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

Zooplankton volumes per cubic meter, March, 1920

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Owing to the tendency of the zooplanktonic community as a whole to congregate in the upper 100 meters of water during the warm months, but at the same time to keep some few meters down (p. 24), the seasonal difference between the volumes of plankton per cubic meter present in March, on the one hand, and in July and August, on the other, is actually much greater than the ratio arrived at by any calculation which fails to take account of its vertical stratification. A more nearly correct picture of the summer state results from the assumption that the entire catch of zooplankton in the vertical net at that season was taken below 10 meters at each station, but that it was only one-third as dense as the ostensible volume per cubic meter below 100 meters, and correspondingly concentrated above that level. The results of such a calculation for 1914 are given in the following table:

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

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

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

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

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

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

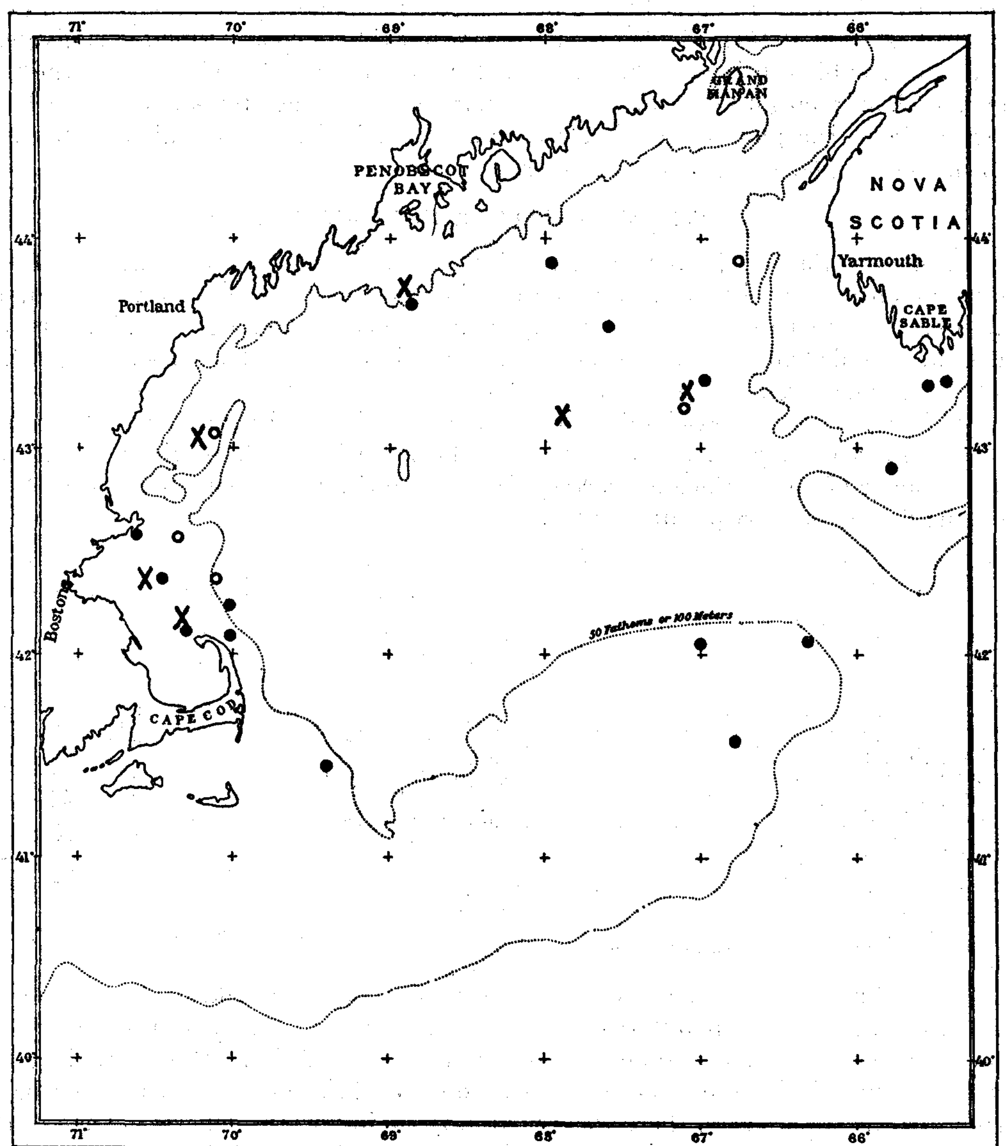

FIG. 39.—Locations where vertical hauls have taken more than 2 cubic centimeters of animal plankton per cubic meter at different seasons, calculated by the method described on page 94. X, September to November; O, May; ●, July to August 15

23, 1914 (station 10224, about 5 cubic centimeters per cubic meter); in the eastern basin on September 1, 1915 (station 10309, approximately 3.5 cubic centimeters per cubic meter, assuming some stratification); and at the mouth of Massachusetts Bay in July, 1916 (station 10342, at least 4.5 cubic centimeters per cubic meter); but occasionally it is much more dense than this at one level or other, the volumes just listed being the minima possible. For example, a horizontal haul of 15 minutes' duration at 40 meters depth, with a net 1 meter in diameter, off Cape Cod on July 22, 1916 (station 10344), yielded over 6 liters, mostly copepods, which is equivalent to about 12 cubic centimeters per cubic meter for the water fished through (the tow covered about one-third of a mile). In fact, it was the richest tow-net catch we have ever made in the gulf, although the vertical haul indicated only about 2.8 cubic centimeters of plankton per cubic meter.

ANNUAL VARIATIONS IN ABUNDANCE

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

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

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

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

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

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

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

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

PLANKTON AS FOOD FOR WHALES AND FISHES

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

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

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

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

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

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

The North Atlantic right whale (*Eubalæna glacialis*), once common in New England waters though now unhappily nearly extinct there (and with it the glories of the New England coastwise whale fishery), subsists largely on euphausiids, notably on Thysanoessa (Kükenthal, 1900). Collett (1909), indeed, found nothing else in right whales taken off the Hebrides and off Iceland. The only eyewitness's account of its feeding habits in New England waters, for which we must turn back nearly 200 years (Dudley, 1734, quoted by G. M. Allen, 1916) tells of "this whale, in still weather, skimming on the surface of the water to take in a sort of reddish spawn or brett, as some call it, that at some times will lie on the top of the water for a mile together." From its geographic situation and mode of occurrence this was probably Calanus or other copepods. Unfortunately, little is known of the habits of the Atlantic right whale, but it is well established that the pollock whale (*Balænoptera borealis*) feeds chiefly on copepods at certain times and places, for Collett (1886, p. 26) found the stomachs of several, killed off East Finmark in July, "filled with a fine gritty mass, which consisted entirely of *Calanus finmarchicus*," with the Calanus occurring "in great numbers and in a tolerable state of preservation" among the hairs of the baleen plates; and since he gives excellent figures of these copepods, their specific identification is assured. In West Finmark, however, this same whale has been reported as subsisting chiefly on euphausiids (Collett, 1886). Kükenthal (1900) likewise states that it feeds on these shrimps, and Andrews (1916) writes that most of the specimens which he opened in Japanese waters contained euphausiids only, while a few had eaten fish. G. M. Allen (1916) and Millais (1906) are therefore fully justified in crediting it with a mixed copepod (Calanus and Temora) and euphausiid diet.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

In North European waters the hyperiid amphipods are a major food for herring (Brook and Calderwood, 1886), but although the genus Euthemisto is widespread and at times locally abundant in the Gulf of Maine, I have found no record of herring feeding on it there, and have recognized none in the stomachs of the Gulf of Maine herring I have opened. Probably this is due to the mutual geographic distribution of the two animals, Euthemisto being most plentiful offshore and herring along the coast. These amphipods may be expected to form an important item in the diet of herring on Georges Bank. This is certainly true of the mackerel there, for Dr. W. C. Kendall found the latter feeding on Euthemisto on the northern part of the Bank in August, 1896 (Bigelow and Welsh, 1925, p. 201). Mackerel taken near Woods Hole in summer have also contained Euthemisto (Rathbun, 1896), and Rathbun (1889) found mackerel feeding largely on amphipods off Virginia and Maryland in the spring. European mackerel also feed on Euthemisto, and, generally speaking, the latter are no doubt more important as a source of fish food over the outer part of the shelf and along the continental edge (where they are constantly abundant) than in the inner part of the Gulf of Maine; but no evidence is at hand that any Gulf of Maine fishes depend on them to the extent to which the long-finned albacore (*Germo alalunga*) does off the French coast (Le Danois, 1921).

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

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

The shell-bearing pteropods, represented locally by *Limacina retroversa*, are seldom plentiful enough in the Gulf of Maine to be of much importance as a possible food supply for the schooling fishes there, but when these mollusks do swarm mackerel would no doubt feast on them, for they are an important food for this fish off the west coast of Ireland (Massy, 1909). According to Rathbun (1889), mackerel eat *L. retroversa* off the Middle Atlantic States, and mackerel taken off No Mans Land (an islet near Marthas Vineyard) have been recorded as full of them. In Norwegian waters, according to Nordgaard (1907), this pteropod also enters into the dietary of the herring, but as Limacina seems not to have been recorded as herring food elsewhere in north European seas it probably does not so serve to any great extent in the Gulf of Maine. Lebour's (1920) observation that young fish of various species not only had not eaten Limacina, although the latter were plentiful in the tow, but refused them when offered in the aquarium is interesting as suggesting that the mackerel is rather an exception in feeding on this pteropod. Naked pteropods are never plentiful enough in the Gulf of Maine to be of any importance as food for larger animals.

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

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

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

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

With the young fry of the whole fish population of northern seas dependent for their existence on the supply of plankton, it is but natural that many attempts should have been made to correlate the movements and migrations of the more important food fishes with local and temporal fluctations in the supply, either of the plankton as a whole or of such members of it as serve as the chief diet of the particular species in question, as well as with the far-reaching physical phenomena that may be looked on as the ultimate causes of such fluctuations. Thus, to mention only a couple of examples, Bullen (1908) has established at least a plausible causal relationship between the fluctuations in the amount of zooplankton present in the sea and in the seasonal and yearly catch of mackerel, corroborated by experience for herring, also, in the Irish Sea (A. Scott, 1924); and E. J. Allen (1908) aroused an interesting discussion by his tentative hypothesis that the abundance of mackerel at any given locality depends on the amount of sunshine during the previous months, sunny weather favoring the multiplication of diatoms and thus affording a rich pasture for copepods, an abundant stock of which attracts mackerel. Dr. C. B. Wilson, in a letter, suggests that the diurnal migrations of copepods upward toward the surface at night and downward by day may be the reason why mackerel and herring most often school at the surface at night, following the daily migrations of their prey.

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

FOOD OF THE PLANKTON

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Murphy (1923, p. 450) writes that the copepod *Oithona nana* ate kelp and diatoms in the aquarium, and we have recognized remnants of Thalassiosira in sundry specimens of Calanus, and Thalassiosira, Chætoceros, and Biddulphia in Metridia from Massachusetts Bay at the time of the vernal diatom flowering. Diatom fragments have also been detected repeatedly in the excreta of copepods, which are familiar objects in the catches of tow nets, but Esterly's (1916) discovery of an occasional nauplius and copepod fragment in copepod stomachs proved that they are not exclusively vegetarian. Lebour (1922) has more recently found that the large blue copepod Anomalocera may feed largely on micro-Crustacea, while smaller copepods form a considerable item in the diet of Temora. Calanus, however, she found chiefly vegetarian, and Pseudocalanus perhaps exclusively so. Marshall's (1924) more recent study of the gut contents of large numbers of Calanus taken throughout the year in the English Channel corroborates this, diatoms proving the chief article of diet in spring and autumn with peridinians (curiously enough, however, no Ceratium) in summer. Silicoflagellates were also eaten in small quantities, while a few of the Calanus had eaten other copepods, molluscan larvæ, and tintinnids.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

THE MORE IMPORTANT GROUPS OF PLANKTONIC ANIMALS

MOLLUSKS

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

Cephalopods

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

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

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

Since more is known of the life history of Loligo than of Illex, it may be considered first. Loligo is common in the Woods Hole region from April or May until November but disappears during the winter. During the 10-year period, 1900 to 1909, the earliest captures ranged from April 16 to May 7 (Sumner, Osburn, and Cole, 1913a), which probably applies to Massachusetts Bay, though, taking one year with another, this squid appears there later in spring and disappears earlier in autumn than it does along the southern coast of New England. During the late spring, summer, and early autumn Loligo is extremely common both south and north of Cape Cod, passing part of the time on or near the bottom, but often seen swimming in shoals near the surface, and it is taken in great numbers in fish traps and weirs and even in eelpots. Many specimens have likewise been dredged. Along the shores of southern New England it breeds from May until September, or later. I am informed by W. F. Clapp that he has frequently found its eggs in Duxbury and Plymouth Bays from June until October, and in the Bay of Fundy its eggs and larvæ are reported by Doctor Leim in August and September. Since Verrill (1882) notes the capture of considerable numbers in breeding condition near Cape Ann as early as May in 1878, it is safe to credit it with a breeding season enduring throughout the warmer half of the year over the major part of its range. The eggs, which adhere together in bunches of hundreds of gelatinous capsules, attached to some fixed object, are laid chiefly (perhaps not exclusively) in depths varying from just below tide mark down to 50 meters or so and have been trawled in large numbers on every sort of bottom south of Cape Cod (Verrill, 1882; Sumner, Osburn, and Cole, 1913a). It has been estimated that individuals of the European representatives of this genus may lay as many as 40,000 eggs.

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

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

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

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

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

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

Whenever and wherever found, these squids are extremely voracious, and the schools that run ashore often do so in pursuit of fish fry. At the mouth of the Bay of Fundy, both in summer and in early autumn, I have seen them eagerly following the schools of young herring, which in their turn are feeding upon shrimps (euphausiids), often so common in the surface waters there (p. 135). I can corroborate Verrill's observation that squid stomachs are then often distended, both with shrimp and with fragments of herring, having found this to be the case in dozens of specimens. Young mackerel, too, suffer from their attacks, and we owe to Smith and Harger (quoted by Verrill, 1882, p. 306) a graphic account of their pursuit of the latter among the wharves of Provincetown Harbor during the month of July. Particularly interesting is their activity at such times, the ferocity of the attack, and the deadly nature of the single bite. The cannibalistic habits of Illex have likewise been commented upon, its own young being a common article of diet. This squid, like so many of the pelagic fishes, is very erratic in its appearance, being here to-day in hordes and gone to-morrow, perhaps to reappear in a few days.

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

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

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

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

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

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

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

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

PTEROPODS

Limacina retroversa Fleming[59]

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

58 Information supplied by Doctor Huntsman.

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

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

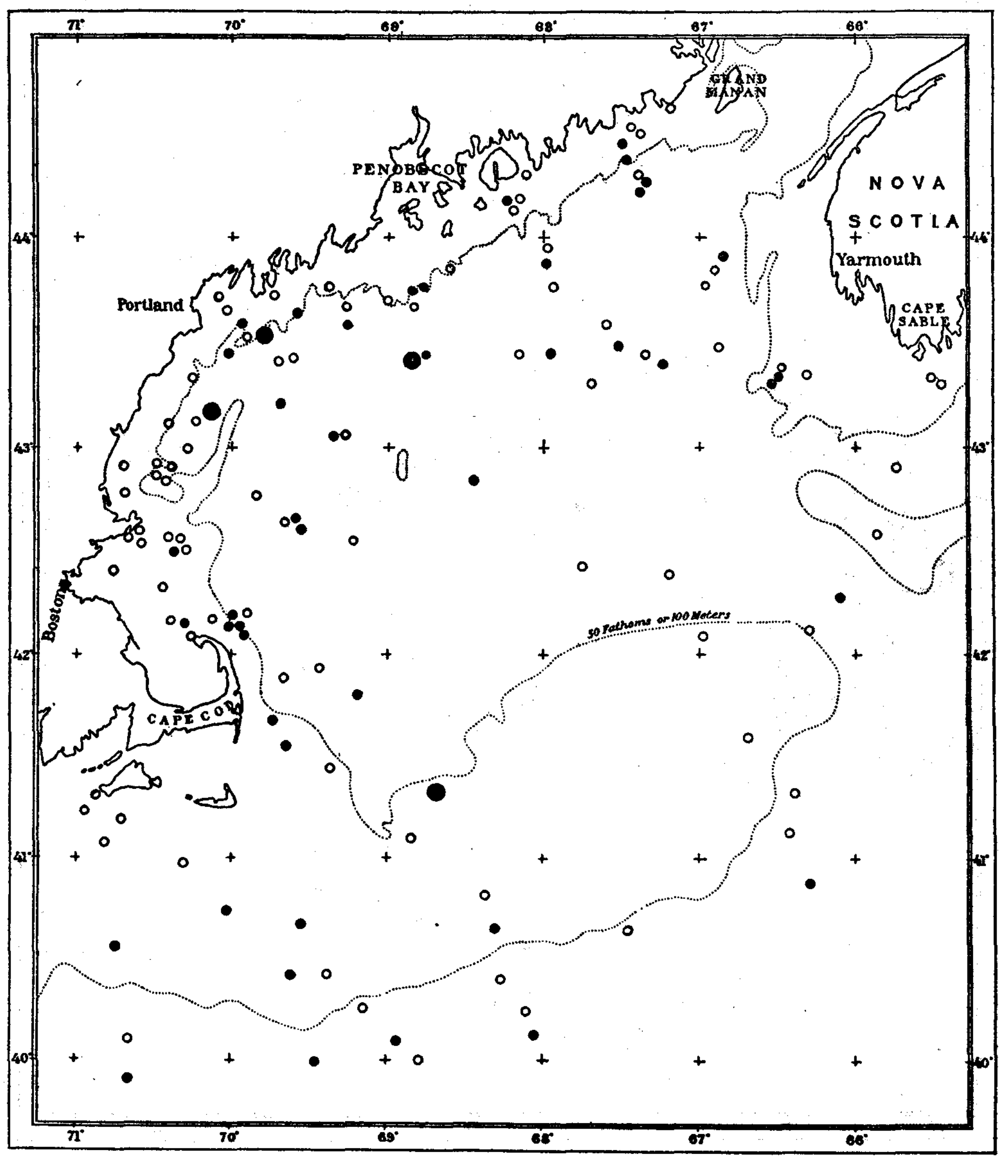

FIG. 43.—Occurrence of the pteropod *Limacina retroversa* from July to September, 1912 to 1922. ●, occurred; ⬤, swarmed; ○, not taken

our records are most extensive) it has appeared at rather more than half of all the stations, but the regularity of its distribution differs from summer to summer. For example, it was practically universal over the deeper parts of the gulf in August, 1913 (Bigelow, 1915, p. 302), whereas in July and August, 1912, we found it only in the northwest part of the gulf, on the one hand, and over German Bank, on the other (Bigelow, 1914, p. 120). At the same season in 1914 we found no Limacina

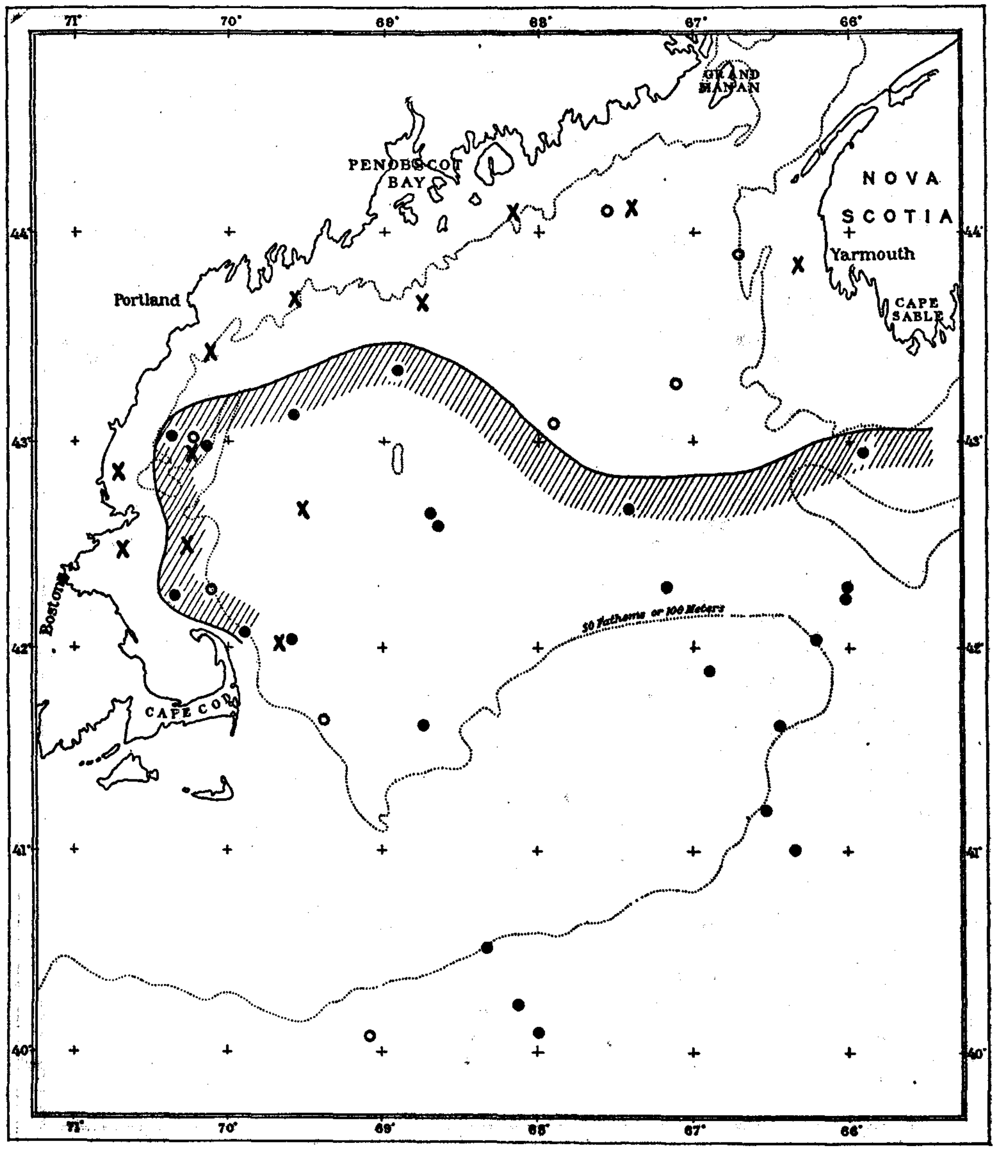

FIG. 44.—Occurrence of the shelled pteropod *Limacina retroversa* in winter and spring. X, locality records for December, 1920–January, 1921; ●, February to April, 1920; ○, May of 1915 and 1920. The hatched curve incloses its area of occurrence in early spring up to May

off Penobscot Bay, where it had been plentiful during the two summers preceding, but towed numbers of them in the northeastern corner of the gulf (stations 10246 and 10247) not far distant, and likewise in the Eastern Channel, over the northwest part of Georges Bank, and off Cape Cod (Bigelow, 1917, pp. 298 and 299). We have not taken Limacina on Browns Bank either in spring or in summer, but since it has appeared at several of our stations over the shelf farther east, as well as on German Bank, in June, July, and August, and in the eastern basin of the gulf in March and April, it is more likely that our failure to find it on Browns Bank was accidental than that this pteropod does not occur there.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Temperature may also determine the bathymetric occurrence of Limacina. For example, we found it comparatively abundant on the surface over the outer part of the shelf abreast of Cape Sable early in the summer of 1915 (station 10294, June 23), when the superficial water had warmed to 9° to 10°, but with temperatures as low as 2° to 3° only 40 meters down it was certainly scarce at deeper levels. In fact, it may not have occurred at all, for the few specimens brought in by the deep hauls may have been picked up by the nets close to the surface on their journey down or up; and the scarcity, if not absence, of this species in the coldest water along Nova Scotia is sufficient evidence that it is not an immigrant to the Gulf of Maine by that route. The general thesis that it is not at home in water of Arctic temperatures is further corroborated by Doctor Huntsman, who informs me that *Limacina retroversa* is scarce, if not wanting, in the Gulf of St. Lawrence, where, by contrast, its larger Arctic relative (*L. helicina*) is very plentiful.

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

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

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

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

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

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

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

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

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