, about 55,000—results probably not far from the truth, judging from the evenness of the frequencies from summer to summer. About 30,000 to 40,000 specimens of this copepod would then be a reasonable expectation for the average frequency below each square meter of the surface of the gulf in midsummer, though actually with extremely wide variations from station to station—that is, from hardly a trace to upward of 200,000. This is a decrease by more than one-half from the most prolific period and region of May (p. 194) and a considerable shrinkage from the stock existing generally in the gulf in May and June. Correspondingly, the richest July or August catch for the period 1912 to 1914 was less than half the richest May catch, and while we have never found less than 7,000 Calanus per square meter in May, several August catches have contained fewer than 100. In some summers, however, the stock remains very high or may even continue to increase until well into July, as exemplified by the year 1916, when vertical hauls yielded an average of about 147,000 Calanus[99] (approximately 71,000 of them being large adults) among 210,000 copepods of all kinds for six stations in Massachusetts Bay, off Cape Cod, and in the southwestern part of the basin (Bigelow, 1922, p. 136).

In September, 1915, for which month vertical hauls were made at nine stations, including the Massachusetts Bay region, the average per square meter (about 35,900), with frequencies per square meter of 4,400 to 138,400, about equaled the expectation for August; but the individual counts, station by station, show a tendency toward dispersal of the local shoals of Calanus by the general circulation of water in the gulf during early autumn, resulting in equalization of the stock, a phenomenon which often accompanies, though is not necessarily a sign of, a cessation of active reproduction.

If the counts for 1915 may be taken as typical, Calanus may be expected to increase again in numbers from September to October, the average per square meter being about 51,000 for the latter month with three of the vertical hauls more productive than 100,000 and none producing less than 7,500. This period of reproduction, if it be one, must be brief, with the stock dwindling rapidly later in autumn, for the yields of the horizontal tows taken during December, 1920, and January, 1921, were uniformly scanty. The volume of the catches, however, suggest that *C. finmarchicus* was more evenly distributed over the inner parts of the gulf at that season than we have usually found it during its period of greater abundance in spring and summer. Unfortunately, however, these stations do not afford numerical data.

Density of aggregation.—Calanus finmarchicus, being the most plentiful copepod in the Gulf of Maine, and, thanks to its comparatively large size coupled with its numbers, by far the most important source of crustacean food for the plankton-feeding fishes, the local abundance in which it gathers is of importance in the natural economy of the region. The numbers present per square meter are not a direct index to this, for the specimens living under that or under any other unit of the

[99] Assuming Calanus to have constituted 70 per cent of the catch, which is probably below the actual figures.

surface of the sea may be scattered sparsely through a great depth or concentrated in a shoaler stratum, depending both on the depth of water at the station in question and on whether they are more or less stratified or are evenly distributed from the surface downward.

In spring the latter state may be said to apply generally down to 175 meters; and assuming that practically the whole catch (in the case of the deeper hauls) was made above that level, as seems justified for the reasons outlined above (p. 24), we arrive at an average of about 48 Calanus per cubic meter for March, 1920, and 69 for April, with extremes of 1 to 654 and 4 to 624, respectively, for these two months. Thus it seems that a slight general increase took place from March to April, cor-

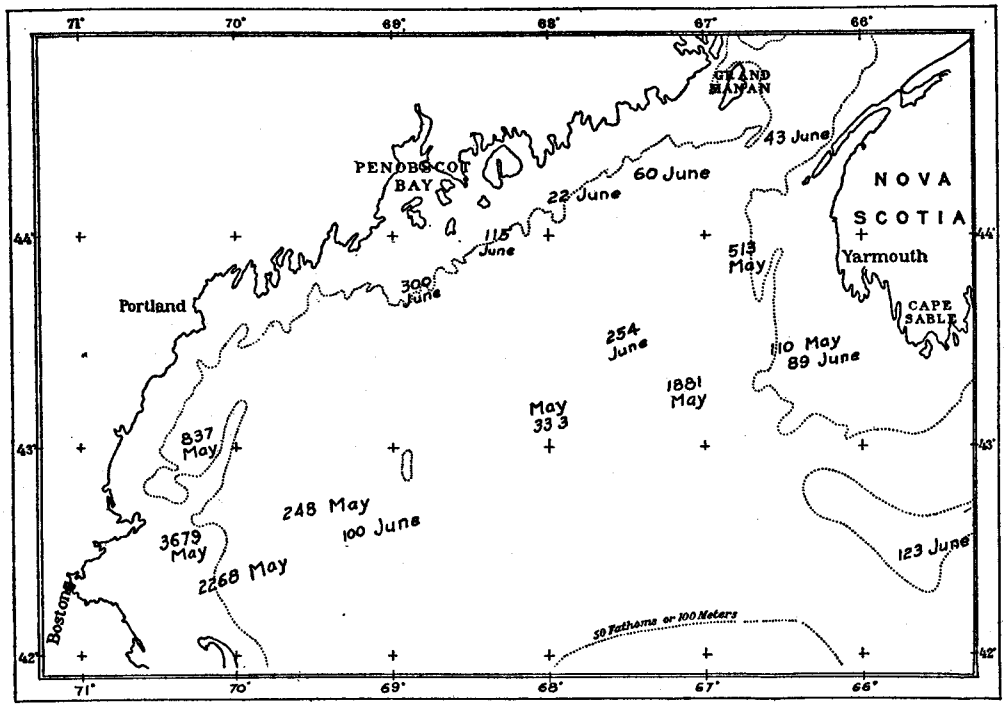

FIG. 67.—Numbers of the copepod *Calanus finmarchicus* per cubic meter of water in May and June, 1915, as calculated from the vertical hauls, assuming that all were living shoaler than 175 meters depth

responding to the beginning of the vernal wave of reproduction of the species, but irregularly from station to station and reversed at many stations, without apparent correlation between the relative density of aggregation and the depth of water or the locality in the gulf.

As might be expected, the great increase in abundance of this copepod which takes place in May is accompanied by a corresponding increase in the numbers present per cubic meter to an average of about 500 for all the May and June stations of 1915 and 1920 combined (fig. 67)—that is, to more than seven times the April average—and with a well-defined cleavage into "rich" and "poor" regions. In the western parts of the gulf and along a line toward Cape Sable Calanus then averaged

about 1,000 per cubic meter, with 2,300 and 3,700 at two stations at the mouth of Massachusetts Bay, these being among the densest aggregations of the species yet demonstrable from our vertical hauls.

In marked contrast to this rich region and to a second center of abundance in the eastern basin (1,900 per cubic meter), there was a sparse stock of Calanus along the coast of Maine east of Penobscot Bay (40 to 100 per cubic meter) in June, and it was only moderately abundant on Browns Bank (120 per cubic meter, station 10296).

In the cool year of 1916, when it is probable that the vernal cycle in the lives of planktonic animals lagged behind its normal schedule, Calanus was extremely plentiful in the Massachusetts Bay region and off Cape Cod in July, as already described (p. 195); and while the numbers per square meter fell somewhat short of the maximum for May, the numbers per cubic meter—both maximum and average—were slightly greater because of the shoalness of the localities where the vertical hauls were made.

Numbers of copepods and Calanus finmarchicus per cubic meter, assuming the latter to average 70 per cent of the former, July 19 to 22, 1916 [1]

Station	Depth in meters	Copepods per cubic meter	Calanus per cubic meter	Station	Depth in meters	Copepods per cubic meter	Calanus per cubic meter
10340	45	2,066	1,446	10345	150	930	651
10341	80	3,312	2,318	10346	62	2,987	2,791
10342	55	6,145	4,301				
10344	80	2,240	1,568	Average		3,113	2,179

[1] The exact proportions of the several species of copepods have not been determined as yet for these hauls, but preliminary examination suggests at least 70 per cent Calanus and probably more.

The copepod population being confined largely to the deeper layers, as evidenced by the comparative poverty of the surface catches, *Calanus finmarchicus* was evidently more densely aggregated locally than even these amounts per cubic meter would suggest. For example, the haul at 40 meters (station 10344), with the 1-meter net, yielded about 6 liters in 15 minutes, chiefly copepods, and contained upward of 2,500,000 large Calanus (Bigelow, 1922, p. 136). This compares favorably with 200,000 in a five-minute haul near Iceland, listed by Paulsen (1906) as one of his richest.

In the daytime the stock of Calanus at, say, the 10 to 30 meter level, becomes to some extent enriched by the tendency of this little crustacean to sink when the sun is high; at night it is correspondingly impoverished.

The July hauls for 1916 represent the richest Calanus pasture for mackerel, herring, etc., that has come to our notice, and hence may be regarded as containing about the maximum number per cubic meter to be expected in any part of the gulf at any season, except in years for some reason unusually productive. When and where this crustacean food supply is at its best, therefore, a plankton-feeding fish finds at least 2,000 Calanus per cubic meter at some level, and probably many more at others, for this copepod has often been reported in shoals. On such occasions every few mouthfuls of water taken by an adult mackerel, herring, alewife, or shad

would contain at least one and sometimes two or three large oily adult Calanus, even without the voluntary selection of such morsels which these fishes regularly practice, and the fish may be expected to be (and often are) packed full of this "red feed."

At any time from early May until midsummer there exists a sufficient stock of Calanus, which is dense enough in some part of the gulf to afford a bountiful food supply. Our hauls point to the outer part of Massachusetts Bay, with the neighboring waters along Cape Cod to the south, offshore to the east, and probably northward to Cape Elizabeth, as on the whole the subdivision of the gulf where it appears most abundantly during the spring and early summer, both absolutely and per cubic meter of water. Secondary centers of abundance have been recorded in the eastern basin, the northern channel, and off the southeast slope of Georges Bank, but the last of these was certainly transitory, (p. 193) and the others may have been equally so.

In warm summers, when the peak of abundance for *Calanus finmarchicus* has passed before July, fewer are to be expected per cubic meter. In August, 1913, when the percentage of Calanus in the vertical hauls was determined by Dr. C. O. Esterly (Bigelow, 1915, p. 286), this copepod averaged only 244 per cubic meter at 14 stations generally distributed over the northern half of the gulf, even assuming that all of them were taken above 175 meters, the figures being as follows:

Station	Number per cubic meter	Station	Number per cubic meter
10087	293	10098	91
10089	94	10099	324
10090	229	10100	309
10092	503	10101	411
10095	104	10102	176
10096	330	10103	274
10097	160	10105	123

The average at the Gulf of Maine stations inside the continental edge for July and August, 1914,[100] was about 600 Calanus per cubic meter, varying from less than 100 to upward of 2,000. These calculations show that in late summer most parts of the gulf offer by no means as fertile a feeding ground for the fishes that eat Calanus as it does two or three months earlier in the season.

In the offshore parts of the gulf there is less variation in the number of Calanus per cubic meter of water, from station to station, in August than in May, with no definite contrast between "rich" and "poor" regions; but in the coastal belt the extremes, represented by very barren hauls between Mount Desert Island and the mouth of the Bay of Fundy and by upward of 2,000 at one station close to Cape Sable (station 10243), are perhaps as far apart as at any season. The fact that Calanus about tripled in number at the locality last mentioned during the interval from July 25 (station 10230) to August 11, in 1914, shows that rapid changes take place.

Nine vertical hauls for September, 1915, distributed over the eastern half of the gulf along the coast of Maine and in Massachusetts Bay give an average of approxi-

[100] A table of the number of copepods and large Calanus per square and per cubic meter for that year is given in an earlier report (Bigelow, 1917, p. 315). The present calculation for 1914 is based on an estimated average of 70 per cent Calanus, which is probably below the true figure.

mately 300 per cubic meter, paralleling the calculations for August as closely as could be expected with an animal distributed so irregularly.

Numbers of Calanus finmarchicus per cubic meter, September and October, 1915

Station	Date	Depth in meters	Number	Station	Date	Depth in meters	Number
10309	Sept. 1	200–0	692	10324	Oct. 1	150–0	225
10310	Sept. 2	190–0	482	10325	Oct. 4	175–0	634
10311	do	60–0	205	10326	do	145–0	325
10315	Sept. 7	80–0	264	10327	Oct. 9	60–0	126
10316	Sept. 11	60–0	265	10328	do	60–0	237
10318	Sept. 16	70–0	63	10329	do	60–0	245
10319	Sept. 20	35–0	380	10336	Oct. 26	50–0	2,050
10320	Sept. 29	70–0	273	10338	Oct. 27	80–0	1,528
10321	do	40–0	170	10339	do	75–0	343
10323	Oct. 1	80–0	288				

Six stations between Massachusetts Bay and the mouth of the Grand Manan channel gave about the same average (298) for the first week of October, with but little variation from station to station (see table above), evidence that, as judged by the number per cubic meter—that is, the density of aggregation and availability for fishes—*Calanus finmarchicus* was distributed with comparative uniformity over the inner parts of the gulf during the late summer and early autumn of 1915, a year probably fairly representative. Vertical hauls off Cape Cod and in Massachusetts Bay on the 26th and 27th of the month yielded it in much larger numbers, rivaling the denser communities of the species in spring and early summer.

We have no data on this subject for the months of November, December, or January, but the catches of the horizontal nets, at depths of 15 to 240 meters during the cruise of December to January, 1920–1921, were so small that Calanus must then have been distributed very sparsely, indeed, and probably in no greater numbers per cubic meter than in March (if as great), judging from the volumes of the catches of the horizontal hauls, which consisted chiefly of copepods (see table, p. 304, for percentages of Calanus). Thus the whole Gulf of Maine supports a much sparser community of Calanus in winter and until May than it does from late spring to October, with the maximum density of aggregation for this copepod falling from May to July, the seasonal fluctuations in this respect paralleling those of the actual numerical strength of the local stock.

Percentage of occurrence.—The degree to which *Calanus finmarchicus* predominates over all other copepods in the Gulf of Maine basin may best be illustrated by the percentages of this species in the total catches of copepods. The vertical hauls of 1915 1920, and 1921, combined, averaged about 55 per cent *C. finmarchicus*, inclusion of the surface hauls for the spring of 1920 and the horizontals made during the summers of 1912 and 1914 bringing theprecentage up to about 60. Furthermore, *C. finmarchicus* is the only copepod that has occurred at every tow-net station in all parts of the gulf at all seasons and in almost every haul, vertical or horizontal, and the only one that we have ever taken in 100 per cent purity. The three instances of this among the surface tows for 1920 (stations 20100, 20111, and 20112, see table, p. 303) are not especially significant, the total catch being so small in each case that other less common species occurring side by side with Calanus might easily have been missed by the net.

Among 246 hauls, vertical and horizontal, for which the proportionate representation of different copepod species has been determined, 51 have contained 90 per cent or more of C. *finmarchicus*. At 12 of our 42 tow-net stations for July and August, 1912, this was the only copepod detected by Doctor Esterly in the subsurface hauls. Its dominating rôle in the copepod community of the gulf may be further emphasized by the statements that it has been an unusual event for any other species to form as much as 50 per cent of the catch, and that we have never found as many as 50,000 of any other copepod per square meter, though there are often upward of 100,000 Calanus.

The frequent dominance by *C. finmarchicus*, especially in spring and early summer, not only over other copepods but of the entire community of planktonic animals, is commented on in an earlier chapter (p. 37). If the seasons of 1920 and 1921 can be taken as representative, *C. finmarchicus* is at its lowest ebb (compared with other copepods, as well as absolutely) during January and February, when it constituted 30 to 90 per cent (average about 55 per cent for the two months) of the copepods caught in horizontal and vertical hauls in the inner parts of the gulf (tables, pp. 299 and 304), but only 2 to 10 per cent over the western end of Georges Bank or outside the continental edge to the southward. The average percentages for March (58 per cent) and April, 1920 (57 per cent), were about equal, but experience in 1915, 1916, and 1920 proves that the percentage of Calanus among the total copepods increases notably as the spring advances, consequent on the active vernal multiplication of this species (p. 194), which no other local copepod rivals. In 1920 the relative augmentation of *C. finmarchicus* far outstripped the general augmentation of the copepod community as a whole[1] in the southwestern part of the gulf and on the western portion of Georges Bank. The percentage of Calanus in the vertical hauls at the May stations for the two years combined averaged about 80 per cent for the more prolific parts of the gulf.

Direct comparison can not be made between the percentages for May and for June (average 56 per cent), because most of the stations for the latter month were located in the northern corner of the gulf, where we have not towed in May. Consequently, the difference may be a regional phenomenon, not seasonal.

The vertical hauls for August, 1913—14 in number—give an extreme range of from 87 per cent to 12 per cent Calanus, averaging 50 per cent, and 4 August hauls for 1915 average 46 per cent Calanus, suggesting that this species is proportionately less dominant in the general copepod population of the gulf in late summer than in spring. Forty-five horizontal hauls at various depths generally distributed over the gulf, including Georges Bank and out to the continental shelf, for July and August, 1914, averaged 71 per cent Calanus, with 100 per cent on several occasions, in both surface and deep hauls—that is, about the same percentage that resulted from the vertical hauls for May, 1920 (table, p. 302), and only slightly less than for that month in 1915 (table, p. 297). It is therefore doubtful whether any decided diminution in the percentage of Calanus, relative to other copepods, is a regular phase in its annual cycle in the gulf during the period June to August, though there may be a considerable variation in the percentage of Calanus from summer to

[1] Compare stations 20044 to 20047 with stations 20127 to 20129, table, p. 299.

summer, consequent on fluctuations in its actual abundance, and in the abundance of the other species of copepods. Twenty-one vertical hauls at as many stations for September and October, 1915, give an average of only 38 per cent and 42 per cent of Calanus, respectively—that is, little more than half of the May percentage.

The percentage of Calanus averaged somewhat higher in the horizontal hauls of December, 1920 (about 58 per cent; table, p. 304). However, this does not reflect an increase in the actual abundance of the species (which, on the contrary, decreases markedly in numbers during the late autumn and early winter), but a still more pronounced decrease in the local stock of other species of copepods. Thus, while curves for the actual and for the relative abundance (percentage) of *C. finmarchicus* would be similar for the spring, they would be contradictory for the September–December quarter, and to this extent the percentages taken by themselves would give a totally false picture of the seasonal fluctuations of the species in the Gulf of Maine.

From the economic standpoint this means that any copepod-eating fish in the Gulf of Maine is likely to make Calanus its chief diet from May until August and in October, but to depend less on it and more on other copepods during the early autumn and again in late winter and early spring.

The average percentages need further qualification to bring out the great irregularity in the relative abundance of the species which we have encountered from station to station on most of the cruises and from month to month at individual stations, irregularities connected with the streaky way in which *C. finmarchicus* often occurs, and with the formation and dissipation of its shoals. In Massachusetts Bay, for example, the percentage fell from 80 to 45 at one locality off Gloucester between March 1 and April 9, 1920, but increased from 6 per cent to 50 per cent off Boston Harbor, near by, during approximately the same interval. In the western basin, at three successive stations, the percentage of *C. finmarchicus* was 90 on February 23, 25 on March 24, 75 on April 18, and at three stations along a line running out from Ipswich Bay toward Platts Bank, on April 9 and 10, the percentages were alternately 75, 25, and 80. Seventy-five per cent of Calanus in the southwestern part of the basin on February 23, but only 2 per cent on the neighboring part of Georges Bank the same day, was evidence of a corresponding difference in the actual number of *C. finmarchicus* per square meter—respectively, 6,562 and 25—but on the southeastern slope of the bank the percentage fell only from an average of about 75 per cent on March 12 to 60 per cent on April 15, although this interval saw the dissipation of a very dense swarm of Calanus, occasioning a shrinking in the number per square meter from 103,000 to about 600.

Apart from the question of vertical stratification (p. 24), the percentages of Calanus have proved more nearly uniform over considerable areas in the later spring and summer. In early May, 1920, for example, it constituted 60 to 80 per cent of the copepods at most of the stations in the southwestern part of the gulf and on the western end of Georges Bank (table, p. 302). In July and August, 1914, its percentages in the horizontal hauls at most of the stations inside the continental edge approximated the average (71 per cent) for all the stations, irrespective of regional variations in the actual abundance of the species. In September and the

first half of October, 1915, considerable differences were noted in the percentages from station to station, but during the last week of the latter month the percentage of Calanus (50 per cent) was nearly uniform at the several stations off Cape Cod and in Massachusetts Bay. In December, 1920, and January, 1921, considerable regional differences obtained in the horizontal hauls, with extremes of 90 per cent of *C. finmarchicus* in the western basin (station 10490, table, p. 304) but only 10 per cent in the eastern basin (station 10502).

The only definite regional subdivision that can be drawn in summer, from the standpoint of the percentages of *C. finmarchicus*, is between the gulf proper (including its offshore banks) and the waters outside the continental edge. Calanus is usually dominant in the copepod community of the former, but is only a very minor element in that of the latter. Experience suggests that the farther out in the Atlantic basin abreast the gulf, the less important relatively and the less plentiful absolutely is this copepod. It is probable that this is equally true throughout the year, but it is certain that the line of demarcation lies farther out from the continental edge in late winter and spring than in the warm season, when the high salinities and temperatures of the inner edge of the Gulf Stream are closest in to the banks—witness the notable dominance of Calanus off the southeastern slope of Georges Bank in March and April, 1920, and the increase in its percentage in the catches off the western end of the bank from February (5 and 6 per cent) to May (80 per cent, station 20129; table, p. 303).

The data so far gathered show that this species may attain a very high percentage anywhere in the inner parts of the gulf. When the local copepod plankton is more intensively studied, characteristic regional differences may be developed there, too.

Vertical distribution.—The vertical distribution of *C. finmarchicus* in the Gulf of Maine varies somewhat with the season of the year. In spring, as exemplified by the February to May cruises of 1920, it was taken in all but one of the surface hauls, irrespective of the time of day. The numbers of specimens per haul do not suggest any diurnal migration upward by day and downward by night, such as this copepod carries out in summer (p. 204), the average being somewhat greater for hauls made between 7 a. m. and 6 p. m. (average, 521 Calanus per haul in February and March; 1,458 in April and May) than for those made between 6 p. m. and 7 a. m. (average 263 for February and March; 838 for April and May). Whether Calanus actually is as plentiful at the surface during the spring months as it is at the lower levels can hardly be determined from the data available.

Further evidence that the surface stratum is as productive of Calanus in spring as are the underlying waters is afforded by the average percentages of occurrence, which for the surface hauls [2] are about the same as for the verticals for the several months, and show a corresponding increase with the advance of the season (p. 201), as follows. Note, also, that the only spring hauls yielding 100 per cent Calanus in 1920 were at the surface (stations 20100, 20112, and 20113).

[2] Taken in hauls uniform in duration and in the diameter of the net employed.

Date	Percentage in surface hauls	Percentage in vertical hauls
March	53	58
April	63	57
May	76	80

It is probable that a certain number of *C. finmarchicus* exist right down to the bottom of the trough of the gulf in spring, as they do in summer, though no direct proof of this is yet at hand. However, were it as plentiful below, say, 175 meters as it is above that level, the deepest vertical hauls—that is, those filtering the longest columns of water—would on the average have yielded the largest catches of Calanus, which was not the case. Actually, the average numbers (about 11,000 per square meter) taken in 15 vertical hauls from depths of 200 to 340 meters in the basin, and in one off the southeastern face of Georges Bank from 1,000 meters,[3] during February, March, and April, 1920, were less than the yields of 20 shoaler vertical hauls from depths of 100 to 175 meters (average approximately 18,000 *C. finmarchicus* per square meter)—evidence that there were not enough Calanus below 175 to 200 meters to add appreciably to the catches. The two richest catches for March and April [4] were in hauls from depths of only 150 and 125 meters, respectively.

With the increasing intensity of the sunlight and progressive warming of the water which accompany the advance of the season, the surface stratum evidently becomes less favorable for Calanus, for in summer it is usually decidedly scarce or even wanting in the surface hauls, even at localities where it swarms a few meters down; but at other summer stations it has been taken in abundance at the surface. I have already pointed out (Bigelow, 1915, p. 290) that its absence on the surface in the regions where it swarms in deeper water is not caused altogether by sunlight, for while it probably does tend to descend during the most brilliantly illuminated hours, on several occasions we have made rich catches on the surface when the sun was high in the sky. Such was the case off the entrance to Gloucester harbor on July 22, 1912 (station 10012), when nearly a liter was taken in the 4-foot net on the surface at about 3 p. m. Again, on August 14, 1914 (station 10251), we made a rich surface catch of Calanus at about 2 p. m. off Cape Elizabeth; in July, 1916, a month when *C. finmarchicus* was notably abundant, surface hauls yielded considerable numbers off Cape Cod at 4 p. m. (station 10345), and off Marthas Vineyard at 5 p. m. (station 10351). Willey (1919, p. 181) records the presence of this copepod in abundance on the surface in the Bay of Fundy between 3 and 4 p. m. under a bright sun; but, as he further remarks, this is unusual. Willey suggests that in the Bay of Fundy the active stirring of the water by tidal currents may be instrumental in bringing the Calanus up at an hour when they ordinarily shun the surface, an explanation that may apply to the particular case in point but not to the other instances just mentioned, which were in regions of weak vertical circulation and certainly not of upwelling.

This station touched the swarm of Calanus already described for that location.

103,300 and 78,000 per square meter, stations 20068 (southeast slope of Georges Bank, Mar. 12) and 20105 (Northern Channel Apr. 15, 1920, station 20078).

Most of the other surface catches of Calanus in the gulf that can be classed as "rich" have been made during the hours after the sun has declined below an altitude of about 8 to 10°, or before it has risen that high in the morning. More specifically, five of these rich surface catches were at 6 to 7 p. m., two at 8 to 10 p. m., five at 10.30 p. m. to midnight, two at 1 to 2 a. m., and two at 6 a. m. Cases in point are stations 10024, 10027, 10038, and 10042 in July and August, 1912; a swarm off Gloucester on July 7, 1913; stations 10093, 10097, and 10100 in August, 1913; and stations 10246, 10247, and 10254 during August, 1914. Thus in the Gulf of Maine Calanus shows some tendency in summer to diurnal migration upward toward the surface at the approach of sunset, which it deserts after sunrise in the morning. Esterly (1911a, p. 142), in his study of the diurnal migrations of *C. finmarchicus* at San Diego, Calif., where the surface was practically barren of it during the day, found it "overwhelmingly more abundant at the surface about twilight or immediately after" than at any other hour, with its plurimum at about 7 to 8 o'clock in the evening; but the fact that we made as many rich catches about midnight as about sunset suggests that in the Gulf of Maine it is as likely to swim upward at one hour of night as another. It has been as scarce at the surface at most of our night stations, even when plentiful deeper down, as it usually is in the daytime, evidence that the vertical movement is only carried out at particular times and places, or that it usually fails to bring any large percentage of the Calanus right up to the top of the water. For example, "Calanus certainly did not come to the surface off Cape Cod during the night of August 5 [1913], for surface hauls taken at 2 a. m. and at practically the same locality at 8 a. m. (station 10086) yielded very few Calanus, although the deep haul caught thousands" (Bigelow, 1915, p. 290). Other instances of the same sort for other hours between sunset and sunrise might be mentioned.

Our few stations (10399 to 10404) in the western part of the gulf for October 31 to November 8, 1916, indicate a similar tendency on the part of Calanus to shun the surface by day but to ascend by night during the autumn as during the summer, for the one surface haul moderately productive of large Calanus was at 4 a. m. (station 10402), while juveniles were taken in numbers on the surface at 6 a. m. (station 10400). At the other stations (10 a. m., 2 p. m., and 3 p. m.) the surface hauls yielded few, though it was moderately plentiful at 50 to 180 meters.

During the winter, as the water continues to cool and the sun is low, the surface must gradually offer a more favorable environment to Calanus, resulting in its occurring as regularly and probably as plentifully there by March as deeper down, irrespective of the time of day. How early in the winter this takes place remains to be learned, however.

These observations corroborate Esterly's conclusion that when Calanus does carry out a vertical diurnal migration it is not induced thereto solely by the time of day, but that the direction of its vertical swimming (or sinking) is governed by geotropism, which changes with physiological changes in the animal itself. Esterly's experiments pointed to varying degrees of solar illumination as governing these changes, thus bringing its reactions into line with those of other copepods. (See, for example, Parker, 1902, on Labidocera.) This explanation, however, does

not cover its constant presence on the surface in the gulf at all hours of the day in spring, contrasted with its absence from the surface by day in autumn (p. 204), the illumination being about as bright at the one season as at the other.

It is possible that temperature, combined with light, may be a factor in the case—that is, Calanus may tend to sink in warm, brightly illuminated water, but to rise in pale illumination, irrespective of its temperature—but until this interesting subject has been studied more thoroughly I need only emphasize that the reactions of Calanus in their local application to the gulf result in its being far less plentiful in the surface stratum than below 10 meters or so by day, and often by night, during the half of the year when the temperature is highest and the solar illumination brightest.

Horizontal hauls locate the zone of chief abundance for this copepod in the gulf at 25 down to about 100 meters depth during the months of July, August, and September, showing that it tends to avoid the deepest waters of the gulf in summer as well as in winter and to congregate in the mid depths. I have pointed out elsewhere (Bigelow, 1915, p. 290) that in the summer of 1913 much larger catches of Calanus usually were made in hauls from 30 to 40 meters than from 100 to 170 meters at stations where we towed at three levels—surface, intermediate, and deep—with the shallower catches "usually two to four times as large in bulk as the deep ones, a difference too great to be charged to the difference in mouth area between the 4-foot and the Helgoland nets. And this source of error was further checked by occasionally alternating the two nets." The only exceptions to this rule during that cruise were at three stations in the eastern half of the gulf (10093, 10097, and 10100), where Calanus was about equally abundant in the deep and shallow hauls and plentiful right up to the surface. Again, on July 19, 1916, a much larger quantity of *C. finmarchicus* (upward of 1½ liters) was taken in Massachusetts Bay in the 30–0 meter haul than at 83–0 meters. The next day a 40–0 meter haul off Cape Cod (station 10344) yielded upward of 2,500,000 large Calanus (Bigelow, 1922, p. 136),[5] not to mention smaller ones, while the 88–0 meter haul took not over one-twelfth as many, estimated by their bulk (6 liters in the one case and less than one-half liter in the other).

The catches of Calanus in the open horizontal nets likewise averaged from two to three times larger from above 100 meters than from greater depths during the cruise of July and August, 1914; and though stations 10246, 10248, and 10254 were exceptions, with several times as many Calanus and other copepods taken in tows at 150 to 225 meters as at 50 to 75, it was only above 100 meters that notably large catches were made (Bigelow, 1917, p. 312).

The chief zone of abundance for *C. finmarchicus* in the Norwegian Sea also lies above 200 meters (Damas, 1905, p. 11), with about 400 meters as its lower limit. Around Iceland Paulsen (1909) found it in great abundance down to 500 meters; Nordgaard and Jørgensen (1905) record it as most plentiful at 200 to 300 meters in the Norwegian fjords in winter; and Damas and Koefoed (1907) found it down to at least 1,200 meters depth between Norway, Spitzbergen, and Greenland.

[5] Our largest catch of large Calanus.

In the San Diego region Esterly (1911) took it in abundance as deep as 400 to 500 meters, to which depth diurnal migration was effective.

Physical factors offer no apparent explanation for the comparative scarcity of Calanus in the deepest water of the gulf as compared with the intermediate levels, both temperature and salinity being well within the optimum for it; and it is more likely that the cause lies in the distribution of the food supply, Calanus tending to congregate at the levels where the microscopic plants on which it feeds are most abundant.

Reproduction.—It is now well known that *Calanus finmarchicus* deposits its eggs singly in the water, where they float until the young copepod hatches in the "nauplius" stage. Being of characteristic appearance (Damas, 1905), Calanus eggs are easily recognized in the plankton. The larval stages are distinguishable by the number of thoracic and abdominal segments and developed legs, as well as by their size. The stages are described by Lebour (1916). Damas's (1905) notation of them, now generally adopted, is as follows:

Stage	Thoracic segments	Abdominal segments	Fully developed legs
I	2	2	2
II	3	2	3
III	4	2	4
IV	5	3	5
V	5	4	5
VI, adult female	5	4	5
VI, adult male	5	5	5

The proportionate numbers in which the different stages in development have occurred in the many samples, American and European, which have now been studied by various authors, indicate that *C. finmarchicus* passes most of its existence in the late postlarval stages, living only for a short time as an adult, to perish shortly after breeding; but much is yet to be learned of its breeding habits in detail.

Only a few scattered observations have been made on the occurrence of eggs or juveniles of *C. finmarchicus* in the Gulf of Maine; enough, however, to show that it is regularly endemic there and that the local stock is chiefly the product of reproduction in the Gulf, though more or less recruited by immigration from colder waters to the east and north.

As previously remarked (p. 194), swarms of copepod nauplii and young copepods appeared off Gloucester during the first week of May, 1915, a decided increase in juvenile Calanus took place in the neighborhood of the Isles of Shoals during the first half of the month, and there were great numbers of young Calanus in Massachusetts Bay off Magnolia on the 17th. In 1920, again, copepod nauplii newly hatched swarmed in the surface waters of the bay on May 4 (stations 20120 and 20121, fig. 27 and 28), and on the 16th juveniles of *C. finmarchicus* were identified among a rich catch of young copepods off Gloucester (station 20124).[6] The fact that the Calanus that swarmed off Cape Ann on May 4, 1915 (p. 297), were mostly in the younger, intermediate stages of growth is sufficient evidence that a production

[6] These juvenile stages were taken chiefly on the surface and in some abundance in the vertical hauls as well (see table, p. 297).

of nauplii such as that just mentioned does actually presage the great augmentation of *C. finmarchicus* that takes place in that side of the gulf during the late spring and early summer. In other words, the Massachusetts Bay region and neighboring waters are actually important centers of reproduction for the species, and of growth, leading to a dominance of adults in July. Willey (1921) has remarked that this part of the Gulf of Maine would seem to be the southern headquarters for the production of *C. finmarchicus* in the northwestern Atlantic, and it is not unlikely that the Calanus population of the gulf as a whole originates chiefly in the area bounded by Cape Elizabeth on the north, Cape Cod on the south, and the western basin offshore.

Judging from the data for 1915 and 1920, the production in this region must be very large to account for the local abundance of this copepod in May and July, but it is probably not to be compared with the tremendous production that takes place in the Norwegian sea, for Calanus eggs have not occurred in notable numbers in any of the samples in question,[7] whereas Damas (1905, p. 12) describes them as locally so abundant between Norway and Iceland that in certain regions they are one of the principal elements in the plankton, even to the exclusion of everything else.

No attempt has yet been made to determine the presence or absence of the early stages of *C. finmarchicus* in the samples from other parts of the gulf. Probably it breeds to some extent over the whole of it (Willey (1921) mentions juveniles in Passamaquoddy Bay in April), but the preliminary study of the tow nettings points to the region just outlined as by far the most productive center of local production. It is also safe to say that spring, from late April on, is the chief breeding season for Calanus in the gulf, and that breeding probably continues actively through June to account for the abundance of juveniles in various stages which we found off Cape Cod on July 9, 1913 (station 10057; Bigelow, 1915, p. 291),[8] and in Provincetown Harbor on July 20, 1916 (station 10343). It is certain that no production comparable with the vernal wave takes place later in the summer, though positive evidence (in the form of eggs and juveniles) as to whether Calanus spawns at all in the gulf during July, August, or September is yet to be sought among the masses of copepods collected on our cruises. Doctor Esterly's [9] report of many juveniles at two stations off southern Nova Scotia on July 29 and August 6, 1914 (stations 10235 and 10237), shows that Calanus breeds well into the summer east of Cape Sable.

In 1915 the increase in the numbers of *C. finmarchicus* in the gulf during early autumn was preceded during the first half of September by an abundance of development stages of copepods in the tow. (See table, p. 298.) If these larval stages actually were *C. finmarchicus*, as seems probable from the constant dominance of the copepod fauna by that species, this points to a second but less productive breeding season in autumn, an interpretation corroborated by the presence of a large proportion of juveniles of this species in the surface tows near the Isles of Shoals and in the western basin on November 1, 1916 (stations 10400 and 10401). Development stages of some copepod were likewise recorded in comparative abundance for January, 1921,

[7] No special attention has yet been paid to the eggs in the Gulf of Maine tow nettings—a task for the future.
[8] These were identified by Dr. C. O. Esterly.
[9] In a letter.

by Dr. C. B. Wilson (table, p. 305), but the fact that no decided multiplication of the later stages of Calanus takes place during late winter (p. 39) suggests that these belonged to some other species of copepod and that *C. finmarchicus* breeds little, if at all, in the gulf from September or October until the following April.

In north European seas generally, where the biology of this copepod has attracted the attention it deserves, it is primarily a spring or summer breeder, the spawning season commencing soon after vernal warming of the water is appreciable and consequently varying with latitude and with oceanic conditions. Thus Gran (1902) found it in full breeding condition on the northwestern coast of Norway (latitude about 67° N.) in April and May; Damas (1905) in June in the Norwegian sea, where the Arctic and Atlantic currents meet, and in May and June around the Faroes. Paulsen (1906) states that the reproductive season south of Iceland lasts from March into June; Damas and Koefoed (1907) describe this copepod as spawning in late June along Norway and in the fjords of Spitzbergen; while With (1915) found it in breeding condition in June in Denmark Strait, in May south of Iceland, in June and July off West Greenland, and as late as the last days of July off eastern Greenland. Thus With justly interprets the term "spring," as descriptive of the chief breeding period of *C. finmarchicus*, to mean the period at which the waters reach a certain temperature and salinity, and which varies according to the latitude from March (February?) to August (east Greenland). The April to June spawning in the Gulf of Maine thus parallels the breeding period of this copepod in the southern parts of the northeastern Atlantic area.

Although most European authors have credited *C. finmarchicus* with one comparatively brief period of reproduction annually, Paulsen (1906), with whom With (1915) agrees, has pointed out that it probably breeds to some extent at other seasons also in Norwegian and Icelandic waters, just as it certainly does in the Gulf of Maine, because adults of both sexes have been found at other times of year almost everywhere in northern seas where towing has been carried out at appropriate depths.

If it proves characteristic of *C. finmarchicus* to have two distinct periods of active reproduction in the Gulf of Maine—a major in spring and a minor in autumn—as a preliminary study of our samples suggests, and only one in north European and Arctic seas, the difference may simply be one of latitude, the first spawning occurring so early in the year in the gulf and autumnal cooling commencing so late that there is opportunity for a part of the product of the spring hatch to mature and breed before the temperature of the water falls too low for sexual development. Thus, it is probable that for most of the stock breeding is an annual event and the individuals survive for a year; for others it is biennial, with the autumn hatch passing the winter in the late postlarval stages, as Paulsen (1906) suggests, and enough irregular reproduction taking place at any time from early spring until well into the autumn to maintain the variety of stages in development that have been seen throughout the year. More intensive study of the Gulf of Maine samples may be expected to throw light on this question that would be important not only as bearing on the life history of the species but with regard to the natural economy of the gulf, of which *C. finmarchicus* is the most important planktonic inhabitant.

The chief value of the foregoing notes on the reproduction of Calanus is their demonstration that this copepod is regularly endemic in the gulf just as it is in the Gulf of St. Lawrence (Willey, 1919). How far west of Cape Cod Calanus breeds in any abundance is still to be determined. Judging from its constant presence off southern New England (p. 188) and from the fact that juveniles were numerous over the inner part of the shelf off Long Island and off New York on August 1 and 26, 1916 (stations 10362 and 10396; Bigelow, 1922, p. 143), it is probable that considerable production takes place that far west. The rich catches of Calanus made farther south during that summer consisted in the main of very large individuals, which apparently did not succeed in reproducing to any extent because young stages were scarce or absent west and south of Cape Cod in the following November.

There is reason to believe that the Calanus stock of the eastern part of the Gulf of Maine is recruited to some extent by immigration around Cape Sable from more northerly breeding centers. Thus, a swarm of large Calanus with comparatively few young stages, in the eastern basin on May 6, 1915 (station 10270), might (so far as internal evidence goes) as well have represented an immigration as a late stage in a local reproduction cycle, the unmistakable westward extension of the Nova Scotian current at the time giving the first alternative an *a priori* probability which our failure to find any great production of young Calanus in this region in April, 1920, tends to corroborate. The swarm off the southeast slope of Georges Bank in March, 1920, had probably drifted thither from the east or northeast.

At present it is impossible to state how regularly such immigrations into the gulf take place, or their precise source, but it is probable that in the maintenance of the stock of this copepod existing in the Gulf they are of far less importance than local production.

Such data as are available suggest, furthermore, that the northern and eastern parts of the gulf are kept supplied with Calanus chiefly by the dispersal of the swarms of young produced in the southwestern side, the general circulation of the gulf indicating a general anticlockwise drift eastward along the northward side of Georges Bank and thence northward and westward around the gulf. Nor is a drift of this sort inherently improbable, for Calanus regularly carries out far more extensive involuntary migrations from its chief breeding centers in north European and sub-Arctic seas.

Relationship to temperature and salinity.—Most authors have described *C. finmarchicus* as eurythermal, which is certainly true within very wide limits. In the Gulf of Maine it occurs regularly over a range of from fractionally above 0° to 20° (station 10254, surface, Calanus plentiful). I do not know the highest range in which it has ever been found, but on August 30 and 31, 1913, the *Grampus* took occasional specimens (living) in 24.44° on the surface off Delaware Bay, where by sinking 20 meters or so it could have found much cooler water of 11 to 12° (Bigelow, 1915, p. 290). Although apparently it is able to exist in such high temperatures, much evidence has been accumulated to the effect that somewhat cooler water offers a more favorable environment for it, whether as it effects the growth of the Calanus itself, its reproduction, or its food supply. This was unmistakably the case in the

southern extremity of its range during the summer of 1916, when there was a very close correspondence between the limits occupied by abundant Calanus on the shelf south of New York, vertically as well as horizontally, and water of 4 to 7°. With one exception it swarmed only in water of 6° or colder (Bigelow, 1922, p. 143, figs. 45 to 47).

In general it may be said that along the North American seaboard *C. finmarchicus* is abundant and dominates the plankton only in temperatures lower than 12 to 15°, or where it can have ready recourse to water as cool as this by sinking or by swimming downward a few fathoms. The fact that in 1916 Calanus was not as definitely concentrated in the deeper water between Marthas Vineyard and Delaware Bay in November as in August, is in line with this general thesis, for the equalization in its vertical distribution corresponds to the vertical equalization of temperature (and of salinity) which takes place there in autumn; and it suggested that "the failure of the southern Calanus swarm to migrate to the surface during the mid-summer nights, as it so often does in the Gulf of Maine and elsewhere, was due either to the very high surface temperature, or possibly to the very low surface density" (Bigelow, 1922, p. 145). With the advance of autumn both these barriers are weakened by surface cooling, until in winter, thanks to the vertical uniformity of the water, the only physical factors governing vertical migration are sunlight and geotropism.

At the other extreme, while *C. finmarchicus* probably can survive in the very lowest temperatures obtaining anywhere at sea, the isotherm of 2° has been found to mark approximately the lower level to its regular occurrence in the northern part of the Norwegian Sea (Damas, 1905). Damas and Koefoed (1907) found it more plentiful in the intermediate strata in the seas between Spitzbergen and Greenland at temperatures of 1 to 2° and upward than in the colder water below.

It is probable that *C. finmarchicus* requires a somewhat higher temperature for its successful reproduction. Thus the abundance of early postlarval stages in the Gulf of St. Lawrence during June, July, and August (Willey, 1919) suggests that breeding takes place there chiefly after the end of May, by which season the upper 20 meters or so have warmed by several degrees from the winter minimum. This is certainly the case in the Massachusetts Bay region, where nauplii did not appear in any abundance in 1920 until the whole column of water, down to 70 meters, was warmer than 2.7° and the upper 25 meters warmer than 4.5°.

The relationship between the breeding range of this copepod and temperature is similar around Iceland, for in spring it spawns abundantly to the south of the island in water of 4° and upward; but apparently it does not do so at all to the north, where the temperature remains as low as 1 to 3° throughout May, though enough Calanus drift westward around Iceland to make this copepod extremely abundant along the northern coast in summer (Paulsen, 1906). As Damas and Koefoed (1907) have pointed out, *C. finmarchicus* is therefore less Arctic in its relationship to temperature than is *C. hyperboreus*, probably finding the lower limit to its active reproduction at about 2 to 3°; and the same for its rapid growth, though it is able to survive through long periods of lower temperature, growing slowly if at all.

C. finmarchicus is likewise indifferent to changes in salinity within wide limits, but I have been unable to learn that it is regularly abundant anywhere in water more saline than about 35.3 per mille[10] (Farran, 1910). Thus high salinity is probably a more effective barrier to its dispersal seaward abreast of the Gulf of Maine and thence southward along the continental edge of North America than is high temperature, though, to quote from an eminent student of this group (Willey, 1919, p. 176), "the factor which determines the limit of southern dispersion of *C. finmarchicus* is clearly neither a simple physical constant nor a single organic tropism," but "includes the biological factors of food-supply and propagation."

C. finmarchicus is regularly and abundantly present in considerably less saline water (31 to 33 per mille) in the western side of the North Atlantic than Farran (1910) set as the lower limit to its plentiful occurrence in the North Sea region (33.5 per mille), and apparently it was spawning actively in a salinity of only 29 to 30 per mille in Massachusetts Bay in May, 1920. Judging from its status in the entrances to the Baltic, however, and from its rarity within the latter, probably it can not exist long in water much fresher than this, though it may reach brackish situations as driftage.

Economic importance.—The importance of *C. finmarchicus* in the general economy of the Gulf of Maine and of all other seas where it abounds can hardly be overestimated. Certainly it is no exaggeration to call it the most important single planktonic animal, probably more important in the gulf in its relation to both larger and smaller organisms than all other copepods combined. It is the basic food for the local mackerel, and is certainly a major article in the diet of the herring, alewife, and shad while these are at sea. All the other fishes of the offshore waters of the gulf that eat plankton at all may be expected to feed on Calanus more than on any other single item. Through the medium of the herrings, which are nourished on it, Calanus helps support the finback and humpback whales, *Balænoptera physalus* and *Megaptera nodosa* (the only whalebone whales now common in the gulf), though neither of these feeds directly on copepods, their whalebone being too coarse (p. 97). On the other hand, it is probable that Calanus makes greater inroads on the planktonic plants on which it preys than do all other copepods combined, and conceivably it may practically exterminate them locally and temporarily.

Calanus gracilis Dana

Dr. C. B. Wilson contributes the following note:

This species has been reported from the western part of the Mediterranean and from the Indian and Pacific Oceans as well as the Atlantic. Cleve (1900), in discussing the distribution of Atlantic Copepoda, gave the northern and southern limits of this species as from the 44th parallel north to the 35th parallel south. The Gulf of Maine, therefore, is about its northern limit, and it would not be expected to appear in large numbers. Neither would it be widely distributed. It is worthy of note that Pesta has reported it from a depth of 1,200 meters in the Adriatic, while Giesbrecht gave 1,500 meters as the maximum depth limit. The few specimens found in the present plankton were obtained in October from shallow water rather close to the shore [at two stations off Marthas Vineyard and at one in Massachusetts Bay (see table, p. 298)].

[10] Willey (1919, p. 176) records abundant Calanus at a salinity of 35 per mille in the edge of the Gulf Stream between the Scotian and Newfoundland Banks on June 1, 1915.

This species was not found in the Woods Hole region by Wheeler (1901), nor did Dr. C. O. Esterly detect it among the tow nettings of the *Grampus* made between the Gulf of Maine and Chesapeake Bay during the summer of 1913 (Bigelow, 1915, p. 287), but Willey (1919, p. 218) reports it from two stations outside the continental edge off Cape Sable, July 22, 1915. It has no regular place in the fauna of the Gulf of Maine, where it is only a stray.

Calanus hyperboreus Krøyer

This is an Arctic species with its chief center of distribution in polar seas, where it is probably circumpolar and universal, having been taken at many localities off the northern coasts of Europe, Asia (to longitude 136° E.), and America (north coast of Alaska, Dolphin, and Union Strait; Willey, 1920). It is described by Damas and Koefoed (1907) as the commonest surface copepod in the Greenland sea. It drifts southward past Iceland with the east Icelandic current over a well-defined tongue (Farran, 1910), spreading thence in small numbers over the southern part of the Norwegian sea to the Skager—Rak and the southern Norwegian fjords, where Sars (1903) regards it as a "relict" species. A few are also carried southward in the cold bottom current across the Wyville Thomson ridge into the North Atlantic, where it has been recorded southward to latitude 51° N., longitude 11° 43′ W., off the mouth of the English Channel.[11] On the American side it occurs generally and abundantly over Davis Strait (With, 1915) and Baffins Bay (Aurivillius, 1896). Curiously enough, Herdman seems not to have had it on his two traverses of the Labrador current abreast the Straits of Belle Isle during the summer of 1897,[12] but the Canadian fisheries expedition of 1915 found it generally distributed over the Gulf of St. Lawrence as well as between Nova Scotia and the Newfoundland Banks and over the continental shelf along the Nova Scotian coast to abreast of Cape Sable. On their summer cruise, however, it was not found at the stations outside the continental edge west of Sable Island (Willey, 1919). It has been taken at many localities in the Gulf of Maine, shortly to be discussed, but Georges Bank and Cape Cod mark the limit to its occurrence as anything more than an accidental stray in this direction. South of this our only record for it is one specimen off Delaware Bay on August 12, 1916, in a haul from 70 meters (Bigelow,1922, p. 148).

Regional and seasonal occurrence in the Gulf of Maine.—Judging from our experience in 1915 and 1920, *Calanus hyperboreus* is, to all intents, universally distributed over the gulf during the late winter, early spring, and early summer. Thus it appears at about 80 per cent of the stations in Doctor Wilson's lists for February to May, 1920, at localities covering all parts of the gulf from the immediate coastal zone, on the one hand, out to the continental edge, on the other, and indifferently from the eastern side to the western, irrespective of the depth of water (fig. 68); and since a species as comparatively rare as *C. hyperboreus* might easily be missed by the vertical hauls, probably it was actually present at every station. Similarly,

[11] For further details see Gran (1902), Paulsen (1906), Damas and Koefoed (1907), and Farran (1910).

[12] Unless possibly some of the Calani listed by Herdman, Thompson, and Scott (1898) as *C. propinquus* were actually *C. hyperboreus*.

it occurred in the vertical hauls at all but one of the May and June stations for 1915 (table, p. 297), covering the basin and coastwise waters of the gulf and Browns Bank as well.

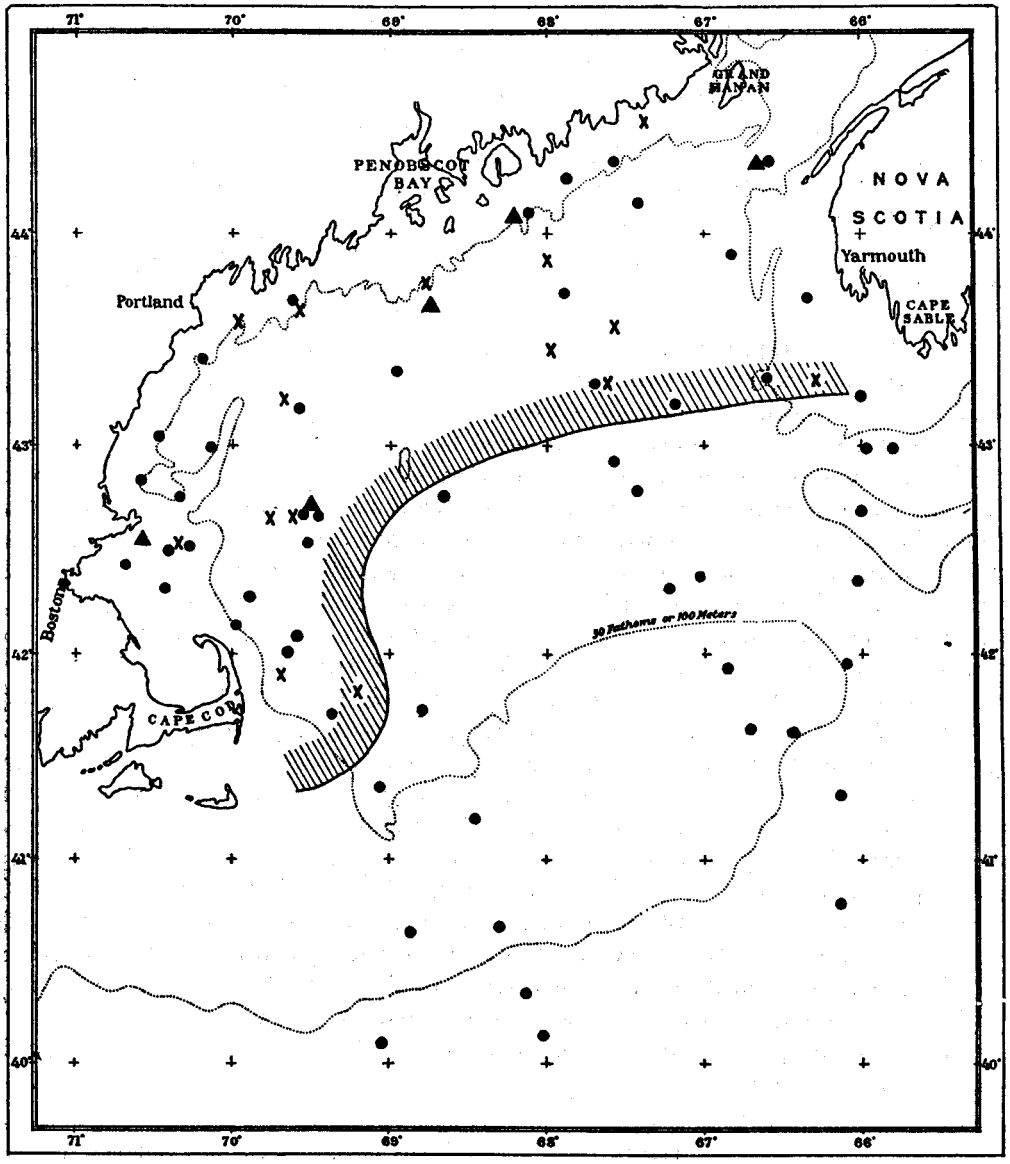

FIG. 68.—Occurrence of the copepod *Calanus hyperboreus* at different seasons. ●, locality records, February to May; X, July to November; ▲, December and January. The hatched curve marks the offshore limit to the occurrence of this species in summer

During the summer and early autumn it continues widespread in the northern and western parts of the gulf [13] over a belt some 60 to 70 miles wide paralleling the

[13] In addition to the localities marked (fig. 68), Willey (1921) found it forming about 8 per cent of a sample of copepods collected in a 10-fathom tow off Eastport, Me., Aug. 2 1916.

coast; but during the July and August cruise of 1914 we failed to find it at any station in the southeastern part of the basin, in the eastern and northern channels, on Georges or Browns banks, or near Cape Sable, indicating that at this season the *C. hyperboreus* of the Gulf of Maine are entirely cut off from the more northerly centers of abundance along the outer coast of Nova Scotia, though continuous with them and drawing from them by immigration earlier in the year (p. 217). During December and January it occurred in the horizontal hauls in the western basin, off Penobscot Bay, off Mount Desert Island, and in the Fundy Deep in 1920 and 1921 (table, p. 304); also at three stations off Gloucester in the winter of 1912–1913 (Bigelow, 1914a, p. 409); and Willey (1921) records it in some abundance in the mouth of the St. Croix River from November to February during the winter of 1916–17, but not in January, 1920, though two specimens were noted in a tow taken on the 25th of March in that year. Unfortunately our November–January cruises have not extended to the offshore banks.

Thus, the geographical range of *C. hyperboreus* in the gulf narrows from the sea shoreward in summer and expands offshore again at some time (just when remains to be discovered) during autumn or winter.

Numerically *C. hyperboreus* is never more than a minor element in the plankton of the gulf, though its economic importance may be considerable because of its large size. Thus the average percentage of *C. hyperboreus* at the stations where it was detected in the vertical hauls was only about 4.5 per cent for March, 1920; 7 per cent for April, 1920; 2 to 3 per cent for all the May stations; and 7 per cent for all the June stations (see tables, pp. 297 and 299). In July, 1915, it averaged 2½ per cent of three vertical hauls, and in 1913 about 1 per cent of two hauls (80 and 270 *hyperboreus* to 8,800 and 5,400 *finmarchicus*). In 1912 there was 1 *hyperboreus* to 50 *finmarchicus* in a sample from one station (10023), and 6 *hyperboreus* among thousands of *finmarchicus* in another (10040). On July 22, 1916 (station 10345) only one specimen was detected in a preliminary survey of some thousands of copepods and none at all at neighboring stations. Willey (1919), however, records 8 per cent of *hyperboreus* near Eastport in August. In December, 1920, and January, 1921, it averaged 3.5 per cent at the stations where it occurred (table, p. 304) but only about 1 per cent at all the stations combined. The maximum abundance of *C. hyperboreus* is 45 per cent, but this is at a station where the total catch of copepods of all kinds was extremely scanty (7,500 copepods per square meter off Gloucester on April 9, 1920, station 20090). The vertical hauls for 1915 and 1920 afford only eight instances of *hyperboreus* in percentages as great as 15 per cent.

The numbers per square meter—counting only the stations at which it occurred—are as follows:

Date	Average	Maximum	Minimum
February, 1920	583	1,125	25
March, 1920	403	4,162	0
April, 1920	804	9,100	0
May, 1915, and May, 1920	2,561	20,575	0
June, 1915	1,634	6,450	25

Evidently the numbers of *C. hyperboreus* existing in the gulf increase considerably from February to May and then decrease during June,[14] and later in the summer the species becomes so scarce that we have never found as many as 3,000 per square meter at any station [15] for July, August, September, or October, while none at all have been detected at most of the midsummer and autumn stations. The fact that *C. hyperboreus* has been detected at only about 10 per cent of the towing stations for July and August, notwithstanding its wide distribution at that season, contrasting with its presence at 80 to 100 per cent of the stations during March, April, May, and June (p. 212), is further evidence of its scarcity in the Gulf of Maine in summer. In 1915 it occurred at 10 per cent of the September stations and at one out of eleven stations east and north of Nantucket in October, while in December, 1920, and January, 1921, Dr. C. B. Wilson detected it at about one-third of the stations.

The regional distribution of the richer and scantier catches of *C. hyperboreus* proves interesting from the standpoint of the source of the local stock, whether endemic or immigrant. When the stations are plotted, where appreciably more than the average number per square meter for the respective months were taken, (fig. 69), it appears that during the season of maximum abundance for the species (March to June) it is usually most plentiful in three distinct localities—(1) in the Massachusetts Bay region and thence out to the western basin; (2) in the eastern side of the gulf from the northern channel (but not on Browns Bank) westward over the neighboring basin; and (3) along the southeast face of Georges Bank. In all other parts of the gulf, including the waters intervening between these "rich" centers—that is, all along the coasts of Maine, in the northeastern corner off the Bay of Fundy, in the central and southern parts of the basin, and over Georges and Browns Banks—*C. hyperboreus* has been uniformly much scarcer. Unfortunately the stages in development of the specimens taken in the vertical hauls, on which this chart is based, have not yet been determined; but such a distribution, coupled with the seasonal increase in the numbers of *C. hyperboreus* during the spring, would be presumptive evidence that the western center is a region of local production, drawing little from immigration but contributing to the stock in other parts of the gulf.

If such be actually the case, this would be by far the most southerly spawning ground for this species. Until Willey's (1919) account of the copepods of the Canadian fisheries expedition appeared, such a suggestion might have seemed highly improbable, *C. hyperboreus* having previously been known to breed only in the polar sea; but his discovery of young stages, besides adult females (but no adult males), in the gatherings at many localities in the Gulf of St. Lawrence, southeast of Nova Scotia, and along the continental shelf westward nearly to the longitude of Cape Sable, proved that the regular breeding range of this copepod extends much farther south along the American coast than it does off Europe. Willey has more recently reported adult males—previously known only from the far north—as well as adult females and younger stages at the mouth of the St. Croix River near St. Andrews,

[14] This statement is justified by the fact that the cruises for April, May, and June have covered the parts of the gulf most prolific in this species.

[15] Maximum for summer, 2,700 per square meter off Mount Desert Rock, Aug. 13, 1913, station 10100.

February 23, 1917 (Willey, 1921). He maintains that these individuals would not reproduce where found, but the presence of adults of both sexes of breeding age in

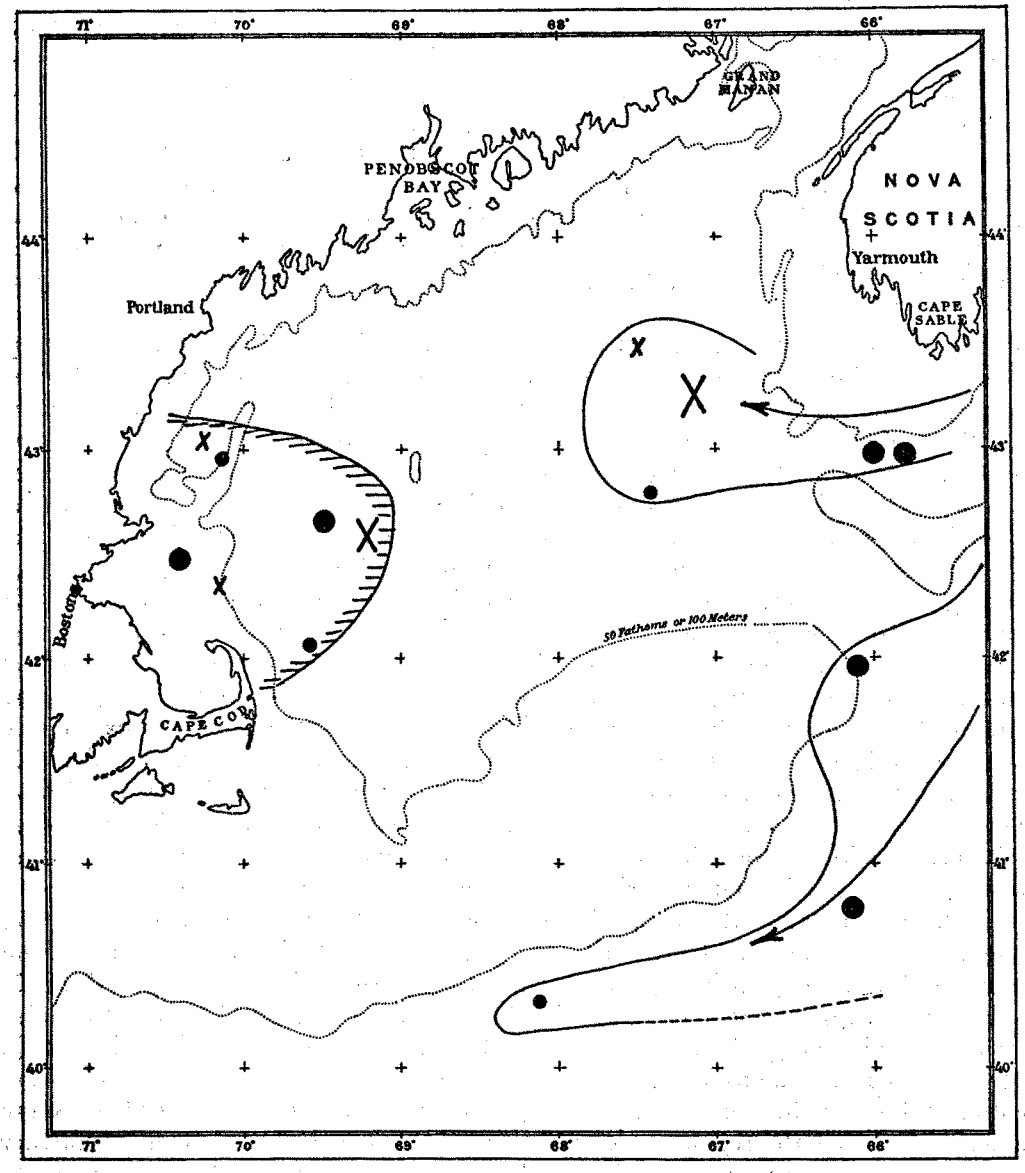

FIG. 69.—*Calanus hyperboreus*. ●, February to April stations with 50 per cent more than the average number per square meter for the respective months; ×, May and June. The large symbols mark three times the average catch or more. The plain curves and arrows indicate the chief lines of migration; the hatched curve the probable site of local reproduction within the Gulf.

the Bay of Fundy becomes more suggestive of local breeding if taken in conjunction with the existence of a more or less isolated center of abundance for the species off

Massachusetts Bay, and makes the hypothesis that the latter is actually a center of local production worthy of consideration.

The two eastern centers are indicative of immigration, being continuous with the more abundant occurrence of the species to the eastward along the outer coast of Nova Scotia. More direct evidence that the comparatively rich gathering made off the slope of Georges Bank on March 12, 1920 (station 20069), was such a wave from the northeast is the fact that it was no more plentiful there a month later (station 20109), though at most localities its numbers had about doubled in the interim (p. 214).

It is, furthermore, entirely consistent with the probable flow of the currents in this region in spring that there should be a drift of *C. hyperboreus* from northeast to southwest along the continental edge and perhaps over the southern edge of Georges Bank during March and April, continuing into June in some years, but the evidence at hand suggests that few pass west of longitude 70° at any season. The large catches in the northern channel and the eastern basin in March, April, and May, contrasted with the scarcity of the species at all our Browns Bank stations irrespective of season, point to the former as the chief route by which *C. hyperboreus* enters the Gulf of Maine. If the data for the two years, 1915 and 1920, can fairly be combined, it would seem that there is comparatively little movement in this direction before the end of April; but with *C. hyperboreus* relatively much more plentiful in the northern channel on March 20 (station 20078), and again on April 15 (station 20105), than in the neighboring parts of the gulf, invasion only awaited the first considerable movement of water westward past Cape Sable, which occurs by the first half of May, for the richest catch of the species yet recorded in the gulf was made in the eastern side of the basin on May 6 (station 10270).[16] A comparatively large catch (about twice the average for the month) in this general region six weeks later (station 10288, June 19) may have been evidence of continued immigration throughout May and into June.

There is nothing in the records of the distribution of the species for summer or autumn to suggest that *C. hyperboreus* rounds Cape Sable in appreciable numbers later in the summer; but to find it doing so would not be surprising, for the stock existing along the outer Nova Scotian coast during the warm months fluctuates so widely from year to year that Esterly did not detect it at all in the *Grampus* tows between the cape and Halifax during the last week of July and first week of August in 1914, whereas Willey (1919) records a moderate representation of the species over the shelf generally nearly to the cape in August, 1915. Willey (1921) has explained the presence of *C. hyperboreus* at St. Andrews in the winter of 1917 as an invasion.

Vertical distribution.—*C. hyperboreus* occurs to some extent on the surface in the gulf in spring (table, p. 303), but more regularly deeper down, appearing in the lists for about 80 per cent of all the vertical hauls during this period but in only about 50 per cent of the surface hauls, though the latter filtered much larger volumes of water. Counting all the stations at which surface hauls were made in 1920 (table, p. 303),

[16] Doctor Wilson's analysis of the catch made in the vertical net at this station proves my earlier statement (Bigelow 1917, p. 292) that *C. hyperboreus* was rare or absent in this general region at the time, to have been incorrect.

there were only about 2 per cent of *C. hyperboreus*, less than half its percentage in the verticals. In the two instances when the percentage rose to 25 and 30 per cent, 500 and 150 copepods of all kinds were taken—that is, only 125 and 45 *C. hyperboreus*, respectively. It has been detected in only one surface haul in the gulf for July, August, or September—that is, off Cape Elizabeth on August 14, 1913 (station 10103; see Bigelow, 1915, p. 293), a locality where the surface temperature was comparatively high (16.11°) and where it was probably brought up to the top of the water by vertical currents. The date when it abandons the uppermost stratum can not be stated, no data being available on this for the May and June cruises of 1915, but probably its sinking is induced by the vernal warming of the surface water.

Relationship to temperature and salinity.—As might be expected from its polar origin, *C. hyperboreus* occurs in greatest number and is most regularly distributed in the gulf in comparatively low temperatures, the great majority of the spring (February to May) records being from temperatures of 1 to 5°. It is doubtful whether any of the specimens taken in June were actually living in water warmer than 7°, and most of the few captures in the later summer have been in horizontal hauls at depths where the temperature ranged from 4.8 to 8°, only one of them in the much warmer surface stratum. The highest temperatures in which the presence of *C. hyperboreus* is definitely established, apart from the one capture on the surface just mentioned (p. 217), are 9 to 10°,[17] a temperature in which probably it could not long survive.

If *C. hyperboreus* actually does succeed in breeding in the western side of the gulf in spring and early summer, probably it does so exclusively in temperatures lower than 3 to 4°, the range of temperature at the rich March and April stations (stations 20087 and 20090, fig. 69) being from 2.25 to 5.09°, and the comparatively large numbers taken there on June 26, 1915 (station 10299), may be explicable as resulting from spawning some weeks or months previous when the temperature was no higher than that. The richest immigrations of *C. hyperboreus* into the gulf so far encountered have been in temperatures falling between 1.9 and 4.6°. It is not probable that the distribution of *C. hyperboreus* is influenced by variations in salinity within the limits prevailing in the open waters of the Gulf of Maine.

Candacia armata Bœck

This large and powerful species may be recognized by the asymmetry of the posterior part of the body, the genital segment being irregularly dilated in the middle, and the first segment of the abdomen having a sac-shaped dilatation turned toward the right side. The frontal margin between the bases of the antennæ is squarely truncated, also. It has been recorded from the coast of Norway, the British Isles, the Mediterranean, the North Atlantic, and the Indian Ocean (Scott, 1911), while Esterly[18] (1905, p. 194) described it as "rather common" at San Diego, Calif. The

[17] Off Penobscot Bay, Aug. 4, 1913, station 10101, temperature at 50 meters about 9.3°; off Seal Island, Nova Scotia, Sept. 2, 1915, station 10311, whole column of water, surface to bottom, 9.4 to 10.1°; off Machias, Me., Oct., 9, 1915, station 10327, whole column 9.4 to 9.8°.

[18] As *C. pectinata* Brady.

Grampus had it in fair numbers at three stations along the outer edge of the continental shelf south of Delaware Bay and off Delaware Bay in July and August, 1913, in hauls from about 40 meters' depth (Bigelow 1915, p. 287). Wheeler (1901) reported a considerable number of specimens of both sexes (as *C. pectinata* Brady) from the "Gulf Stream," 70 miles south of Marthas Vineyard, on July 25 and 29, 1899, and Willey (1919) counted two specimens among 100 copepods off the mouth of the Laurentian channel between the Scotian and Newfoundland banks on June 1, 1915, at a temperature of 10.2 to 13.75° and salinity of upward of 35 per mille. It did not appear in any of the collections made by the Canadian fisheries expedition on the banks or in the Gulf of St. Lawrence, nor did Herdman, Thompson, and Scott (1898) report it between the Straits of Belle Isle and Liverpool.

Candacia armata has not been reported from the Gulf of Maine previously, but Doctor Wilson lists it at two stations outside the continental edge on March 14 and May 17, 1920 (stations 20077 and 20129); also in the eastern part of the basin of the gulf on March 3 (station 20053) and on German Bank on April 15 (station 20103), from vertical hauls (table, p. 299). It likewise appears in one vertical haul in the eastern part of the basin for May, 1915 (station 10270), one off Cape Elizabeth for September (station 10319), and one off Cape Cod for October of that year (station 10336; table, p. 297), but not in any of the surface hauls.

The general geographic range of the species, as summarized above, and its distribution in British waters, where it is most plentiful in the English Channel and penetrates the northern part of the North Sea from the north around Scotland, point to an oceanic origin for the occasional specimens taken in the Gulf of Maine. The localities of record bear this out, being grouped in the eastern side and near shore in the western (fig. 62), like other visitors from the open basin, with no records in the western basin or from Georges Bank. It is a decidedly rare species in the gulf, usually amounting to 1 per cent or less of the copepods, only once reaching 4 per cent, and it is not likely that it is endemic there.

Centropages bradyi (Wheeler)[20]

Dr. C. B. Wilson, in a letter, describes it as "fairly common on the Atlantic coast off the mouth of Chesapeake Bay." Wheeler (1901) obtained both sexes in the Gulf Stream, 70 miles south of Marthas Vineyard, in July. Willey (1919) lists it at three stations outside the continental edge, along the inner edge of the Gulf Stream, off Cape Sable, and off Sable Island in July, 1915, and Esterly (1905) records it from San Diego, Calif.

This species has not been recognized previously in the Gulf of Maine, where it is to be expected only as a straggler from warmer waters offshore. In 1920 it was noted in one vertical haul off Cape Cod for March and one off Gloucester in May (table, p. 299); in 1915 occasional specimens were noted in the eastern basin on June 14 and near Cape Elizabeth on September 20 in vertical hauls. The numbers of specimens concerned are in each case minimal, 1 per cent being the maximum frequency.

[20] This name was given by Wheeler (1901, p. 174) to the species figured by Brady (1883) as *C. violaceus* Claus, but which, as Giesbrecht (1892) pointed out, is quite distinct. It is readily distinguished from the other two species of the genus mentioned here by lacking spines at the posterior corners of the thorax.

Centropages hamatus (Lilljeborg)

This species is so far known from the North Atlantic area between the latitudes of 40° N. and 70° N. (Scott, 1911), including the North Sea and the Baltic—most commonly within a moderate distance of the coast. Sars (1903) describes it as common along the whole west and south coasts of Norway, and, according to Scott (1911, p. 106), it is "one of the more common of the Calanoida met with in the North Sea."

On the American side it did not appear in the towings made south of New York during the summer of 1913 (Bigelow, 1915, p. 287) or 1916, but was taken off that port on August 26, 1916 (station 10394; Bigelow, 1922, p. 146), and near the Long Island shore on August 1, 1913 (station 10083), which, so far as I can learn, are the most southerly records for it along the United States coast. Northward it becomes more plentiful. Williams (1906) found it in Narragansett Bay in January and February, and it is "nearly always present in the tow at Woods Hole, in Vineyard Sound, and in the Gulf Stream south of Marthas Vineyard," writes Dr. C. B. Wilson.[21] Wheeler (1901) also records it as nearly always present in considerable numbers at Woods Hole. Its range includes the Gulf of Maine, as described below. Willey (1919) found it at many localities on the banks and over the deep intervening channel between Nova Scotia and Newfoundland in May, 1915, but not at the more oceanic stations, and restricted to the immediate vicinity of the Nova Scotian coast in July. It is widespread and plentiful in the shoaler parts of the Gulf of St. Lawrence (T. Scott, 1905; Willey, 1919), and Herdman, Thompson, and Scott (1898) report it from the Labrador current off the Straits of Belle Isle out to longitude about 53° W., and again between longitude 28° 24′ W. and the coasts of Great Britain, but not over the intervening stretch of ocean.

Gulf of Maine.—C. hamatus appears only twice in the published lists of Gulf of Maine copepods from the *Grampus* cruises—viz, occasional specimens off Boothbay on July 26, 1912 (station 10016), and off Cape Porpoise on August 18 of the same year (Bigelow, 1914, pp. 115, 116). It was not taken in the vertical hauls during June, 1915, and at only two of the four August stations (table, p. 298), proving it decidedly uncommon in the open waters of the Gulf during the summer, though it may be more plentiful in estuarine situations, where we have made few hauls. It appeared in about 60 per cent of the September verticals for 1915 (Willey (1919) lists it for 3 out of 10 stations near St. Andrews during that month), and it occurred at about half the October stations in the gulf east and north of Nantucket that year, off Gloucester on October 31 (station 10399) and off Cape Cod on November 8 in 1916 (station 10404; Bigelow, 1922, p. 135). No information is available as to its local status in November; but the fact that it occurred at about 50 per cent of the midwinter stations for 1920 and 1921 (table, p. 304) points to its constant and widespread presence throughout autumn and early winter. It was detected in only 2 of the 80 vertical hauls made in various parts of the gulf during the spring season of 1920 (table, p. 299), and there were less than 100 per square meter in every case.

During the month of October in 1915, *C. hamatus* averaged about 9,000 per square meter at the several stations where it occurred to the eastward and northward of

[21] In a letter.

Nantucket, and 7 per cent of the total catch of copepods; but it was much more plentiful, relatively as well as absolutely, in the shoal water south of Marthas Vineyard on October 21 and 22 (stations 10331 to 10333), with 12,240 to 58,500 per square meter (constituting 6 to 25 per cent of the total copepods), and was most numerous at the station closest to the land.

Numerical data as to the occurrence of *C. hamatus* are not available for the early winter, but it formed about the same proportion of the catches in the inner parts of the gulf (2 to 16 per cent, averaging 6 to 7 per cent), at the stations where it occurred in December, 1920, and January, 1921, as in autumn. It has never amounted to more than 1 to 2 per cent of the copepods at any station from February to the middle of September, nor has it been more numerous than about 4,000 per square meter. Obviously this suggests that *C. hamatus* is definitely seasonal in the gulf, occurring with some regularity from September until January but only very sparsely from February until August. Thus, even at the season and in the zone of its greatest abundance, *C. hamatus* is but a minor element in the copepod population of the gulf.

The regional distribution of the captures (fig. 70) is interesting, nearly all being near shore and the majority within a few miles of land, with not a single record anywhere in the central and southern parts of the basin or on Georges or Browns Banks. Although *C. hamatus* occurs across the whole breadth of the continental shelf off southern New England, on the one hand, and from Cape Sable eastward, on the other, its geographic range within the Gulf of Maine[22] has so far proved neritic, as contrasted with oceanic, and closely parallels that of the neritic medusæ (p. 33).

No observations have been made on the breeding of *C. hamatus* in the gulf, but the abundance of developmental stages of copepods of some sort during August and the first half of September, preceding the increase that takes place in the number of adults of this species and of its ally, *C. typicus*, during the last half of September, suggest that both of these species are regularly endemic in the gulf. If this be the case it breeds in comparatively high temperatures, stated tentatively as upwards of 7° in the gulf because of its neritic distribution, chiefly in salinities lower than 32.5 per mille.

Centropages typicus Krøyer

This species is described by T. Scott (1911) as a true Atlantic form, estuarine as well as oceanic. In the eastern Atlantic it occurs from the Mediterranean to northern Norway, being one of the common species in the North Sea region generally, where it often occurs side by side with *C. hamatus;* but it has not been reported from Arctic seas. In the western North Atlantic it has been found on the Louisiana coast of the Gulf of Mexico (Foster, 1904) and occurred commonly over the continental shelf as far south as the mouth of Chesapeake Bay during the summers of 1913 and 1916—was, in fact, the commonest copepod at many of the stations but chiefly in the uppermost stratum of water, as I have described in earlier reports (Bigelow, 1915, p. 293, and 1922, p. 146).

In July, 1913, the *Grampus* took it abundantly off New York, and although Williams (1906) does not list it from Narragansett Bay, Wheeler (1901, p. 173)

[22] Also plentiful in the eastern side of the basin on August 20, 1926.

describes it as "nearly always present in small numbers in the tow taken from the Fish Commission's wharf at Woods Hole and in the neighboring Vineyard Sound."

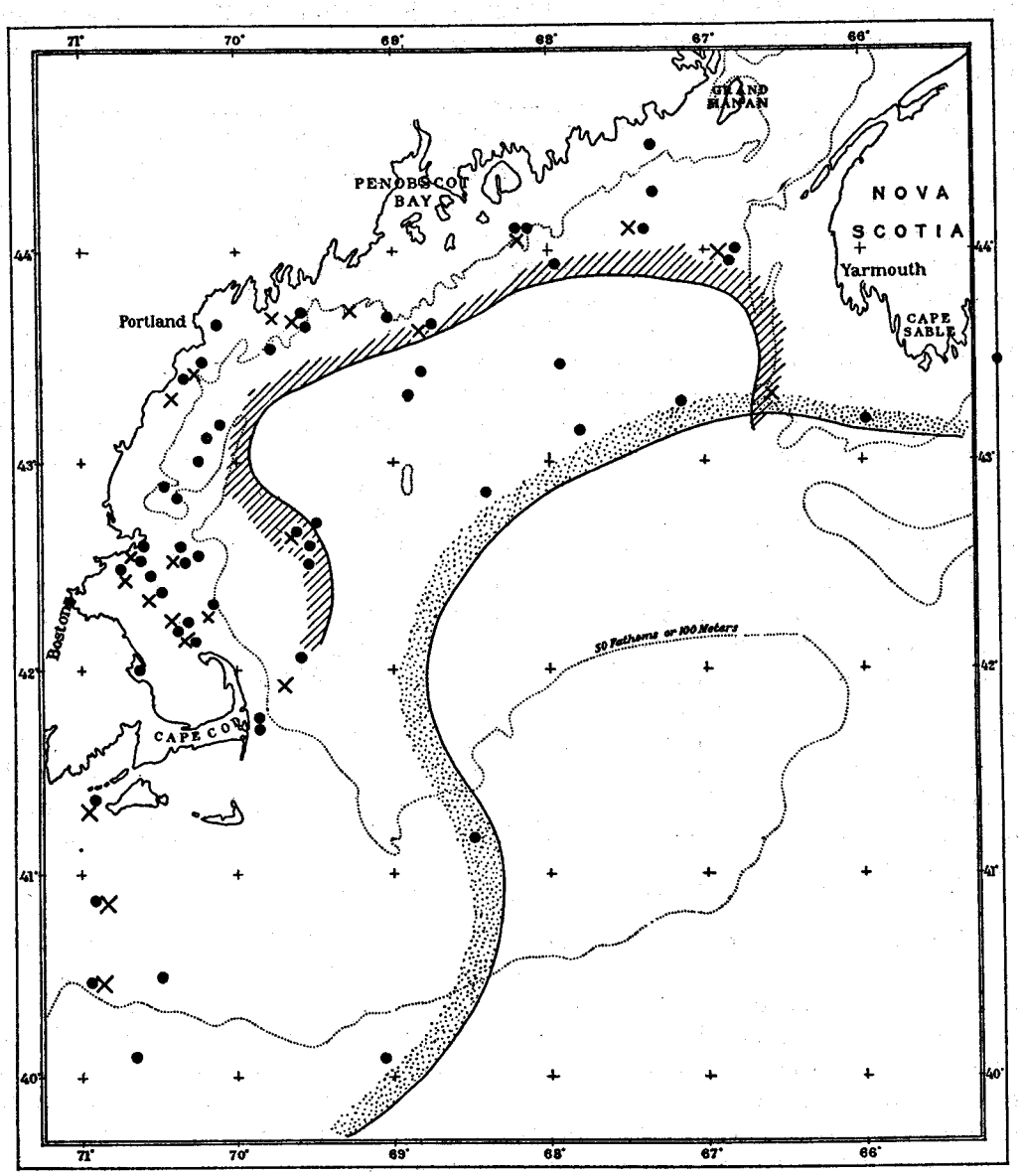

FIG. 70.—Occurrence of the copepods *Centropages hamatus* and *C. typicus*. X, locality records for *C. hamatus*, all seasons; ●, locality records for *C. typicus*, all seasons. The hatched curve incloses the chief zone of occurrence for *C. hamatus* within the Gulf; the stippled curve for *C. typicus*

It occurred abundantly also in the Gulf Stream 70 miles south of Marthas Vineyard. Fish (1925) also took it regularly at Woods Hole.

On July 10, 1913 (station 10062), it swarmed near the 100-meter contour off Marthas Vineyard, and again on October 21 and 22, 1915, it occurred right across the whole breadth of the continental shelf off Marthas Vineyard, most abundantly near shore (see table, p. 298, stations 10331 to 10333), all of which proves it as widespread out to the continental edge off southern New England as it is farther south.

C. typicus has proved to be a decidedly more important member of the plankton of the Gulf of Maine than is its relative, *C. hamatus*, as is described below; but Cape Sable evidently marks the most northerly and easterly limit to its regular occurrence along the North American coast line, for it does not appear in Willey's (1919) lists of copepods collected on and along the slopes of the Nova Scotian and Newfoundland Banks and in the intervening deeps. The *Grampus* did not find it between Cape Sable and Halifax that same summer. It has not been reported from the Gulf of St. Lawrence, nor did Herdman take it west of longitude about 28° W. on his two traverses of the North Atlantic between Liverpool and the St. Lawrence River. Comparison with the known range of *C. hamatus* shows *C. typicus* to be the more southerly of the pair by about 7° of latitude, in terms of its northern boundary.

Gulf of Maine.—When the locality records for *C. typicus* in the Gulf of Maine are expanded to include Georges Bank [23] (fig. 70) there is no evident concentration in the western side or in the eastern.

It is reported from Plymouth Harbor by Wheeler (1901) and from St. Andrews by Willey (1919); hence it would no doubt be found in similar estuarine situations all along the intervening coastline. Apparently it is never plentiful as far east as the shallows west of Nova Scotia and perhaps never reaches Browns Bank or the eastern part of Georges, and one record close to land off Shelburne, Nova Scotia, September 6, 1915 (station 10313), is, so far as I can learn, the most easterly known outpost of the species on the Atlantic coast of North America. The preponderance of records in the inner parts of the gulf, as contrasted with the basin, accords with a nature more neritic than oceanic (p. 35). In fact, its distribution east and north of Cape Cod closely parallels that of the hydromedusa *Phialidium languidum* p. 350); but this applies only to the most northerly part of its range, for off southern New England and thence southward it occurs generally right out to the continental edge.

Seasonal fluctuations.—In its seasonal ebb and flow in the gulf, *C. typicus* closely parallels *C. hamatus*. Thus it was so rare during the spring quarter, as exemplified by the February to May cruises of 1920, that it was detected in only 6 out of 81 vertical hauls (about 7 per cent); it appeared in but one May haul in 1915 and not at all in June. Furthermore, the numbers of specimens concerned have invariably been small on the few occasions when *C. typicus* has figured in the spring lists. On the western part of Georges Bank (February 23, 1920) it constituted 18 per cent of the copepods, but the total number was so small that this percentage amounts to only about 325 *C. typicus* per square meter. The maxima during the February to June period are 2,625 per square meter in the western basin on February 24, 1920 (station 20049), and 4,115 in the eastern basin on May 6, 1915 (station 10270, see tables, pp. 297 and 299), with less than 300 per square meter at the few other stations of record for these months.

[23] Also dominant over northern and eastern parts of Georges Bank, at the surface, August 7, 1926.

There are only two records of *C. typicus* in the gulf in July—one off Cape Elizabeth on the 29th (station 10019) and the other in Casco Bay on the 31st (station 10020)—both in 1912. The records point to a notable increase in August, when it occurred at 23 per cent of the stations (7 out of 31) in 1912, 40 per cent (8 out of 20) in 1913, and at 2 out of 11 in 1914. It is most regularly distributed in the gulf during autumn and early winter, occurring at 60 per cent of the September stations and 66 per cent of the October stations in 1915 and at about 60 per cent of the stations for December, 1920, and January, 1921. The local abundance of the species, as well as the generality of its distribution, likewise increases during late summer and autumn, mounting to an average of about 1,000 per square meter for August, 1913 (counting only the stations where it is actually recorded east and north of Nantucket), about 5,300 for September, 1915 (maximum 18,200 in Massachusetts Bay on the 29th), and to about 8,637 during that October (maximum 24,450 in Massachusetts Bay on the 27th). Off Marthas Vineyard on October 22, 1915, the numbers per square meter ranged from about 58,400 near shore (station 10331) to slightly more than 12,000 on the outer part of the continental shelf (station 10333). Even at its season of maximum abundance, *C. typicus* is usually a minor element in the plankton of the gulf, averaging only 7 to 9 per cent of the total copepod population at the stations where it occurred in September and October, 1915 (table, p. 298). Occasionally, however, it may dominate locally near shore—witness 40 per cent of this species in Massachusetts Bay on September 21 of that year (station 10321)—but probably this never happens out at sea in the gulf.

C. typicus constituted so small a percentage (1 to 8 per cent) of the scanty catches of copepods made during the December and January cruise of 1920 and 1921 as to suggest a shrinkage in its numbers during the late autumn.

The numbers of *C. typicus* present per square meter are further interesting as proving the Massachusetts Bay region generally and the waters off Cape Cod its chief centers of abundance in the gulf during the late summer and autumn. In late winter and spring the largest catches have been made in the western and eastern sides of the basin—2,600 per square meter at the former locality on February 23, 1920 (station 20049), and 41,100 per square meter near German Bank on May 6, 1915 (station 10270). It is also worth noting that this last was the richest catch of *C. typicus* that has ever been recorded east of Nantucket, though at a time of year when the species occurs only irregularly in the gulf and usually in very small numbers.

Breeding.—No observations have been made on the breeding of this species in the gulf, but the fact that its chief center of local abundance lies off Massachusetts Bay, whereas summer immigrants, whether of northern or of Tropic origin, enter chiefly via the eastern side, is strong evidence that the stock is maintained by local reproduction, aided little, if at all, by immigration. The presence of this species within the gulf throughout the year tends to corroborate this. Seasonal fluctuations point to summer as the chief breeding season, as does the fact that in 1915 the autumnal multiplication of *C. typicus* and *C. hamatus* was preceded by an abundance of larval copepods of some sort (see table, p. 298). With only one period of abundance annually, and that well-marked in contrast to the scarcity of the species during the other months, it is safe to assume one chief breeding period for it yearly.

Vertical distribution.—In an earlier report (Bigelow, 1915, p. 293) I have noted that west and south of Cape Cod, *Centropages typicus* is most abundant near the surface, citing as noteworthy examples of this one station (10088) where the surface haul yielded ten times as many specimens as the haul from 80 fathoms, though made with a net of only one-sixth the mouth area, and another (10083) where the surface haul brought in several hundred *C. typicus* and the haul from 20 fathoms only one specimen. Our largest catches of the species have also been on the surface, where it swarmed off Marthas Vineyard on July 10, 1913 (station 10062), and at 15 fathoms off New York on July 12 (station 10066).

Observations of this same tenor were made in the Gulf of Maine during August, 1912, *C. typicus* amounting to about 40 per cent of the copepods at the surface at station 10041 but not over 2 per cent at 40 meters; about 60 per cent at the surface and not found at all at 30 meters at station 10042. At a third station for that month (in Massachusetts Bay, station 10044) it and *C. finmarchicus* each constituted 50 per cent of the copepods on the surface. Our few records for it north of Cape Cod in August, 1914, are also from surface hauls; and while it has figured in a considerable number of hauls at various depths in one year or another, it has never been more than a trifling percentage of the copepod catch in the deeper horizontals, and rarely in the verticals (p. 225). Failure to take it in the surface hauls during the spring of 1920 (table, p. 303) is not necessarily significant in this connection, the species being so rare at that season that it might have been missed by the nets. Consequently it may be classed as typically a surface form in the gulf, most plentiful above 20 meters and perhaps never sinking as deep as 100 meters. It is likewise most numerous near the surface in north European seas.

Relation to physical conditions.—In different seas *C. typicus* occurs over a wide range of temperature and salinity. Along the Atlantic seaboard of North America its presence is established in water as warm as 24.4° (Bigelow, 1915, p. 293) and as cold as 3.05° (station 20104, April 15, 1920). It did not occur in the coldest waters of the gulf, for example in the inner part of Massachusetts Bay, at the season of minimum temperature, and the locations of the few early spring records suggest either that it tends to withdraw from the coastal waters as the latter chill or that the specimens living there perish, leaving only those that are in the parts of the gulf less subject to winter cooling to survive the cold season. The fact that the species did not appear in the surface hauls for March or April suggests that *C. typicus* may sink in the deeper parts of the gulf as the surface chills. In the western basin, for instance, where this copepod was comparatively numerous on February 23, 1920 (station 20049), it might have been in temperatures anywhere between 5.6° and 2.8°, according to the precise depth at which it was living.

However this may be, *C. typicus* increases notably in abundance about when the upper 20 meters or so have warmed to the maximum annual temperature, and the tendency of the species to keep near the surface makes it safe to set 8° to 10° as the lower limit to its active multiplication in the gulf. In autumn it is probable that its numbers fall off after the upper 20 meters have chilled appreciably below this figure, which, speaking broadly and for the gulf as a whole, takes place some time during November.