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

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

IMMIGRANT PLANKTONIC COMMUNITIES

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

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

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

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

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

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

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

TROPICAL VISITORS

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

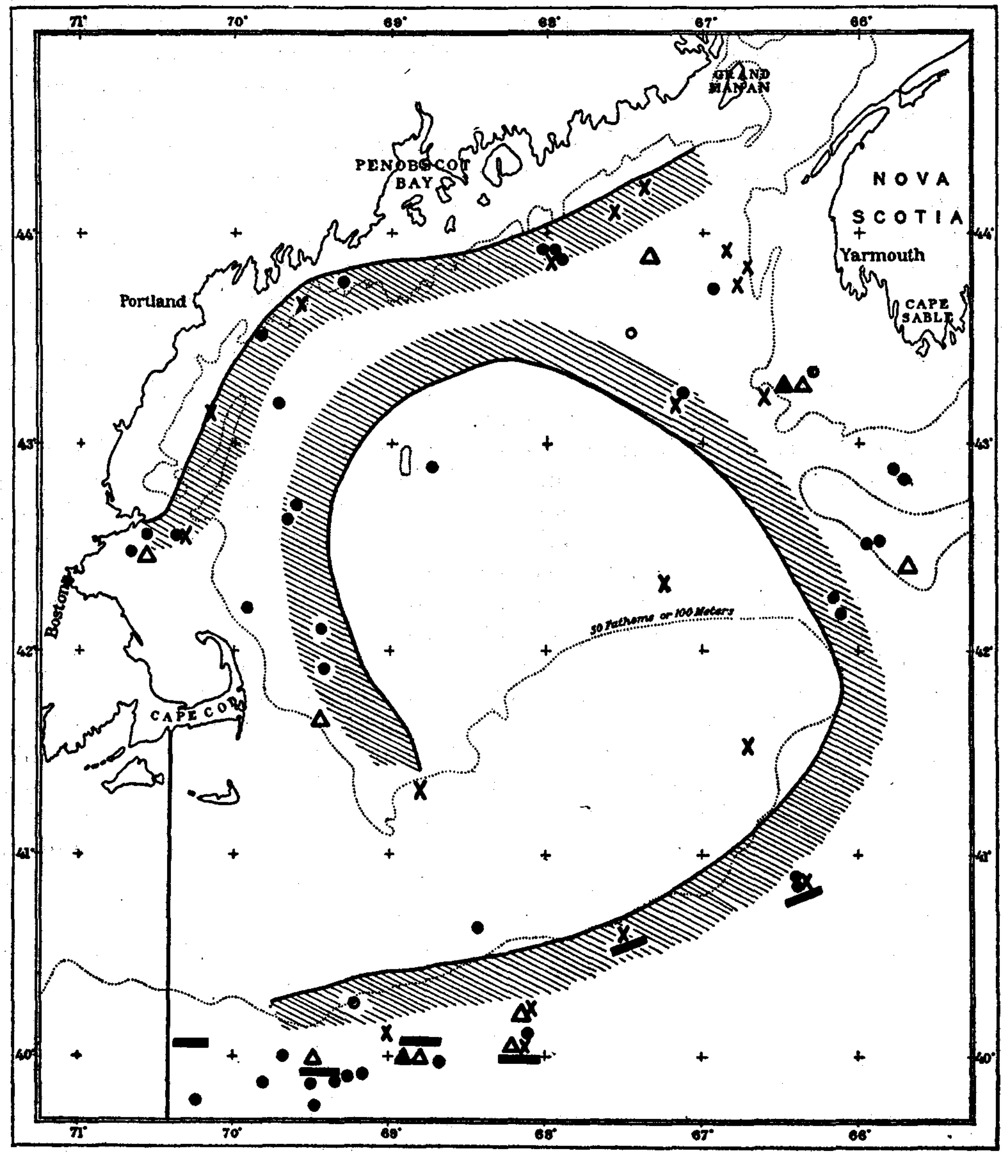

Fig. 31.—Locality records for certain of the more typical planktonic animals of tropical or warm-Atlantic origin. △, Salpæ, ●, *Thysanoessa gregaria*; X, tropical copepods; ○, Portuguese man-o-war (Physalia); ▲ *Physophora hydrostatica*; ⊙, gulf weed (Sargassum); ▬, many tropical species

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

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

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

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

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

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

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

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

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

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

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

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

This was the case with *Salpa fusiformis* near German Bank and off Lurcher Shoal, August 14, 1912 (stations 10030 and 10031), though other scattered specimens were seen floating on the run from one station to the other. A few *Salpa tilesii* were also taken in the tow near Lurcher Shoal, August 12, 1913 (station 10096). Huntsman (1921) records five *S. fusiformis* found on the beach at Campobello Island (New Brunswick) in the autumn of 1913, and two *S. zonaria* taken in that general region (probably near Grand Manan) in 1910. On September 30, 1912, Capt. John McFarland, of the fishing schooner *Victor*, to whom the Bureau of Fisheries is indebted for other interesting tow-net hauls, made a large catch of *S. mucronata* 25 miles off Chatham, Cape Cod; and fishermen reported great numbers of large Salpæ (probably *S. tilesii*) in Massachusetts Bay in November and December, 1913, which, so far as I can learn, are the only occasions when Salpæ have been found in such numbers within the gulf, though they are often reported in abundance south and west of Cape Cod. Local swarms, such as this, probably result from their very rapid asexual multiplication (there is no evidence that they can reproduce sexually in cool waters) in summer and early autumn (A. Agassiz, 1866).

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

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

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

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

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

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

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

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

The locations of the stations of capture and the fact that *S. serratodentata* is usually more numerous in the eastern than in the western side of the gulf (p. 322) are sufficient evidence that its invasion takes place chiefly into the eastern side and from the southwest and south; that is, across the eastern end of Georges Bank and via the Eastern Channel. It is probable (as suggested by Doctor Huntsman in a recent letter) that *S. serratodentata* also comes to the gulf from the east, drifting with recurrent movements of mixed water along the outer edge of the continental shelf off Nova Scotia and entering across Browns Bank or through the Eastern Channel, but there is no reason to suppose that any come by way of the Northern Channel or around Cape Sable across the coastal shallows; in fact, it would be very surprising to find any warm-water species journeying along that route.

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

ARCTIC VISITORS

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

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

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

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

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

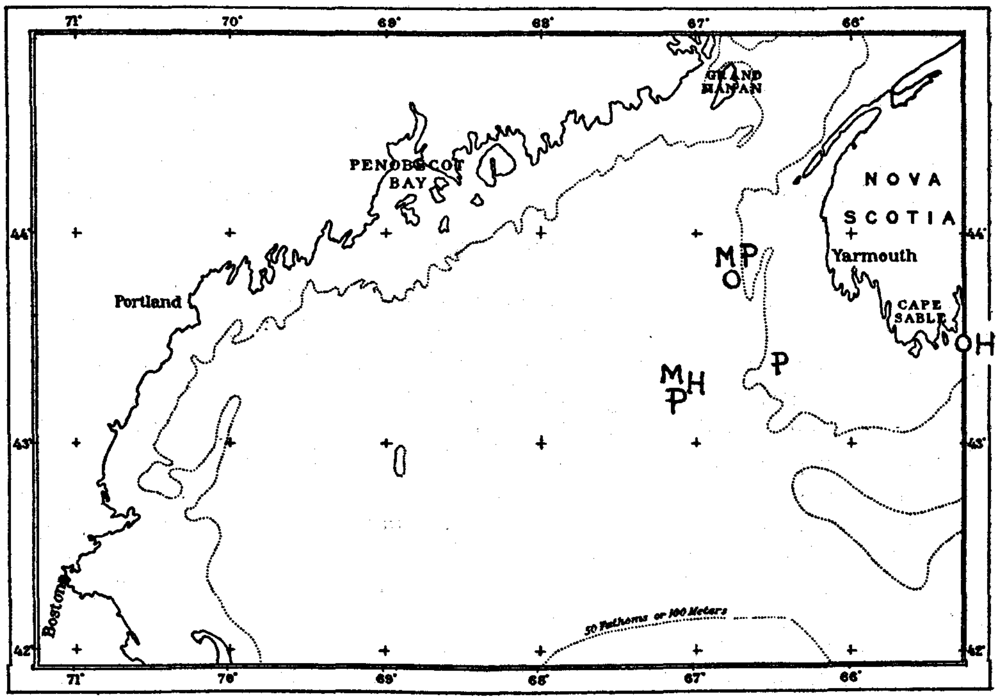

FIG. 32.—Localities at which certain planktonic animals of Arctic origin were taken in May and June, 1915. H, *Limacina helicina;* M, *Mertensia ovum;* O, *Oikopleura vanhöffeni;* P, *Ptychogena lactea*

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

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

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

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

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

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

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

OTHER IMMIGRANTS

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

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

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

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

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

The large and easily recognized chætognath *Eukrohnia hamata* (p. 328) is a characteristic inhabitant of a lower level in the mixed water (say, below 50 meters), though not of the deepest. Its faunal relationship is diametrically opposite to that of its relative, *S. serratodentata,* for while it is widely dispersed over the ocean basins in the mid-depths, it is only in the Arctic or at least in cold seas that it comes to the surface regularly (Apstein, 1911). It enters the Gulf of Maine by the same route followed by *S. serratodentata,* but below it, and is equally unable to breed within the gulf,[80] though in its case this failure is because the temperatures it experiences there are too high instead of too low.

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

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

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

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

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

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

The lines of dispersal followed, respectively, by *Sagitta serratodentata,* Eukrohnia, and *S. maxima* within the gulf correspond closely with the dominant drift of water at as many levels—that is, surface, mid, and deepest—as made evident by the physical data afforded by temperature and salinity and by drift bottles. Thus, while *S. serratodentata* not only spreads widely over the offshore parts of the gulf in its season, it also sweeps right around the coast to Massachusetts Bay (which apparently serves more or less as a cul-de-sac for it, as it has for certain drift bottles released in the Bay of Fundy), and Eukrohnia has much the same distribution except that it lives so much deeper that it is prevented from entering Massachusetts Bay by the contour of the bottom, and, in fact, hardly encroaches at all on the shallow coastal belt within the 100-meter contour. Furthermore, the two agree in their scarcity in the

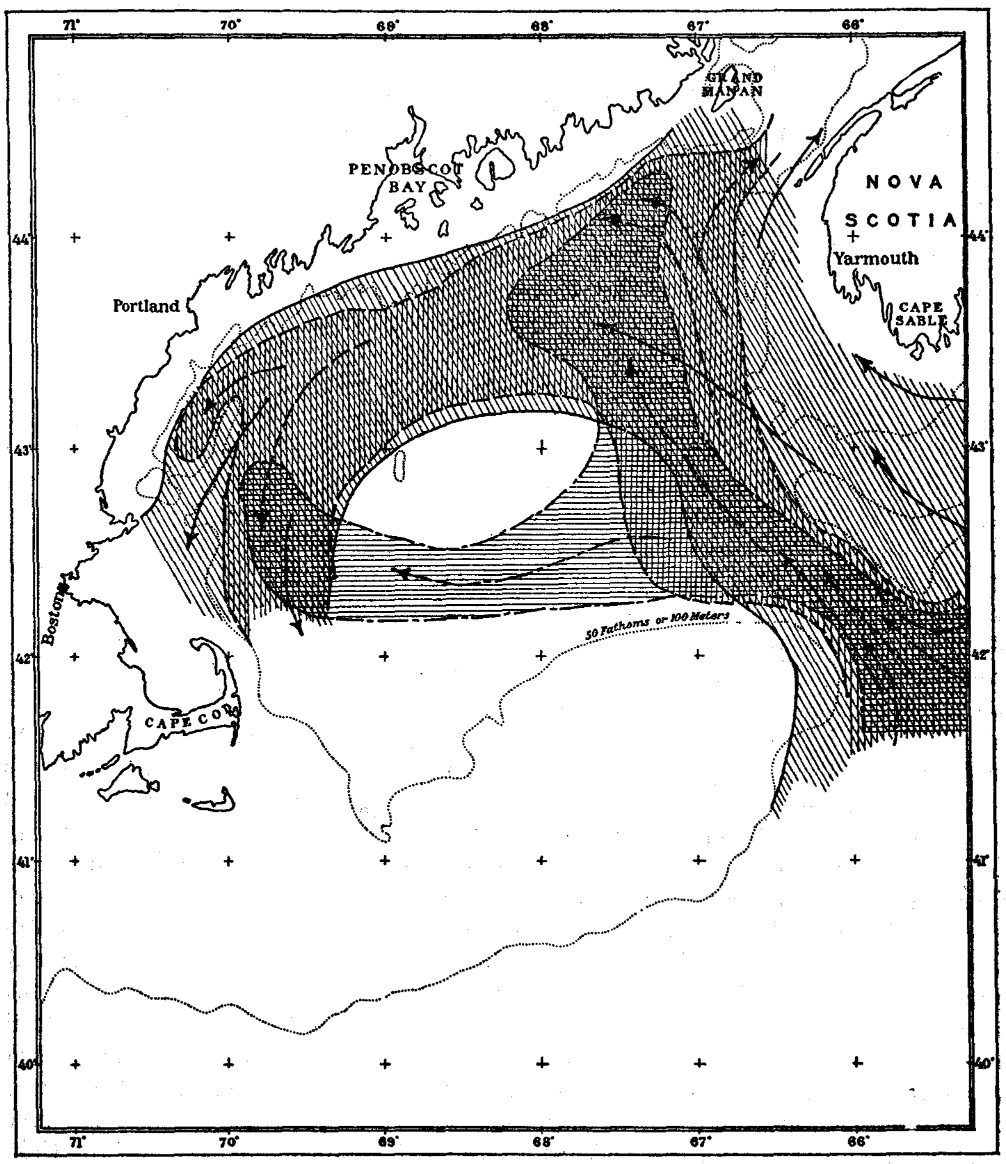

FIG. 33.—Chief routes followed by planktonic immigrants entering the Gulf of Maine at different levels. \\\, immigrants at the surface; |||, immigrants at intermediate levels; ≡, immigrants at the deepest level

southwestern part of the basin of the gulf—that is, just where the physical data, to be discussed elsewhere, locate the "dead water" in the anticlockwise eddy that occupies the gulf. However, *S. maxima*, living in the deepest waters of the basin, must follow its two diverging troughs, in both of which there is a dominant though perhaps not a constant indraft along the bottom, the result being that while its route parallels those of the two preceding species in the eastern part of the gulf, it crosses below them at a lower level in the western, an interesting phenomenon illustrated in the accompanying chart (fig. 33). No doubt this applies in general to the three bathymetric groups which these three chætognaths typify.

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

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

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

It is a fortunate chance for the oceanographer that many of the bathypelagic animals are so distinctively colored, because their presence in any numbers anywhere in shoal water over the continental shelf would be the best of evidence of an upwelling of Atlantic water from the mid-depths or deeper, a type of oceanic circulation that has evoked considerable discussion as a possible factor in maintaining the low temperature of the coastal waters off the eastern United States. Consequently, the presence or absence of the black fish-red prawn community within the Gulf of Maine is a question of some moment, and it is in the hope of encouraging others to keep a sharp lookout for it there that I have devoted the preceding lines to the general appearance of its members. No doubt this planktonic community is represented at the appropriate level all along the continental slope off the United States, for it occurs generally over the whole Atlantic basin from high latitudes to low. We encountered it over the 1,500-meter contour off Cape Sable on March 19, 1920 (station 20077), the following being a partial list of its more noticeable representatives in hauls from 500 and 800 meters: Several black lantern-fishes (genus Myctophum); a specimen of the curious deep-sea snipe eel (*Serrivomer beanii*), 45 centimeters long;[32] the wine-red medusa *Periphylla hyacinthina;* 13 specimens of its chocolate-colored relative *Æginura grimaldii;* the iridescent medusæ *Halicreas papillosum* and *Rhopalonema funerarium;* and many red prawns; side by side with the chætognaths Eukrohnia and *Sagitta maxima*, the large copepod *Euchæta norvegica*, and the euphausiids Nematoscelis and Thysanoessa, besides boreal animals such as *S. elegans*, Tomopteris, *Limacina balea*, and Calanus.

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

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

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

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

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

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

No doubt one or other member of the plankton might be found to represent every conceivable intergradation from utter failure to perfect success in colonizing the waters of the Gulf of Maine (for all members of the plankton are colonists in the last analysis) were the known record sufficiently complete. The copepod genus Euchæta, for example, may be taken as representative of animals that breed indifferently and grow equally large along the continental slope, in the Eastern Channel, and in the gulf wherever the depth is sufficient, as proven by the occurrence of sexually adult males, of females with large egg clusters, and of juveniles. For this copepod the gulf basin is simply a diverticulum from its general geographic range. Most successful of all are those that find a more favorable environment in the inner parts of the gulf than in the waters immediately tributary to it, and it is to this group that such members of the local zoöplankton as the copepods *Calanus finmarchicus* and *Pseudocalanus elongatus* and the chætognath *Sagitta elegans* belong. It is true that most, if not all, the animals of this category have equally prolific centers of abundance elsewhere (chiefly to the eastward and northward), connected with the gulf by a continuous zone of occurrence, but all of them are regularly more abundant in the particular temperatures, salinities, densities, etc., that characterize the Gulf of Maine than immediately outside it, whether to the east or the west or offshore. Indeed, such multitudes of several of these species (Calanus, especially) are produced there that the small accessions which the gulf may receive from the north must be far outnumbered by the emigrants that emerge from it to journey either northward along the inner edge of the continental slope, on the one hand, or around Cape Cod to the westward and southward over the outer part of the continental shelf, on the other. It is probable that the boreal winter plankton of the coast water south of New York draws more from this source than from local production.

MIGRATIONS OF PELAGIC FISH EGGS AND LARVÆ

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

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

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

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

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

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

It is, of course, possible that the northeast part of the gulf is so ill fitted for a fish nursery that only a small proportion of the pelagic eggs spawned there ever hatch or the resultant larvæ survive. The researches carried on during the past few years at the Canadian Biological Laboratory at St. Andrews point unmistakably to the conclusion that few if any floating eggs of any groups of animals hatch success-

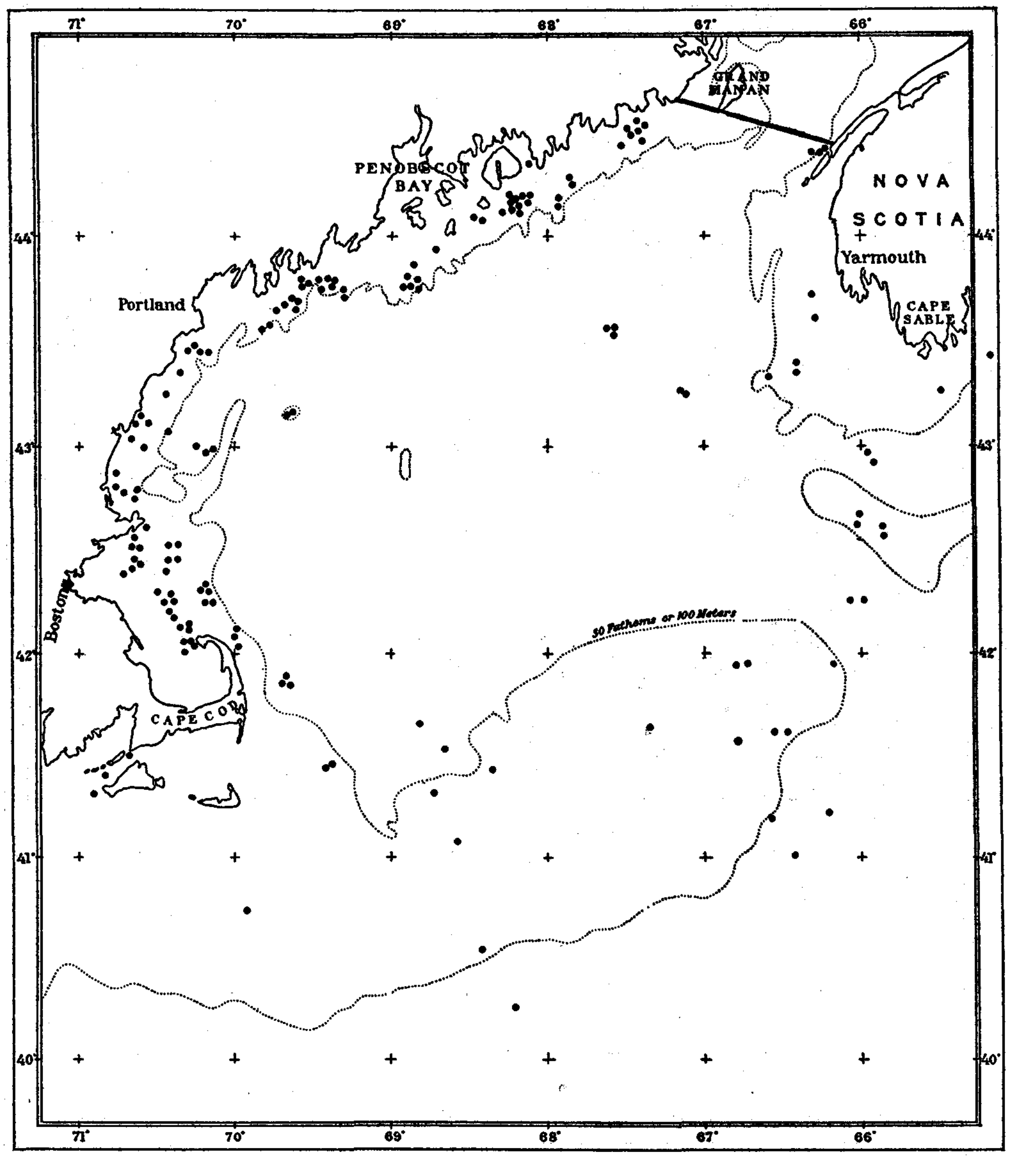

FIG. 34.—Locality records for buoyant flounder (pleuronectid) and gadoid eggs combined (a dot for each record of each species), 1912 to 1922

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

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

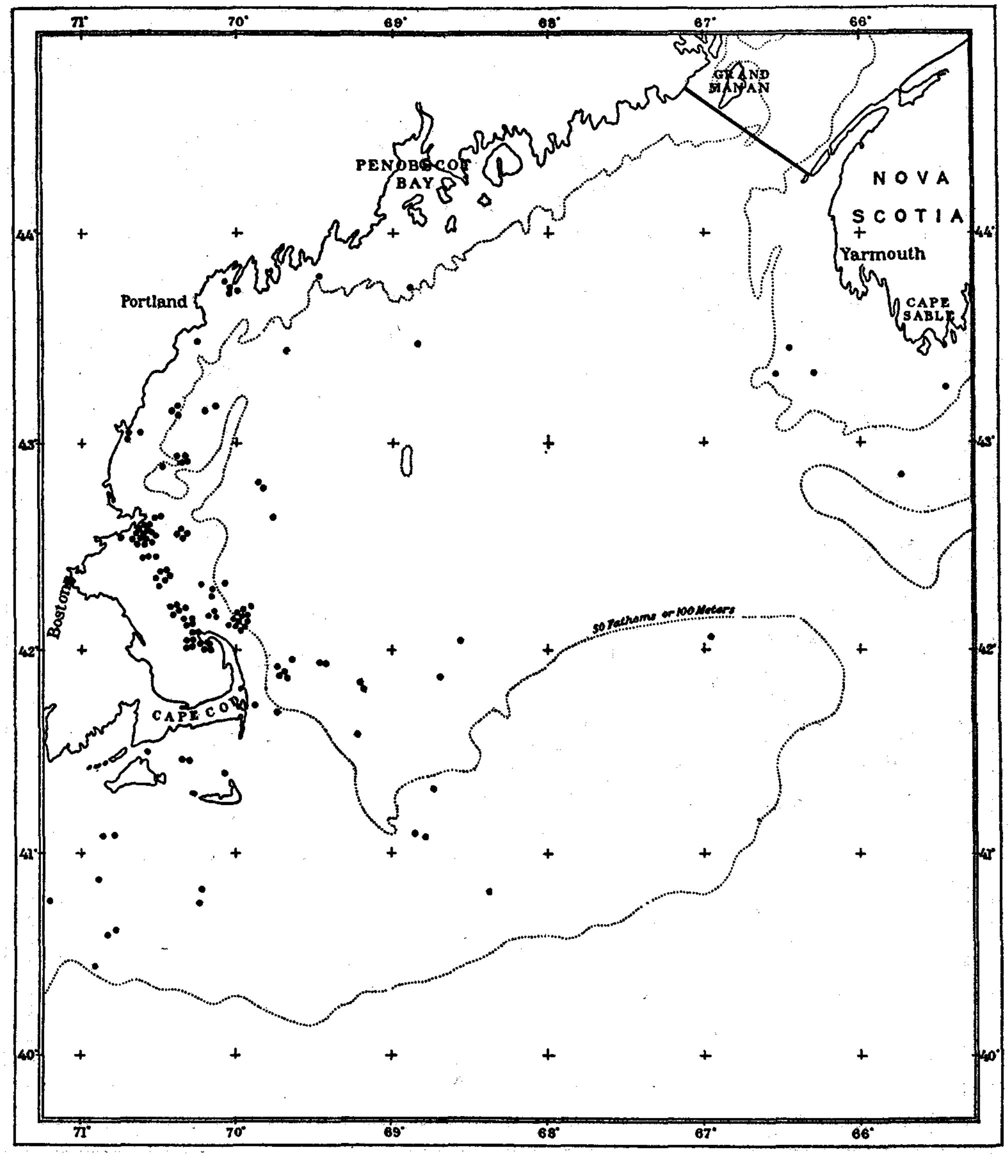

FIG. 35.—Locality records for flounder (pleuronectid) and gadoid larvæ (a dot for each record of each species) to illustrate the probable drift of buoyant fish eggs and larval fishes

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

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

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

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

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

From Mount Desert eastward the coastal belt of the gulf more and more closely approximates the Bay of Fundy hydrographically, owing to the increasing strength of the tides and the consequent activity of tidal mixing. Correspondingly, the general neighborhood of Mount Desert Island is the most easterly location along the northern shores of the gulf where we have found gadoid or flatfish eggs in any numbers.

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

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

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

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

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

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

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

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

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

Similarly, the abundant occurrence of young pollock at Woods Hole in late spring (fry so small that they are evidently the product of the previous winter's spawning) is clear evidence of a migration southward along and around Cape Cod from the very productive spawning grounds at the mouth of Massachusetts Bay, because no important spawning is known for this fish south of the Massachusetts Bay region (Bigelow and Welsh, 1925).

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

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

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

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

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

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

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

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

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

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

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

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

QUANTITATIVE DISTRIBUTION OF THE ZOÖPLANKTON

To give an adequate quantitative picture of the plankton would require a far greater number of vertical hauls than have yet been made in the Gulf of Maine. Not only are the seasonal gaps in the series serious, but hauls should be located closer together than has been feasible for us, even in July and August, unless the plankton is more uniform than our work suggests. However, even a cursory examination of the zooplankton, if extended over a considerable area or through a considerable period of time, is certain to reveal wide fluctuations in abundance as well as in its qualitative composition, both from season to season and from place to place; and inasmuch as an understanding of the causes of the fluctuations in the numerical strength of any group of marine animals would clarify the interaction of the many physical factors that govern pelagic life in the sea, information along this line is never amiss.

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

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

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

[34] The larger the better.

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

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

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

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

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

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

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

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

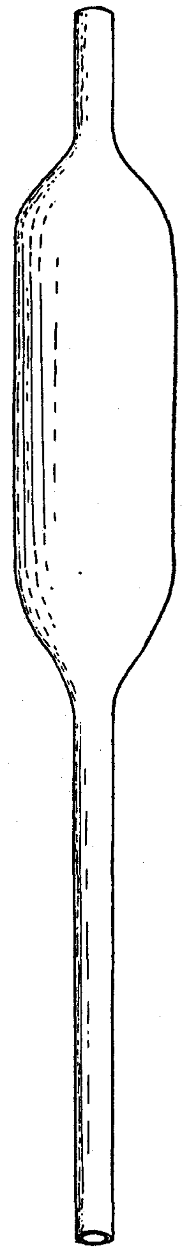

FIG. 36.—Volumetric pipette used for sampling copepods for counting

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

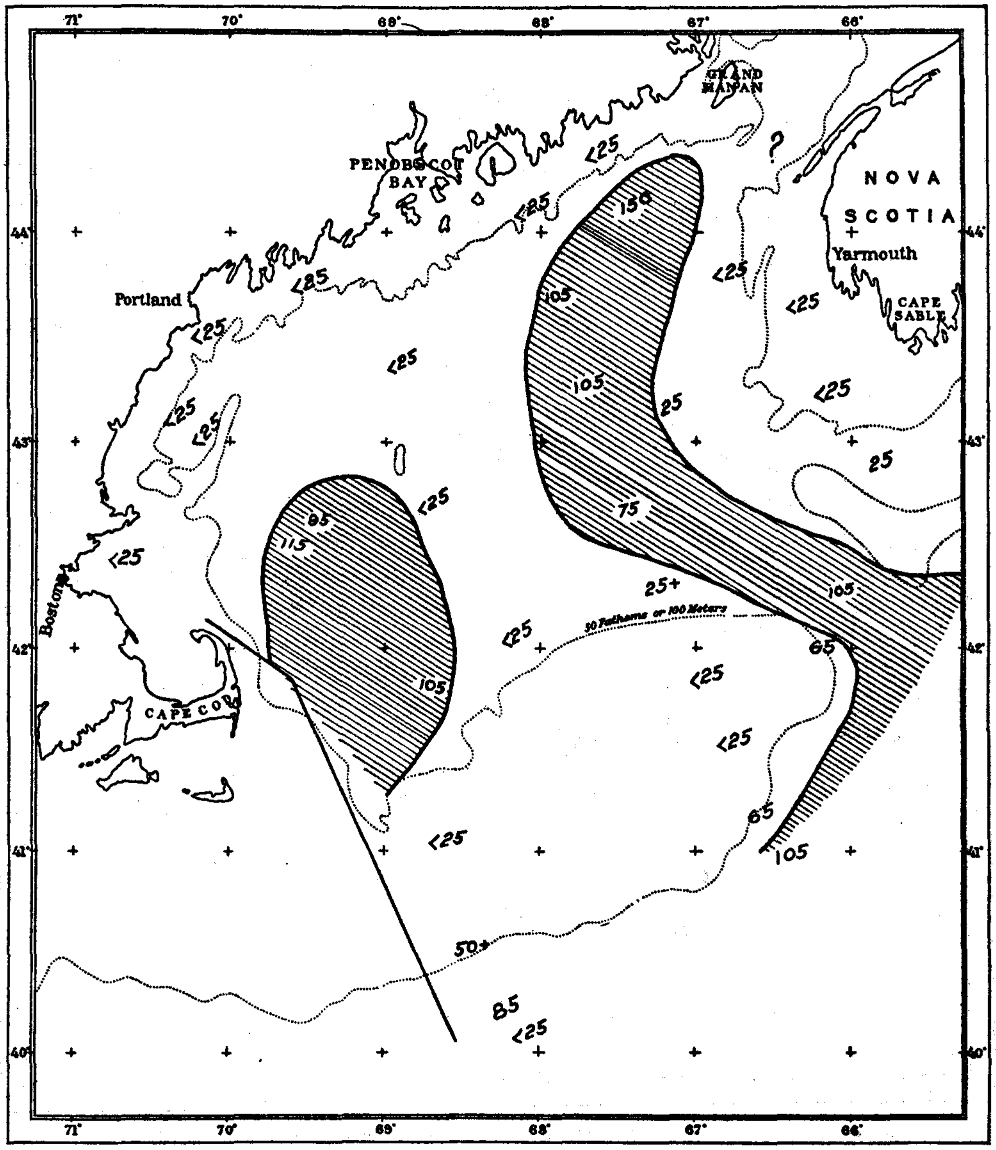

FIG. 37.—Volumes of plankton, in cubic centimeters, below each square meter of the surface of the sea in February and March, 1920, as calculated from the catches made in the vertical hauls. In the shaded area the volumes were uniformly greater than 75 cubic centimeters.

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

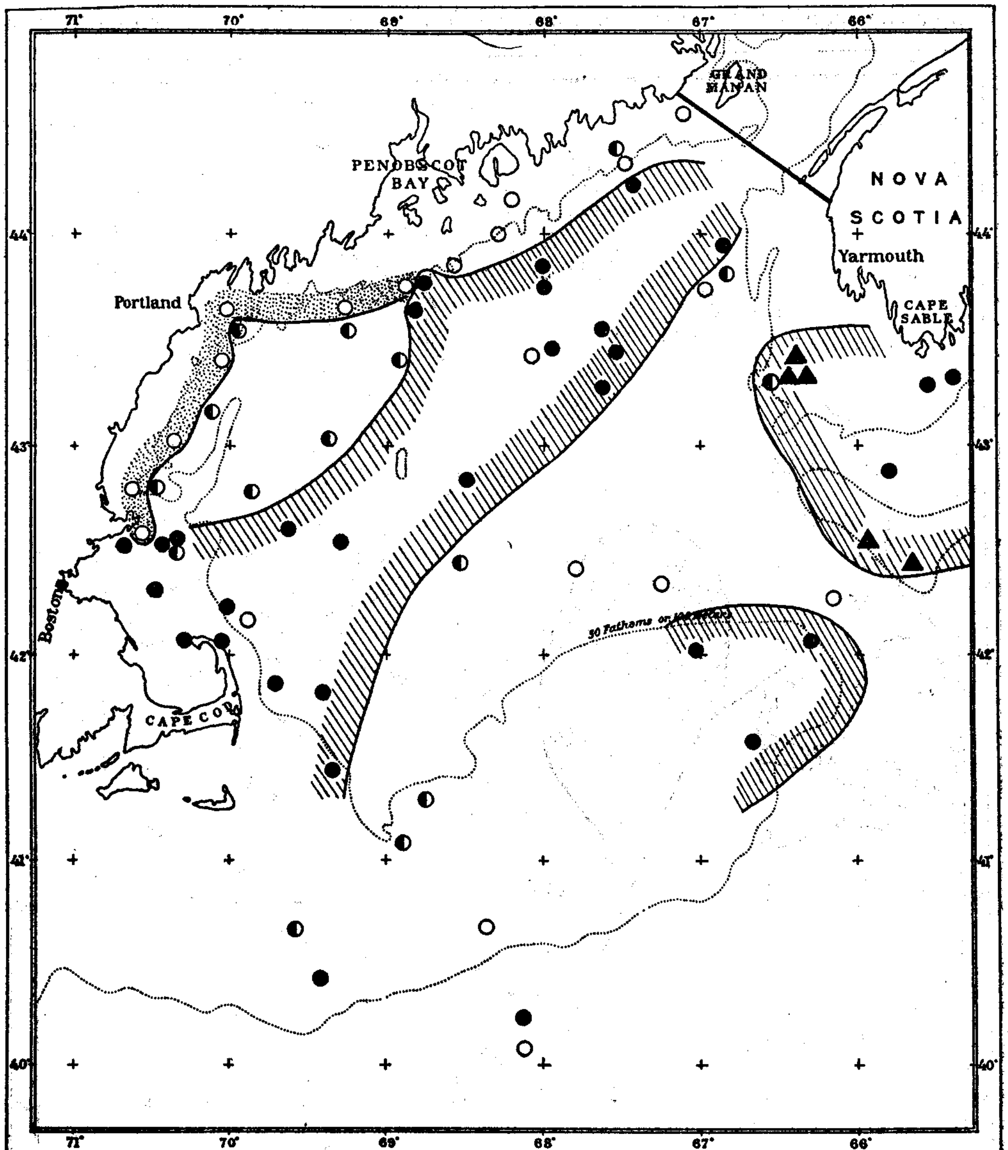

FIG. 38.—Volumes (cubic centimeters) of animal plankton below each square meter of the surface of the Gulf of Maine in summer, as calculated from the vertical hauls made in 1912–1916. ●, 100 cubic centimeters or more per square meter; ◐, 50 to 100 cubic centimeters or more per square meter; ○, 50 cubic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

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

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

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

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

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

Zoöplankton volumes, mouth of Massachusetts Bay

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

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

We have made no quantitative hauls in the gulf during the period between October and late February, but the comparative scantiness of the yields of the horizontal nets in Massachusetts Bay during the cold months of 1913 (Bigelow, 1914a) and at all our inshore stations from Cape Cod to Yarmouth, Nova Scotia, in December, 1920, and January, 1921, points to an ebbing zoöplankton as characteristic of the coastal belt in late autumn and early winter, leading progressively to the extremely barren state of the water typical of the first weeks of spring (p. 82). Hauls made near Mount Desert Island and in the northeast corner of the gulf from January 1 to 5, 1921 (stations 10497, 10500, and 10502) were equally unproductive,[43] but I hesitate to conclude from this that the water was actually so barren there, because horizontal hauls were hardly more productive in that general region in March, 1920, although the vertical nets yielded large catches, a fact suggesting that the former missed the level at which the plankton was most concentrated. However this may be, it seems that in winter and early spring the zoöplankton is far more plentiful in the western side of the basin than near shore, because we made a rich horizontal catch there on December 29, 1920 (station 10490), a rich vertical haul (though a rather scanty horizontal) on February 23, 1920 (station 20049), and a rich horizontal and a comparatively rich vertical on March 24 of that year (station 20087).

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

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

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

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

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

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

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

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

Volumes of plankton per square meter, western basin

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

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

DENSITY OF ASSOCIATION OF THE ZOÖPLANKTON

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

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