SECTION 2.—GENERAL SURVEY OF THE PLANKTONIC PLANTS (PHYTOPLANKTON) AND UNICELLULAR ANIMALS

Unicellular pelagic plants, or, to use the more convenient term, "phytoplankton," play as large a rôle in the natural economy of the Gulf of Maine as in other boreal seas. Strangely enough, however, systematic collection and examination of them in this particular region date back only to 1912 (Bigelow, 1914). Since then many hauls of phytoplankton have been made in the offshore parts of the Gulf of Maine, but time and the assistance available have so far allowed only a preliminary examination of these. Besides these records for the open sea in the gulf, McMurrich (1917), Bailey (1910, 1915, and 1917), Bailey and Mackay (1921), and Fritz (1921) have published valuable surveys of the phytoplankton (particularly the diatoms) from the estuarine waters near the Canadian biological station at St. Andrews in the Bay of Fundy, and in addition Doctor McMurrich has very kindly allowed the use of his unpublished notes, to which frequent reference will be found in the following pages.

Gran (1912) has recently given such an excellent and readable account of the phytoplankton of the high seas as a whole and of the rôle it plays in the economy of nature that no general survey is called for here. Suffice it to say that these unicellular algæ are the chief marine producers (organisms, that is, capable of elaborating organic compounds from inorganic substances in sunlight) and the only producers over the high seas outside the narrow coastal zone within which seaweeds flourish. I do not know who first paraphrased the expression "all flesh is grass" with the words "all fish is diatoms," but if not taken too literally it expresses the fundamental truth that the whole system of animal life in the sea (as on land) depends on plants in the last analysis and chiefly on the tiny unicellular algæ, which we often capture in millions in our tow nets.

The groups that play the major rôles in the phytoplankton of the Gulf of Maine, as well as in other northern seas, are the diatoms and the peridinians, which alternate in more or less regular seasonal succession, to be described below; and since the value of the following account depends chiefly on the correct identification of the several species, a word on this subject will be germane here. The diatoms are proverbially a "difficult" group because fresh and brackish waters support a multitude of species, which are separable one from another only by most painstaking study with the microscope. Fortunately, however, although the planktonic diatoms are probably the most numerous of all marine organisms in number of individuals, the species occurring regularly in the plankton of northern seas are comparatively few,[21] while those that dominate the northern planktonic communities at one time or another (and these are, of course, the most important from both the geographic and the

[21] Gran (1908) lists about 170 species as typically pelagic in boreal-Arctic waters.

ecologic standpoints) are fewer still. Until comparatively recently the identification of even these few could hardly be attempted by anyone not a specialist in the group, but thanks to Gran's (1908) excellent synopsis, to Meunier's (1910) beautiful figures, and to the fact that most of the important species are distinguished by rather precise characters, they are now no more difficult to name than are other planktonic groups; far less so, for instance, than the smaller copepods. A certain number of species, of course, are hardly to be determined except under most favorable circumstances. For example, certain members of the genus Chætoceras are separable only when carrying their resting spores, but these are in the minority. It chances that most of the diatoms that are prominent numerically in the phytoplankton of our gulf at one time or another—for example, the members of the genera Thalassiosira and Rhizosolenia and most of the predominant members of the genus Chætoceras—are characterized by such well-marked structural features that no one trained in systematics in general and in the study of marine plankton in particular should experience any unusual difficulty in referring them to their respective species by Gran's (1908) tabular keys. What is required for this is close observation of small characters, often under high powers of the microscope; but the technique is simple, amounting usually to nothing more than examination in water or in formalin—at most to the drying process employed by Gran (1908, p. 6) or to one of the modes of mounting described by Mann (1922). The complicated methods of cleaning, so valuable in the study of estuarine and bottom-living diatoms as a whole, are not essential when the object in view is merely the identification of the comparatively large and already well-known species of marine planktonic diatoms preserved in formalin as taken from the tow net.

Since no attempt is made in the present paper to contribute to the systematics of marine diatoms, the nomenclature follows Gran (1908) strictly, except as noted below. The identification of the representative lists (p. 423) having been verified by Dr. Albert Mann, a leading student of the group, they are offered with some confidence, although the catches still await final examination.

The peridinian element in the plankton of the gulf is represented chiefly by members of two genera—Ceratium and Peridinium—genera so unlike in appearance as to be separable at a glance; and while a good deal of discussion has centered about the relationships, specific, varietal, or genetic, of the numerous representatives of Ceratium (which is usually the dominant peridinian in the Gulf of Maine), it is not difficult to refer the specimens in question to the proper subgroup—call it species or what you will—by the use of Paulsen's (1908) recent synopsis. The following identifications follow him strictly. Fortunately the naked peridinians,[22] which are not only far more difficult to discriminate among but apt to be mashed past recognition in the nets, have never been prominent in our tows; in fact, never detected except for a brief period in the spring (p. 417).

[22] For descriptions and beautiful figures of these the reader is referred to Kofoid and Swezy's (1921) monograph.

PHYTOPLANKTONIC COMMUNITIES

Although our studies in the Gulf of Maine are in their infancy, as compared with the intensive surveys that have been made in north European waters, they have progressed sufficiently to give a general idea of the groups of microscopic plants primarily concerned, and of their seasonal alterations; and although periodic or sporadic fluctuations are to be expected in the composition of the pelagic communities, the seasonal cycle here outlined and the accompanying charts, based on our tow-net hauls, are offered with some confidence as representing what may be called the basic status of the phytoplankton of the Gulf of Maine.

It is necessary to select some arbitrary starting point in describing the general seasonal succession of diatoms, peridinians, and other groups, though necessarily this is an artificial one because the planktonic cycle is uninterrupted from year's end to year's end. Perhaps the most convenient is the status late in February or during the first days of March, when the phytoplanktonic community falls to its lowest ebb over the Gulf of Maine as a whole, just prior to the vernal awakening that takes place in the sea as well as on the land. Unfortunately our data for the open gulf at this season are not all that could be desired, for although the *Albatross* made a general planktonic survey of the gulf between the 22d of February and the 24th of March in 1920, this, as it proved, did not altogether forestall the earliest flowerings of diatoms. But from this cruise, added to winter tow nettings made in 1912 and 1913 (Bigelow, 1914a), and during December to January, 1920–1921, and from the counts of diatoms tabulated by Fritz (1921), it is safe to assert that when the temperature of the gulf is at its minimum for the year, just prior to the first trace of spring warming, its offshore waters as a whole and the estuarine tributaries of the Bay of Fundy [23] support only a very scanty phytoplankton, in which peridinians (p. 407) and oceanic diatoms mingle (fig. 104), except that vernal flowerings of diatoms are already under way locally along its northwestern shore and over the western part of Georges Bank. In 1920 this description applied to the entire basin of the gulf as well as to the eastern part of Georges Bank, at least up until the middle of March. But flowerings of diatoms, resulting in local swarms so dense as to be the most spectacular event in the yearly planktonic cycle, were already under way along a narrow coastal zone between Cape Ann and Cape Elizabeth by the first week of that month (stations 20059 and 20060), and their future expansion was foreshadowed even thus early in the season by the fact that diatoms in small numbers had replaced the peridinians as far east along the coast as Mount Desert Island, on the one hand (stations 20056 and 20058), and bulked about as large as the peridinians in a very sparse phytoplankton off Gloucester on March 1, on the other (station 20050; genera Coscinodiscus and Thalassiosira). On March 4, 1913, diatoms dominated near this last locality, and on March 5, 1920 (station 20061), we found a pure diatom plankton with only an occasional peridinian; but on both these occasions the total catch of phytoplankton was still very scanty. As April 3 (Bigelow, 1914a, p. 405) is the earliest date when we have found diatoms in great abundance at the mouth of Mas-

[23] No planktonic data are yet available for other inclosed waters or harbors around the gulf at this season.

sachusetts Bay, it is not likely that the vernal flowerings become active there until after the middle of March—that is, at least three weeks later than in the waters between Cape Ann and Cape Elizabeth, or in Cape Cod Bay (p. 396).

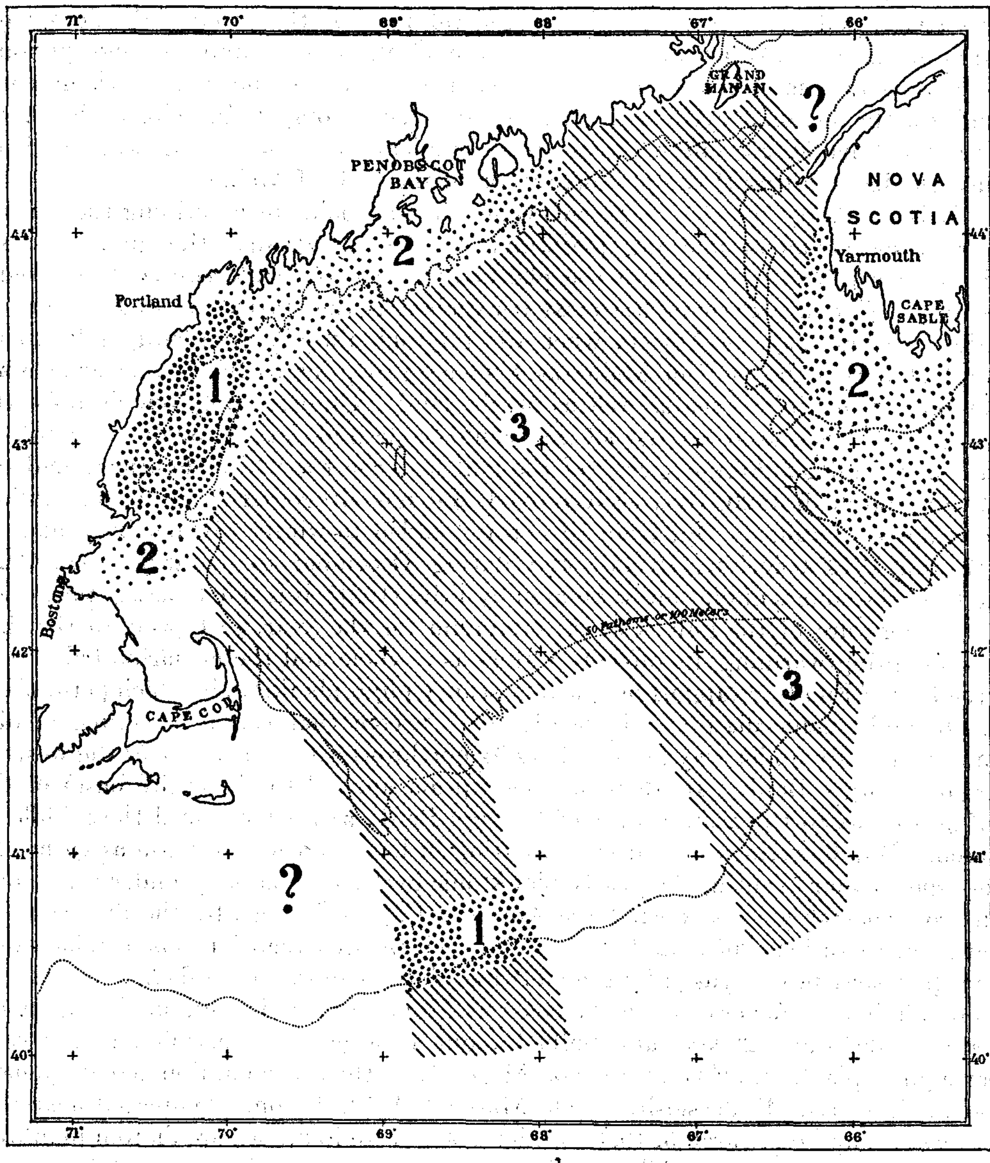

FIG. 104.—Distribution of the more characteristic types of phytoplankton, February to March, 1920. 1, rich diatom; 2, sparse diatom; 3, sparse Ceratium and diatom

The shallow waters off western and southern Nova Scotia, out to and including German and Browns Banks, are the site of a second center of propagation for diatoms late in March, for though the phytoplankton was still very scanty there on the 23d of that month in 1920 (stations 20078 and 20082 to 20085), it consisted chiefly of diatoms with few peridinians; and by April 15 (stations 20101 and 20103 to 20106) the waters in this part of the gulf were cloudy with neritic diatoms of the species listed below (p. 427). A rich diatom community was also discovered by the *Albatross* on the southwestern part of Georges Bank even earlier in the year (February 22, station 20046).

The diatom flowerings of the western side of the gulf expand in all directions and at the same time multiply so rapidly during the last half of March that their numbers are soon countless. By the 3d of April we have found them so abundant in Massachusetts Bay as to cloud the water and clog our nets (Bigelow, 1914a, p. 405), a state again observed from the 6th to the 9th of April in 1920 (stations 20089 and 20090); and by that season diatoms swarm from Cape Cod on the south to Cape Elizabeth and Casco Bay on the north, as far out from land as the 200-meter contour at the inner edge of the western basin (fig. 105). Fritz also found diatoms augmenting suddenly and to an extraordinary abundance at St. Andrews between the end of March and the end of April. Meantime the eastern diatom community vastly augments in numbers over the whole coastal bank off southwestern Nova Scotia and out across Browns Bank to the eastern channel (stations 20103 to 20107), where we found them swarming on April 12 to 16 in 1920.

A rich gathering of diatoms off the southeast slope of Georges Bank on that date (station 20109) is especially interesting because there were comparatively few (and these of more oceanic species) in the waters over the neighboring parts of the bank (stations 20108, 20110 to 20111). The presence of the abundant flowering in question at just that place therefore points to a drift from Browns and the other shallows to the eastward, as did a shoal of Calanus at that same locality the month previous (p. 189). However, Georges Bank is itself the site of extremely productive flowerings in April, though we did not chance to encounter them there in that month in 1920, for Douthart's tows yielded a great abundance of several species on its northern part during the last half of the month in 1913 (Bigelow, 1914a, p. 415).

Hand in hand with this vernal multiplication of diatoms, peridinians diminish almost to the vanishing point. As the impoverishment of this group apparently takes place nearly simultaneously over all but the southeast corner of the gulf, and so early in the season that the rich diatom flowerings are still restricted to the coastal waters within the gulf, to the shallows of Browns and of Georges Banks, and to the intervening channel and the continental slope, there is a very sharp contrast during the last half of April between these swarms of diatoms and a very scanty diatom plankton in the central and northeastern deep of the gulf, which is reminiscent of the mixed peridinian and diatom community existing there in March.

During late April the flowerings of diatoms that have originated in the northwest part of the gulf two months earlier (fig. 104) spread eastward beyond Mount Desert Island, while at about this same time a great increase takes place in the numbers of diatoms (though of other species) present in the waters of the Western Basin [24] and thence throughout the center of the gulf generally, where we found

[24] In 1915 diatoms were extremely abundant in the Western Basin and near Cashes Ledge on May 4 (stations 10267 and 10268, fig. 121).

diatoms swarming and peridinians practically nonexistent during the first half of May in 1915 (Bigelow, 1917, p. 324), the result being that the vernal flowerings of diatoms reach their widest expansion at this season.

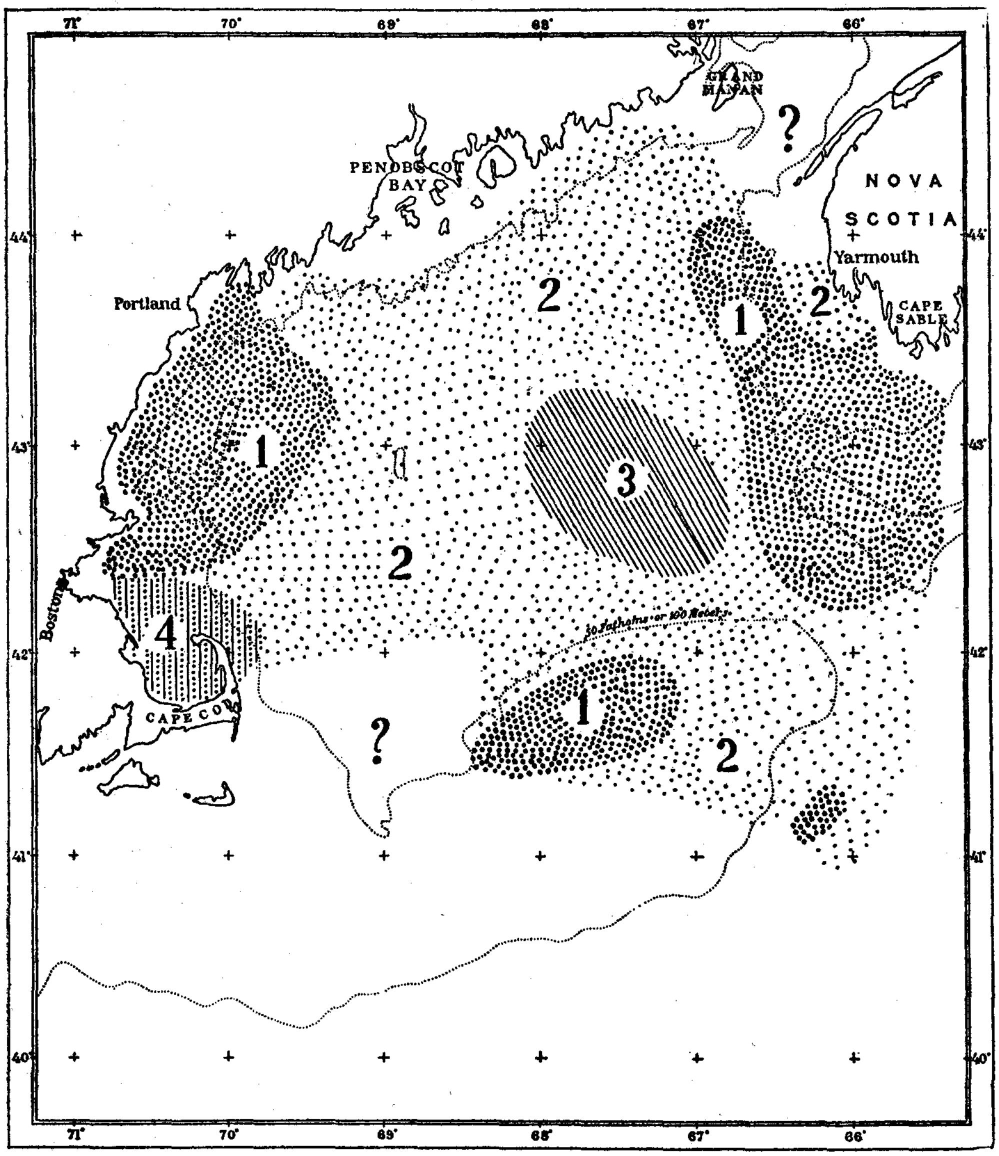

Fig. 105.—Distribution of the more characteristic types of phytoplankton, April, 1920. 1, rich diatom; 2, sparse diatom; 3, sparse Ceratium and diatom; 4, rich Phæocystis and diatom

The unicellular alga Phæocystis may also swarm, even to the extent of monopolizing the surface waters locally, for a brief period during the month of April, but shortly disappear once more, as occurred in the southern part of Massachusetts

Bay and off Cape Cod during the last half of the month in 1920 (p. 458). Although this is the only occasion on which we have actually observed this event, it is to be expected equally in other parts of the gulf, where the peak of abundance for Phæocystis may have chanced to fall between the dates of our successive cruises.

These diatom flowerings of the Massachusetts Bay region are so short-lived and dwindle so suddenly after they have attained their plurimum that we found them reduced to an occasional Coscinodiscus only among a scanty community of Ceratium, Peridinium, and Halosphæra on May 4 to 16 in 1915 [25] and again in 1920, although diatoms continue swarming in the central parts of the gulf and along its northern shore line generally until considerably later. Diatoms vanish equally from the waters along Cape Cod by the middle of May, where only an occasional diatom was to be found among the small catches of Ceratium and Peridinium at three stations on a line run by the *Albatross* from Cape Cod out to the north slope of Georges Bank in 1920 (stations 10225 to 10227, May 16), though the water over the southwestern part of the bank still supported much the same diatom community as the last week of February (p. 383). This late flowering was strictly limited, however, to the shallows of the bank because our tow nettings over the continental slope a few miles to the south yielded little except a sparse gathering of peridinians (station 20128).

In the western side of the gulf the shrinkage of the diatom communities, following their season of abundance, which, as we shall see, foreshadows their eventual disappearance from the plankton, proceeds progressively from south to north during May. Thus tow-net catches made about the Isles of Shoals, where we were able to follow the rise, culmination, and eclipse of the diatom flowerings at close intervals during the spring of 1913, were still exceedingly abundant (almost purely diatom) and very clean up until the first week in May in 1913, whereas there were very few diatoms on the other side of Cape Ann as late as this. From that time forward, however, the plankton of the Isles of Shoals area began to contain noticeable amounts of diatom débris, and as the season advanced the relative amount of dead specimens and variously fragmented remnants grew progressively greater until the 25th of the month, when there were very few living diatoms (Bigelow, 1914a, p. 406), though the nets still yielded large amounts of their débris.

Peridinians, on the other hand, and especially the genus Ceratium, multiplied as the diatoms dwindled (perhaps more relatively than absolutely), changing the general composition of the phytoplanktonic community so rapidly, from rich diatom at the beginning of May to peridinian with but few diatoms at the end of the month in the area bounded on the south by Cape Ann, on the north by Cape Porpoise, and offshore by Jeffrey's Ledge, that it is represented as "mixed diatom and peridinian" on the accompanying chart for May (fig. 106).

The duration of the spring flowerings of diatoms in the shoal waters off southwestern Nova Scotia is likewise brief, for though they filled our tow nets there on April 15, 1920 (stations 20103 and 20105), we found a sparse Ceratium plankton in that general region from May 7 to 10, 1915 (stations 10271 and 10272), with but few diatoms.

[25] Station 10266, May 4, 1915; station 10220, May 1 and 16, 1920.

In the deep offshore waters of the gulf, diatoms do not attain their maximum abundance for the year until some time during the last half of May or first week in June, after which they diminish so rapidly in number that in 1915 (the only year

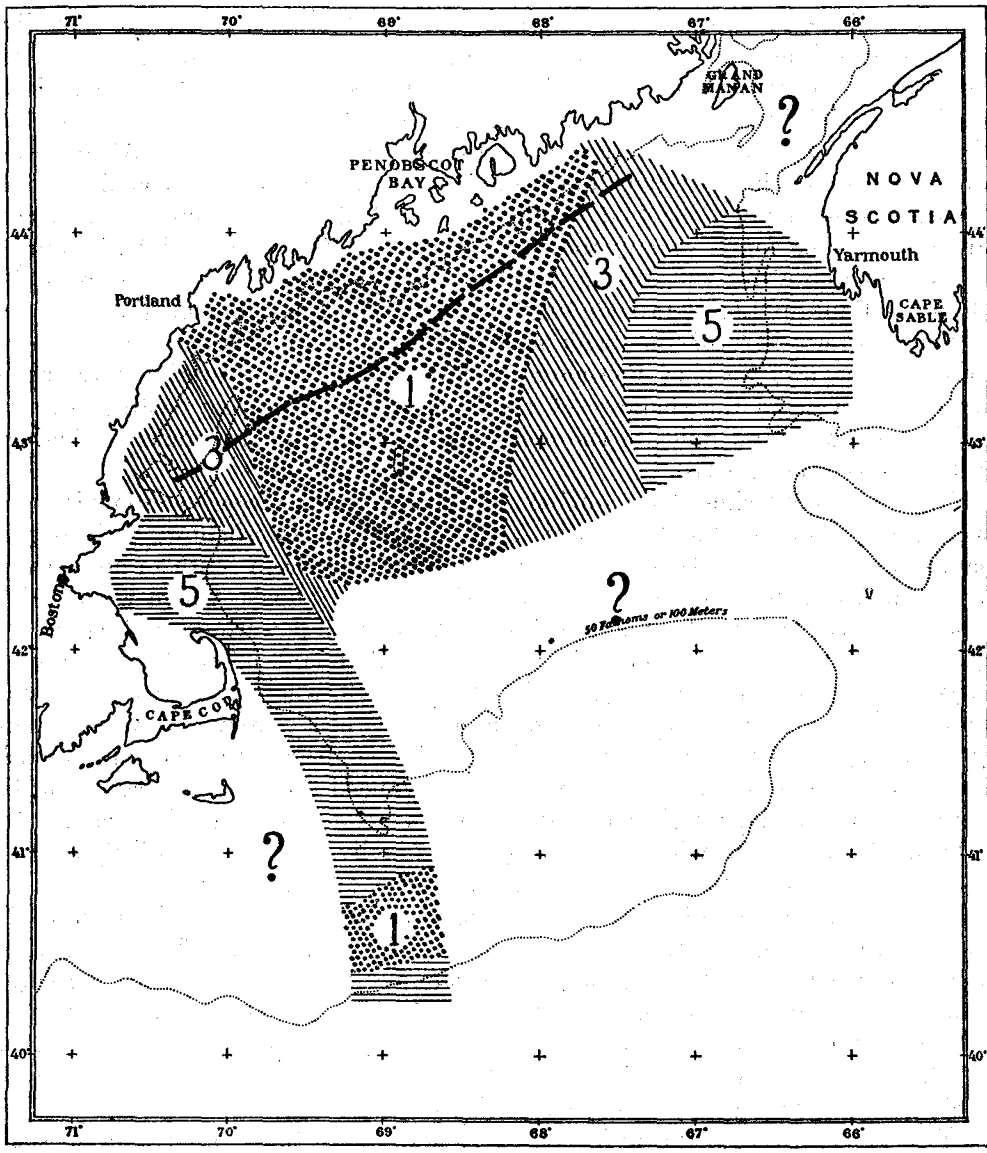

FIG. 106.—Distribution of the more characteristic types of phytoplankton, May, 1915 and 1920. **1,** rich diatom; **3,** Ceratium and diatom; **5,** Ceratium. The heavy broken curve marks the offshore boundary to abundant Thalassiosira

of record) we found that diatoms had practically vanished by mid-June from the tow nettings made in the basin of the gulf south of the line Cape Ann–Cape Sable, having been replaced there by a scanty peridinian plankton. Diatoms had also fallen to a low ebb everywhere in the offshore waters of the northern half of the gulf by June 10 to 19, when they mingled with a scanty community of peridinians. Diatoms, however, were still flowering abundantly in the coastal zone east of Penobscot Bay at that time, for we found them in swarms off Petit Passage on the southern side of the Bay of Fundy on June 10 and again near Mount Desert Island (stations 10285 to 10287) on June 14 in 1915. Fritz (1921) also records diatoms in comparatively large numbers at St. Andrews in June, though not as abundantly as in May, on the one hand, or in July, on the other. It is probable that in June these three localities are local centers of production and not parts of a continuous coastwise belt of rich diatom plankton for two reasons—first, because Fritz found very few diatoms in the open Bay of Fundy on June 15, 1917, and, second, because they were but sparsely represented in our tow in the Grand Manan Channel on June 4, 1915 (station 10281).

Thus, a general and very pronounced diminution in the number of diatoms takes place over the offshore waters of the gulf as a whole and all along its western shore during May and June; but in the year 1915 diatoms reappeared, though not in great numbers, and mingled with peridinians, over the shoal coastal bank off western Nova Scotia during the last half of June (station 10290, June 19). The scarcity of diatoms in that region in May of that year may be assumed to have followed rich April flowerings and coincides with the greatest expansion of the Nova Scotian current in that region. Unfortunately we have made no hauls close in to this part of the Nova Scotian coast during June and have no data on the phytoplankton of the eastern half of Georges Bank, of the southeastern part of the basin of the gulf, or of Browns Bank for May.

As I have pointed out in an earlier report (Bigelow 1917, p. 326)—indeed, the facts outlined above would suggest it—the seasonal history of peridinians in the Gulf of Maine is just the reverse of that of the diatoms. In late February and during March they join with the latter to characterize the sparse plankton of the whole basin of the gulf, this "mixed" zone extending into its northeastern corner, on the one hand, and over most of Georges Bank, on the other, likewise over the shelf abreast of Shelburne, Nova Scotia. But even this early in the season they are entirely dominated in the several centers where diatoms have commenced flowering actively, and by April they are so wholly overshadowed in the regions where the diatom flora is at its climax that only an odd ceratium or peridinian is to be found among the masses of diatoms that clog the nets. Over most of the central and southern parts of the gulf, where diatoms are not yet very plentiful, they are sufficiently so to make the few peridinians a minor element in the tows (though these never wholly disappear from any part of the gulf at any season), leaving only a small area in the southeastern part of the gulf where there are so few diatoms that the few Ceratium still color the plankton of April.

As the flowering of diatoms reaches its climax and then diminishes in its regular seasonal progression, the peridinians (chiefly Ceratium) take their place in constantly augmenting abundance. This happens earliest in the season in the Massachusetts Bay region in the western side of the gulf and off southwestern Nova Scotia in the eastern, where Ceratium dominated the plankton as early as the first week of May in 1915, leaving diatoms still overwhelmingly dominant in the central deeps of the gulf and along its northern coastline. Comparison of the chart for May (fig. 106) with that for April (fig. 105) illustrates the encroachment of these two peridinian centers—western and eastern—on the areas previously characterized by abundant diatoms, the former replacing the latter over the coastal zone from Cape Cod northward across Massachusetts Bay and past Cape Ann, on the one side of the gulf, southward, too, as far as Georges Bank, and offshore over the eastern side of the basin on the other, by the last half of May.

Probably peridinians would also have been found to dominate the phytoplanktonic community right across the southern part of the deep basin of the gulf at that

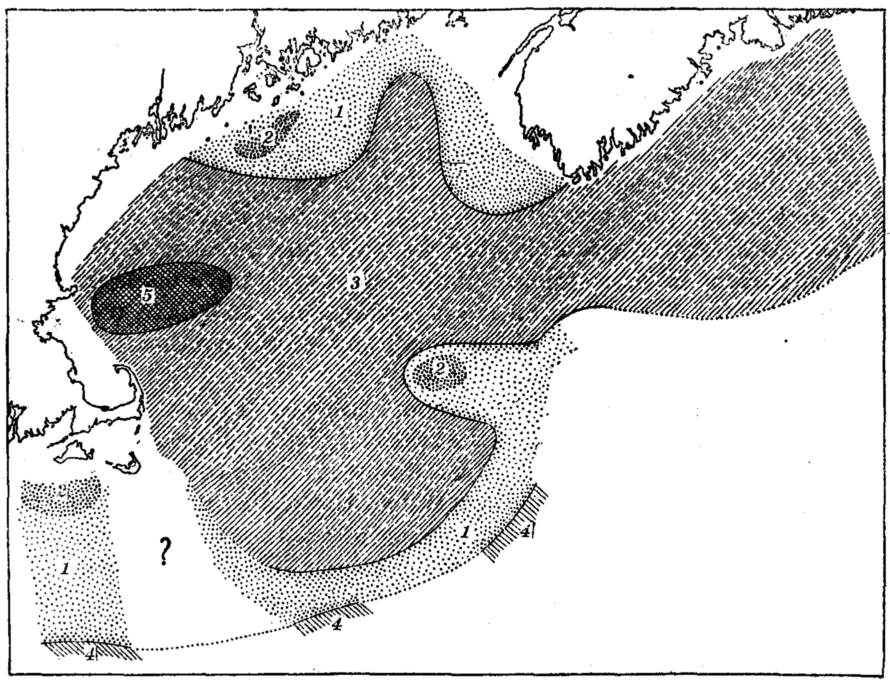

FIG. 107.—Distribution of the more characteristic types of phytoplankton, July to August, 1914. **1**, Ceratium and diatom; **2**, diatom; **3**, Ceratium; **4**, tropical, characterized by Trichodesmium; **5**, Radiolarion. (Reproduced from Bigelow, 1917, fig. 97)

time. This is certainly the case by mid-June, when we have found them in considerable abundance at all our stations near the coast as well as offshore (and this covers the whole northern half of the gulf), except in the rich but circumscribed diatom areas just described for that month, where peridinians were still extremely rare.

No doubt variations from this planktonic cycle are to be expected from year to year, but it is sufficiently established that the vernal flowerings of the pelagic diatoms, followed by their eclipse, with the coincident disappearance and reappearance of peridinians, are as characteristic of the spring season in the offshore waters of the Gulf of Maine as are the spring freshets from the rivers that discharge along its coast, in which, as in so many other ways, the gulf closely parallels other northern seas.

In midsummer (fig. 107) we have usually found the entire basin of the gulf occupied by a peridinian (Ceratium) plankton, with only occasional diatoms, and we have never found diatoms in abundance anywhere in the gulf in July or August except close along the coast, on the one hand, and on Georges Bank, on the other.

We found diatoms flowering in abundance on each of our summer visits to the latter locality, but in different regions in different years. Thus they dominated on the western end of the bank on July 9, 1913 (station 10059) and on July 23, 1916 (stations 10347 and 10348), but when we visited that general locality on July 20, 1914, the water contained very few diatoms but, instead, a characteristic peridinian plankton. Three days later, however, we encountered a rich flowering of diatoms near the northeastern edge of the bank (station 10224). Furthermore, the Georges Bank flowerings of July, 1913 and 1914 (stations 10059 and 10224; see list, p. 430), though far apart geographically, were both dominated by Guinardia. In July, 1916, however, we found no Guinardia on a traverse of the western part of the bank but swarms of Thalassiothrix (p. 455) and Rhizosolenia (p. 444) in its stead. With so little data available it is not possible to outline the normal summer status of diatoms for the Georges Bank region. Nevertheless, the fact that we have found them in such abundance on some part of the bank on each visit in summer, with the abundant flowerings encountered there in February and May of 1920 by the *Albatross* (pp. 383, 387), and in April, 1913, by Douthart (p. 385), shows that swarms of diatoms may be expected somewhere on its extent at any time from late winter until midsummer. It is not unlikely that this applies to Nantucket Shoals also, for Dr. W. C. Kendall writes, in his field notes, that on September 2, 1896, the water "was very full of brown slimy stuff" at latitude 40° 47′, longitude 69° 43′, which could only have been diatoms.

It is not yet clear whether any particular region on the banks is more favorable for the multiplication of diatoms than another, except that we have always found these rich flowerings on its shoaler parts and never close enough to the continental slope to be within the influence of the high temperature outside the edge, which, in its own turn, supports various oceanic diatoms in small numbers mingled with peridinians of similarly Tropic origin.

The fertility in diatoms of the waters over Georges Bank is interesting, not only from the standpoint of the phytoplankton *per se*, but because of the great importance of the bank as a spawning ground for haddock. The prevalence of the genus Guinardia on the bank, contrasted with its absence or rarity in the deeper waters of the gulf to the north, is likewise instructive for its bearing on the circulation of the water in this region.

Turning now to the coastwise belt, diatoms continue a more important factor in the phytoplankton of estuarine situations throughout the summer than they are in the open waters of the deeper parts of the gulf at that season. Owing to the fact that most of our towing has been well out at sea, we have few data to offer on this regional differentiation. It was clearly demonstrable in Massachusetts Bay on August 22 to 24, 1922, however, when several stations close in to the land, following around the coast line from Cape Cod Bay to Cape Ann,[26] were dominated by diatoms

[26] Stations 10633, 10634, 10637, 10639, and 10642.

(chiefly Skeletonema and *Rhizosolenia alata;* pp. 448 and 447), whereas hauls at several stations farther out in the bay or off exposed stretches of the coast line[27] were dominated by the peridinian genus Ceratium (p. 407), as the open gulf as a whole usually is in summer.

We also found the water in Casco Bay, near the Harpswell biological laboratory, so cloudy with diatoms and Peridinium with bright red chromatophores on July 27, 1912, that its transparency was only about 4 meters. Two days later, however, a tow at the same location yielded hardly a diatom and very little phytoplankton of any kind, its place being taken by a fair representation of copepods, small medusæ, and many ophiuran larvæ.

Tows for the years 1912, 1914, and 1915 proved diatoms a major element in the phytoplankton in the neighborhood of Mount Desert Island in August; locally swarming (p. 431). Fritz (1921) also found this to be the case in the St. Andrews region. She also records an abundant July plankton of diatoms in the more open waters of the Bay of Fundy. Our few August tows in the Grand Manan Channel have yielded chiefly diatoms, though the phytoplanktonic community as a whole has been extremely sparse there. Diatoms have likewise shared with the peridinians the domination of our summer tows in the northeastern corner of the gulf off the mouth of the Bay of Fundy, and we have found this condition on German Bank and off Lurcher Shoal during each August when we have visited that region, while there were a few diatoms as far offshore as Browns Bank on July 24, 1914, among the more abundant peridinians that characterized the phytoplanktonic community there. Cape Sable, however, seems to mark the eastern boundary for diatoms as an appreciable factor in the plankton during the latter half of the summer.

Diatoms were a much more important factor in the plankton of the gulf in the summer of 1912 than at that season in 1913, 1914, or 1915. During that July and August they occurred in great abundance all along the coast from Seguin Island (situated a few miles east of Casco Bay) as far eastward as the mouth of the Grand Manan Channel, and were plentiful enough over the whole northeastern corner of the gulf, mingled with the peridinians, to give a distinctive aspect to the catches, instead of being limited to the narrow confines just outlined as the usual bounds to their summer flowerings. More interesting than the unusual abundance of diatoms which characterized that summer is the fact that this was mostly due to a species (*Asterionella japonica*) which has not been found in the offshore waters of the gulf since that time (p. 432). The genera Thalassiosira and Chætoceras likewise were more widespread and numerous in the eastern side of the basin then than we have since found them at that season, reflecting an unusually late continuance of their vernal flowerings (Bigelow, 1914, p. 132).

This much stress has been laid on the midsummer status of diatoms in the Gulf of Maine because of the very important rôle which this group of microscopic plants plays in the economy of the sea earlier in the season; but when all is said, diatom plankton occupies only a small part of the area of the open gulf during the warm months, as contrasted with the much more extensive area which then supports a typical peridinian plankton dominated by the genus Ceratium.

[27] Stations 10630, 10631, 10632, 10636, 10638, 10640, and 10641.

The record of towings is now sufficient to show that this peridinian community, with only an occasional diatom, normally dominates and usually monopolizes the phytoplankton of the whole of the central part of the gulf outside the 100-meter contour during the late summer and early autumn, from off Cape Elizabeth and Cape Cod, on the one side of the gulf, to German Bank and Cape Sable, on the other, and from about the 100-meter contour on the north, southward across the whole breadth of the basin to include the Eastern Channel, though with an admixture of diatoms in the northeastern part, as just noted.

A typical Ceratium plankton, or at least a predominance of Ceratium mingled with the diatoms, has likewise characterized all our summer tows on Georges Bank except for the local diatom flowerings just described. But, judging from St. Andrews and from conditions in north European seas, it is not likely that Ceratium, the peridinian genus that is predominant out at sea in the gulf, ever attains abundance in its estuarine waters, for according to McMurrich (1917, p. 3) none of the dinoflagellates were sufficiently numerous to be an important quantitative constituent of the plankton at St. Andrews at any season, "*C. tripos* only on one occasion being in sufficient quantity to be regarded as frequent." Nevertheless, Ceratium follows essentially the same seasonal pulse there as at our stations out at sea, reaching its plurimum in autumn and practically vanishing from the tows in April and May.

It is impossible to prepare a chart of the mutual limits of the chief classes of phytoplankton in the gulf for midsummer, which shall be as true for one year as for another, because of the yearly fluctuations in the abundance of and area occupied by diatom plankton near its northern coast and of the variable midsummer flowerings of diatoms on Georges Bank. On the whole, however, the state obtaining during July and August of 1914 (fig. 107) seems fairly representative of the offshore waters of the gulf in the summer season, bearing in mind the different locations of the diatom swarms on Georges Bank of July, 1913, and July, 1916. A corresponding chart of the northern part of the gulf for 1912, published in an earlier report (Bigelow, 1914, pl. 8), illustrates a summer more productive of diatoms.

The sporadic occurrence of swarms of acantharian radiolarians in the western part of the gulf in some summers, though perhaps not annually, a conspicuous feature of the chart for 1914 (fig. 107), need be mentioned but briefly here, being discussed below (p. 460).

It is in July and August, if ever, that tropical phytoplanktonic communities may be expected to drift northward from the Gulf Stream across Georges Bank and thus to penetrate the inner parts of the Gulf of Maine. But if our hauls are to be trusted as fairly representative, this rarely takes place, the only positive records of this sort which have yet been obtained for the inner parts of the gulf or even for the shoaler parts of Georges Bank itself being a fragment of gulf weed (Sargassum) picked up on German Bank on September 2, 1915 (station 10311; Bigelow, 1917, p. 246), and an occasional *Ceratium macroceras* detected among other boreal species of the genus off the Merrimac River on December 30, 1920 (station 10492).

Planktonic forms of tropic origin, plant as well as animal, are, of course, more important along the slope south of Georges Bank (p. 54), thanks to the close proximity of the tropic water. Thus gulf weed is often seen floating there in some quantity, as was the case at our outermost stations in the summer of 1914 (stations 10218 and 10220). July and August stations (10218 and 10261) in 1914 over the slope west of longitude 68° W. and south of latitude 42° 10′ N. likewise yielded small amounts of the characteristically tropical alga Trichodesmium, together with *Ceratium macroceras*, which also occurred off the southeast face of Georges Bank in July (station 10220) and in the coastal waters off Martha Vineyard in August (stations 10258 to 10260); but we have never found *C. macroceras* along the continental slope farther east than the Eastern Channel.

Although tropical pelagic plants, both large and miscroscopic, as well as planktonic animals belonging to this same category in their relationship to temperature, may be expected to encroach on the western half of Georges Bank at some time during most summers, just as they do more regularly and abundantly farther west and south, the exact season when this happens varies considerably from year to year, as might be expected from the fluctuations in the location of the inner edge of the Gulf Stream, a fact illustrated by their failure to appear there by the third week of July in 1916. Probably they are hardly to be expected along Georges Bank earlier than the first of that month, even in warm years, and are locally more characteristic of the months of August and September.

Autumnal data on the phytoplankton of the gulf outside the Bay of Fundy are limited to a series of stations covering its northern half for September, 1915, and to occasional October and November hauls between Cape Cod and the Grand Manan Channel during the years 1912, 1915, and 1916. Bailey (1910 and 1917) and Fritz (1921) have also published lists of diatoms from St. Andrews and neighboring parts of the Bay of Fundy, for the autumn as well as for other seasons of the year, and Doctor McMurrich's plankton lists include the status of several genera of diatoms and of peridinians at St. Andrews in autumn. These records, united, show that diatoms practically disappear from the deeper parts of the gulf—not, however, from the Bay of Fundy— after the last days of August, leaving almost its entire area outside the outer headlands occupied by a Ceratium community, with the Mount Desert and Massachusetts Bay regions and the Bay of Fundy alone supporting diatoms in appreciable number. In fact, we have never found abundant diatom plankton anywhere else in the open gulf, either in September or in October, though diatoms were present in some numbers, together with the peridinians, along shore from Penobscot Bay to the Bay of Fundy up until the 9th of October in 1915, and dominated the phytoplankton near Mount Desert Island on that day (station 10328).

Considerable catches of diatoms at the mouth of Massachusetts Bay during the last week of September, 1915, resulted from a rich flowering of Skeletonema. This genus is comparatively rare there in spring (p. 448), but in the summer of 1922 it had commenced flowering in the coastwise belt and among the islands along the northern shore of the bay by August, and the three successive states—spring, August, and September—though for different years, suggest that its normal cycle is to spread offshore as the season advances. Its flowering period was apparently brief in 1915, however, and probably is in most years, having come to an end before October 26 or 27, by which date its place had been taken once more by Ceratium, with only occasional diatoms (Coscinodiscus and *Thalassiothrix longissima*) in the tows on a line across the mouth of the bay (stations 10337 to 10339), where it had dominated the phytoplankton a month earlier.

Bailey (1917, p. 101) also records an abundance of diatoms (Skeletonema) near Grand Manan Island in the Bay of Fundy in early September, and Dr. McMurrich's lists show a rather pronounced maximum of diatoms (chiefly Thalassiothrix) at St. Andrews in September and October, 1916. But during the season of 1917, when Fritz's (1921) counts located the vernal maximum in late April and early May at St. Andrews, with a period of scarcity for diatoms in June, the second maximum fell in July, followed by a sudden diminution in the number of diatoms in August, with much smaller numbers in September. The wide fluctuations in her counts at the same locality on different dates in July and August is an instructive illustration of the streaky way in which shoals of diatoms often occur. Note especially an increase from 632,000 on July 23 to 7,186,000 on August 2, falling to 14,900 on the 8th. It is more likely that the net chanced to hit a streak of diatoms on the occasion of the rich catch, which a haul made shortly previous or later might have missed, than that an active flowering culminated during the two-weeks interval.

It is dangerous to generalize from a small number of hauls, especially for a tide-swept locality, but it seems that a secondary maximum of diatoms is to be expected sometime during the late summer or early autumn both in Massachusetts Bay and in Passamaquody Bay, and therefore probably all along the coast line in estuarine situations; one, however, which is less abundant than the vernal flowering and likewise less regular in the date of its occurrence.

Little change has been noted in the general composition of the phytoplankton of the Massachusetts Bay region during the period November–January, Ceratium dominating. Hauls off Gloucester on November 20, December 4, and December 23, 1912, yielded a scanty plankton, chiefly Ceratium, with few diatoms (Bigelow, 1914a, p. 404). In 1920 the several species of diatoms that are most abundant from spring to early autumn had practically vanished from the whole coastal belt between Cape Cod and the mouth of the Bay of Fundy by December and January; but by contrast the diatom genus Coscinodiscus apparently has a flowering period in midwinter, for it rivalled Ceratium at all the stations occupied by the *Halcyon* off the western and northern shores of the gulf from December 28, 1920, to January 9, 1921, dominated locally off the Merrimac River (station 10442), and was the most numerous diatom genus (though dominated by the peridianians) in the eastern side of the basin, in the Fundy deep, and off western Nova Scotia at this time (stations 10499 to 10502).

Judging from the midwinter data just outlined and from our experience during the first days of March in 1920 and 1921, peridinians are predominant and diatoms—except for Coscinodiscus—fall to a very low ebb out at sea in the Gulf of Maine during the later winter. Fritz (1921) found only very small numbers at St. Andrews from November until the middle of March, compared with the tremendous flowerings of spring. But diatoms may be a considerable element, quantitatively, in the plankton here and there along the open coast even in midwinter, as was the case off Gloucester on January 16 and in Ipswich Bay, a few miles north of Cape Ann, on January 30 in 1913, on which occasions our towings yielded about as great a bulk of the diatom genus Chætoceras as of the peridinian genus Ceratium (Bigelow 1914a, p. 405).

In 1925 Cape Cod Bay was likewise the site of a rich flowering of *Rhizosolenia alata* (p. 447) from the middle of December (appearing between the 10th and 15th) through January. But while the Ipswich Bay diatoms may have been the precursors of the vernal flowerings for the coastal belt Cape Ann–Cape Cod, marking the site of their inception, this flowering of Rhizosolenia can hardly be so classed for Massachusetts Bay, both because the waters in the western and central parts of the latter contained almost no diatoms in January when Rhizosolenia was at its maximum in Cape Cod Bay, and because when flowerings suddenly appeared off Plymouth to the west and near Stellwagen Bank to the north during the last week in that February, the plankton at the latter locality was dominated by Thalassiosira, with very few Rhizosolenia detected in such of the towings for later dates as have yet been examined. So far we have no other record of *R. alata* flowering richly in the Gulf of Maine in winter; in this respect the shoal waters of Cape Cod Bay agree rather with the Wood Hole region, where Fish (1925) has reported winter maxima of Rhizosolenia for two different years.

In summary, diatoms and peridinians alternate in dominating the phytoplankton of the gulf. The former, scarce in the offshore waters of the gulf during late autumn and winter, flower in tremendous abundance during the spring, the flowerings commencing in the coastal belt. Probably they always appear between Cape Ann and Cape Elizabeth as early as the first week in March, perhaps earlier. In early years the vernal flowerings appear in Massachusetts Bay by the last week of February, perhaps not till the last week of March in late years, preceded (at least in some years) by winter flowerings of Rhizosolenia in Cape Cod Bay. Eastward along the coast from Cape Elizabeth to the Bay of Fundy diatoms swarm from early April on. The diatom flowerings are of but brief duration in Massachusetts Bay, having passed their climax in its southern side by the first week of April of 1925, and by the last week of the month in the northern side of the bay in 1913; but the diatom maxima endure till May to the northward of Cape Ann and to some extent throughout the summer along the northern shore of the gulf. At St. Andrews the vernal flowerings continue through May, followed by a period of scarcity in June. On the Nova Scotia side diatoms swarm in April, but only for a brief period, reappearing in some numbers in June (p. 389). Over the central deeps of the gulf the spring flowering reaches its climax in May; and shortly after mid-June diatoms practically vanish from the western basin, though in some summers diatoms are an element in the plankton of the eastern part of the basin all summer. During some years, if not annually, a secondary brief flowering of diatoms takes place in Massachusetts Bay in late August or September, and at some time in late summer or early autumn (the precise date varies from year to year) in the St. Andrews region and likewise in the open Bay of Fundy. Diatoms probably play a more important rôle in estuarine situations generally and close in to the shore than they do out at sea, but I can offer little on this point, most of our towing having been done well out from the land.

Diatoms may also be expected to flower on one part of Georges Bank or another at any season from late winter to midsummer, but nothing is known of their status there in autumn or early winter.

Fish (1925) has pointed out that the waters just west of the barrier of Cape Cod show quite a different seasonal cycle—namely, rich diatom plankton throughout the winter, usually with a brief summer maximum, but with few diatoms in spring—this seasonal distribution corresponding to the Mediterranean, as that of Massachusetts Bay and of the Gulf of Maine generally does to the diatom cycle of the North Sea, Irish Sea, and Skager-Rak. Thus, as Fish (1925, p. 111) emphasizes, the same relationship between the seasonal succession of diatom maxima and the latitude and temperature obtains in the western side of the North Atlantic as in the eastern.

Peridinians dominate the phytoplankton of the open gulf throughout the summer and autumn, but they become very scarce, actually as well as by contrast, during the flowering period of the diatoms. The latter are much the more important group of the two in estuarine situations, where they occur in greater or less abundance throughout the year instead of dwindling almost to the vanishing point between their flowering periods. Peridinians, on the other hand, are seldom more than a very minor constituent of the plankton in estuarine situations.

Finally, before turning to the quantitative records, I may point out that the Gulf of Maine diatoms are chiefly of local origin—that is, that they are produced in the gulf itself and are not immigrants thither from elsewhere. For the western center of dispersal this may be taken as proved; and while the chain of evidence favoring the endemic origin of the diatom plankton of the Nova Scotian side of the gulf is not so complete, there is nothing in our records to suggest that it receives any important accessions from the east around Cape Sable. On the contrary, none of the hauls made east of the cape during March, 1920, June, 1915, or July and August, 1914, have yielded diatoms in any abundance; nor are the diatoms of the eastern side of the gulf more Arctic in their affinities than those of the western, as might be expected if the Nova Scotian current were responsible for their presence there, but rather the reverse.

QUANTITATIVE DISTRIBUTION OF THE PHYTOPLANKTON

When the study is undertaken of the plankton of an ocean area previously virgin ground in this respect, a general qualitative and seasonal survey is the first task. Until we know what groups of organisms are the chief constituents of the pelagic community, at what seasons they reach their maximum abundance, and have outlined their temporal and geographic fluctuations in general, it is difficult to plan counts of the actual numbers in which they occur, to yield results commensurate with the vast amount of labor entailed. For this reason our hauls in the Gulf of Maine have so far been made with the ordinary horizontal nets of appropriate mesh, but I believe that with the information now at hand the time is ripe for more intensive quantitative studies of the phytoplankton of the offshore waters of the gulf, such as Fritz (1921) has undertaken for the St. Andrews region.

In north European waters this stage has long been passed, and since the time when Henson (1887) first focused scientific attention on the productivity of the high seas, quantitative determinations innumerable of marine and fresh-water plankton have been made by methods the reliability of which has steadily increased through the medium of successive trial and criticism. Inasmuch as our Gulf of Maine studies touch only the edge of this field, I may simply refer the reader to Hensen himself, to Lohmann (1903 and 1911), to Steuer (1910), and especially to the summaries by Johnstone (1908) and by Gran (1915),[28] for general accounts of such undertakings. Much of the earlier work of this sort was robbed of part of its value by the impossibility of determining how much of the vertical column of water fished through by the net was actually filtered by it. But thanks to Lohmann's (1911) demonstration that satisfactory counts of many of the most important pelagic plants could be obtained by centrifuging a water sample obtained with an ordinary water bottle, and to Gran's (1912a; 1915) discovery of a satisfactory preservative (Flemming's fluid) for such samples, a simple but exact method for quantitative plankton work is now available, which it is to be hoped American biologists will soon adopt.

While this method gives far more reliable results for the smaller planktonic plants, "many of the larger species," as Lebour (1917, p. 135) points out, "do not get into the water samples in anything like a representative number," and as a rule this method is quite worthless for the larger animal plankton. In fact, no one collecting apparatus can be expected to be equally satisfactory for all the members of the plankton, large as well as small.[29]

Horizontal hauls with ordinary tow nets yield useful information as to the relative abundance of phytoplankton, but only if hedged about by the same precautions as are necessary for the zooplankton (p. 79), the need of which is now universally recognized. For example, we face the impossibility of insuring that all the tows shall fish through an equal column of water, because it is practically impossible to keep even a steamer moving at a uniform rate at the low speed that towing requires. The uncertainty introduced by imperfect filtration is much more serious for phytoplankton than for zooplankton, for the much finer-meshed nets that must be employed become clogged much sooner and to a greater degree. This is especially the case when Phæocystis and certain diatoms swarm (that is, just when information on their abundance is most to be desired), for they often clog the silk so thoroughly that the nets become quite impervious to water after a few minutes, so that the catch becomes the product of the first part of the tow only.

There is also the problem of a method of estimating the amount of phytoplankton caught, on the one hand sufficiently accurate for the results to be instructive and on the other rapid enough to deal in a practical manner with the large amounts which horizontal tows at the surface often yield. The total volume—simplest and easiest measure—is estimated by the same method as for the zooplankton, described above (p. 81), and entails the same sources of error, the worst being the uncertainty as to what proportion of the measured volume represents the actual plankton and how much of its bulk is due to the spaces between its members.

[28] W. E. Allen (1921) has recently formulated a formidable list of sources of error inherent in all collections of plankton taken with tow nets.

[29] Lebour's (1917) tables give instructive examples of the discrepancy between net hauls and collections made with the water bottle off Plymouth, England.

This depends somewhat on the shapes of the plant cells, smooth ones naturally fitting together much more closely than setose or irregular cells or chains (Michael, 1921, p. 564). Unfortunately, measurements of volume have little value as a measure of the phytoplankton for tow nettings containing appreciable proportions of larger organisms (e. g., copepods), unless these be painstakingly picked out. Nevertheless, even the most critical supporter of more rigorous methods must allow a certain value to estimates of the volume of plankton, at least for comparative purposes, especially when diatoms are flowering, for as a rule there is then very little else in the water. At their worst horizontal hauls tell whether the plankton is comparatively rich or scanty, as between stations where similar hauls are made; and when prosecuted over a period of years, as has been done near the Isle of Man under the leadership of Professor Herdman,[30] very instructive results may be expected. Because of their inherent inaccuracy, however, they can not be used as a measure of the absolute amount of plankton present in the water, nor even as a basis of comparison between different areas, unless the requirements of hauls of uniform duration, at uniform speed, and with nets of uniform type be rigorously adhered to.

In midwinter the production of phytoplankton in the inner parts of the gulf is so low that the volumes recorded in December, 1920, and January, 1921, ranged only from 0.5 to 6.5 cubic centimeters;[31] but toward the end of February or early in March of 1920 the vernal flowerings of diatoms on the southwestern part of Georges Bank, on the one hand, and in the immediate vicinity of Cape Elizabeth, on the other, were responsible for catches of phytoplankton 40 to 200 times as great as in the center of the gulf or along its northern and eastern coast, where the catches made during the March cruise of the *Albatross* in 1920 were often too small to measure (fig. 108). During April of that year, the month when the diatom flowerings attain their maximum abundance in the two sides of the gulf, the amount of vegetable matter present in the surface waters of the Cape Elizabeth region in the west and from the shallows off Cape Sable out to Browns Bank on the east is so much larger still, without any corresponding augmentation in the central or northern part of the gulf, that, allowing for the clogging of the nets, which I have repeatedly emphasized, it is not out of bounds to claim plankton volumes a thousandfold greater in the most productive regions than in the more barren localities (fig. 109). Two successive stations located 25 miles west of Cape Sable, where the volume of plankton increased from less than 1 cubic centimeter to at least 380 cubic centimeters (actually, no doubt, much more) during the three-weeks interval between March 23 and April 15 of that spring, is a notable illustration of the rapidity with which the pelagic flora augments in quantity when diatoms are flowering actively. The plankton

[30] See especially Herdman, Scott, and Dakin, 1910.

[31] The volumes here listed are the total yields of surface hauls of one-half hour's duration with a No. 18 bolting-silk net 14 centimeters in diameter, not the amounts in any given volume of water or below any given areas of sea surface. They, therefore, are not absolute measures, though comparable one with another. Since the unavoidable errors preclude accuracy, measurements have been only to the nearest cubic centimeter, and all the larger volumes should be regarded as too small because of the clogging of the net already alluded to. Probably none of the volumes of 200 cubic centimeters or more represent much more than half the amount of plankton that was actually present in the horizontal column of water through which the net was dragged, but through a part of which it failed to fish after its meshes were clogged.

augmented similarly in volume at the mouth of Massachusetts Bay from less than 5 cubic centimeters on March 1 (station 20050) to at least 200 cubic centimeters on April 9 (station 20090), while Fritz (1921) records the numbers of diatoms per haul

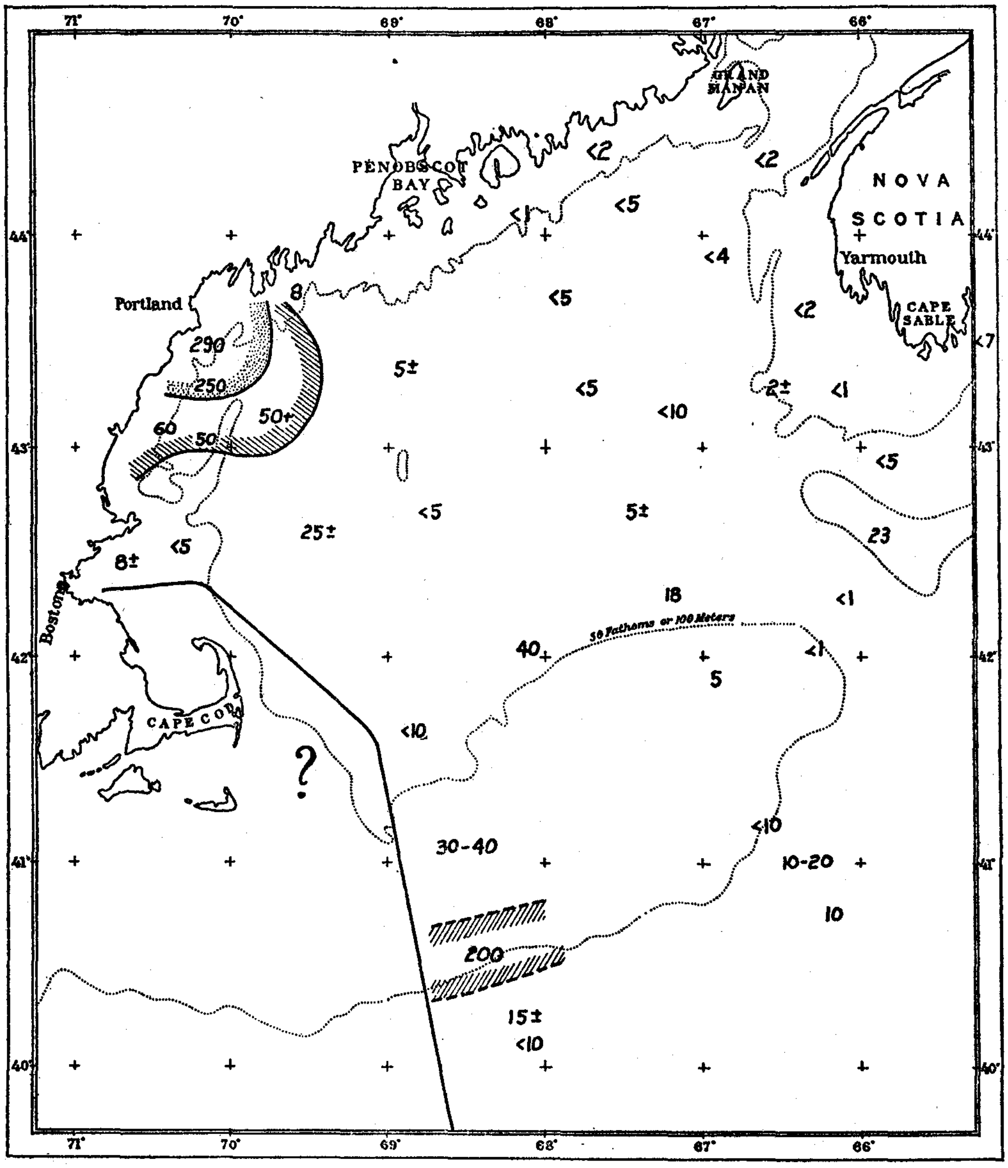

FIG. 108.—Volumes of phytoplankton (in cubic centimeters) per standard surface haul in February and March, 1920. The hatched curve incloses areas with more than 50 cubic centimeters; the stippled curve with more than 250 cubic centimeters

as increasing from about 28,000 on March 15 to upwards of 9,000,000 on May 1 at St. Andrews.[32] When the water is cloudy with diatoms, as is the usual state when

[32] Fritz's counts are for the catches of horizontal hauls that fished through an unmeasured volume of water.

these microscopic plants are flowering most intensively, volumes even as large as those noted (fig. 109) are but a pale reflection of the mass of vegetable matter actually present in the water.

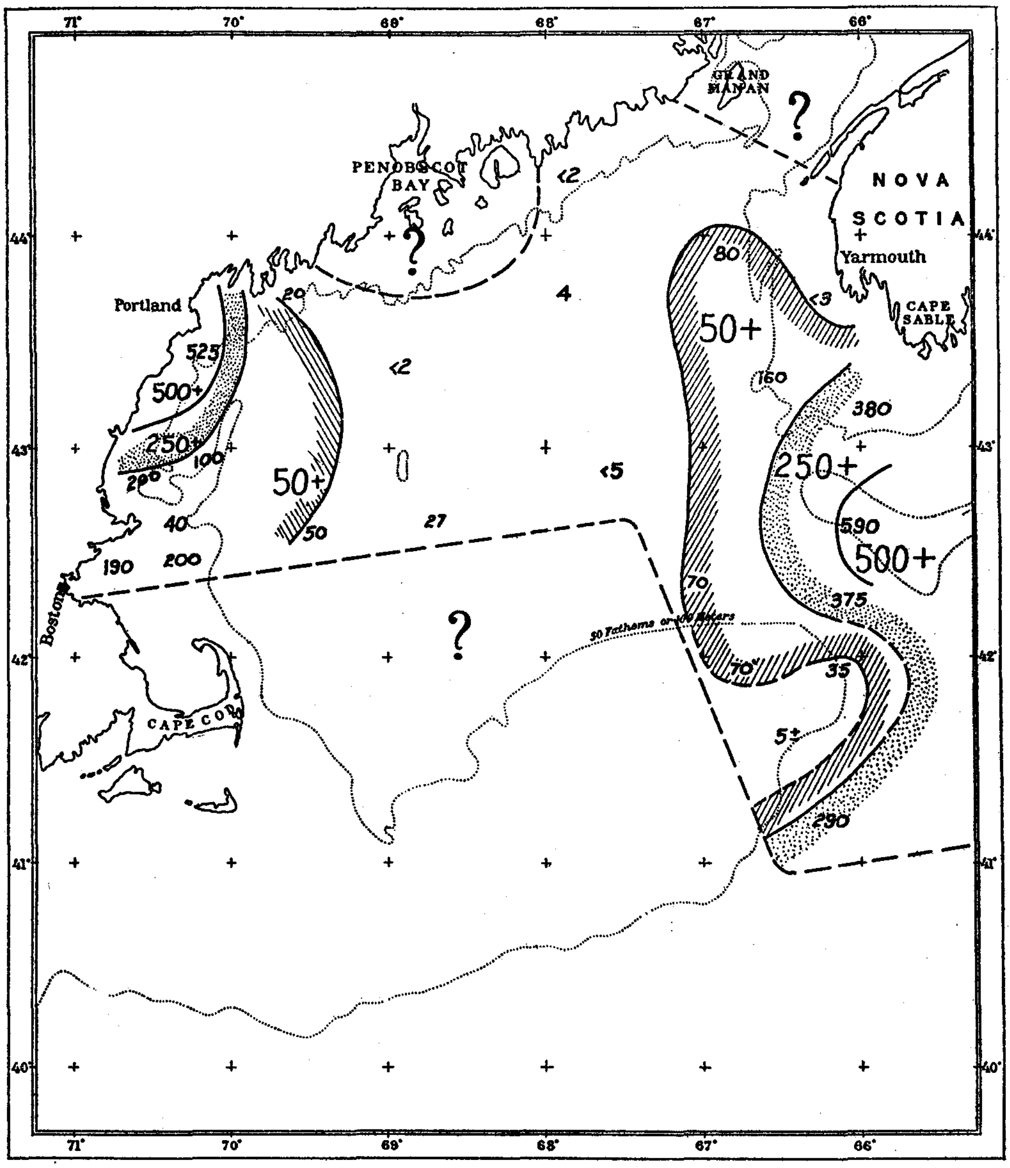

FIG. 109.—Volumes of phytoplankton (in cubic centimeters) per standard surface haul, April, 1920. The hatched curve incloses areas with more than 50 cubic centimeters; the stippled curve with more than 250 cubic centimeters

The accompanying chart (fig. 109) for the last half of April is necessarily imperfect, because records for the several stations ought to be taken simultaneously (which has not been practicable). But the variations that appear there in the local density of the eastern diatom center, reflected by the volumes of plankton, and more especially the rather large volumes along the 100-meter curve west of Nova Scotia contrasted with the barren water both over the basin to the west and close in to the neighboring coast on the east, point directly to a tonguelike drift of diatoms northward toward the Bay of Fundy from the rich center of production off Cape Sable.

The rich catches in the Eastern Channel (375 cubic centimeters at station 20107) and off the southeast face of Georges Bank (290 cubic centimeters at station 20109) similarly suggest another line of dispersal for the Cape Sable–Browns Bank diatoms toward the southwest, a thesis supported by the qualitative uniformity of the April catches in that region, illustrated by the following table:

Diatoms	Browns Bank, station 20106; volume, 590 cubic centimeters	Eastern Channel, station 20107; volume, 375 cubic centimeters	Southeast slope of Georges Bank, station 20109; volume, 290 cubic centimeters
Chætoceras laciniosum	×	×	×
Chætoceras debile	×	×	×
Chætoceras atlanticum	×		×
Chætoceras decipiens	×	×	×
Chætoceras diadema	×	×	×
Chætoceras didymum	×	×	×
Chætoceras convolutum		×	×
Chætoceras criophillum		×	×
Thalassiosira gravida	×	×	×
Thalassiosira nordenskioldi		×	×
Thalassiothrix nitschioides	×	×	×
Coscinodiscus			×
Rhizosolenia semispina	×	×	×
Lauderia glacialis	×	×	×
Fragillaria sp		×	×
Coscinosira		×	×

If such a drift of diatoms from the Nova Scotian center was actually taking place at the time of our April cruise in 1920 it must have been strictly confined to the outer edge of Georges Bank, because the shallows to the northward (stations 20108, 20110, and 20111) supported a phytoplanktonic community not only much less abundant (15 to 120 cubic centimeters per haul), but one of rather a different type, in which the oceanic diatoms *Chætoceras decipiens*, *C. criophillum*, *C. atlanticum*, *C. densum*, and Coscinodiscus were dominant, with the several species of Ceratium continuing as an important factor in April just as they had been in March.

As long as the diatom flowerings continue at their peak, volumes of plankton as large as or larger than those noted on the chart (fig. 109) are to be expected all along the coast north and east of Cape Ann, on the one side of the gulf and over the banks west and southwest of Nova Scotia on the other (Browns Bank yielded one of our largest spring catches, as appears on the chart), locally, too, on Georges Bank (p. 385); and while the central part of the gulf is hardly less barren in April than in March, the spring flowering may be no less intensive there, once it is under full headway, than in the coastal zone. For example, diatoms were so plentiful in the western basin on

May 4, 1915 (station 10267) that every interstice of the fine net was clogged and its silken bag transformed into a cone of slime almost impervious to water after a few minutes submergence at a locality where a net of the same specifications took only 5 cubic centimeters of phytoplankton on March 24, 1920, and 50 cubic centimeters on April 18 of that year. Even a coarse (No. 5 silk) net, 24 centimeters in diameter, yielded over 2,000 cubic centimeters, mostly diatoms of one species, after 20 minutes' towing, though a large part of the phytoplankton must have escaped through it.

Perhaps I should remark in passing that while very rich catches are the rule throughout the areas occupied by the flowerings of diatoms during these periods of abundance, considerable local variations in the volumes of plankton present in the water are to be expected from place to place, for instead of being uniformly and evenly distributed, the congregations of diatoms are often so streaky that one can actually see the net pass through alternate bands of brownish diatoms and of clear water (Bigelow, 1914a, pp. 405 and 407).[33] Conceivably it might miss the productive spots altogether, and very likely this happened off Cape Ann on April 9, 1920 (station 20091), when the catch of phytoplankton was very small though diatoms were then extremely abundant (200+ cubic centimeters) both south and north of the cape a few miles away. In the deeper waters offshore, however, the phytoplankton is much more evenly distributed, and it may even approach perfect uniformity over large areas in the open sea.

The duration of the flowering season of the diatoms determines the period during which large volumes of phytoplankton (say upwards of 50 cubic centimeters per haul) are to be expected anywhere in the Gulf of Maine. After the diatoms pass the peak of their abundance the amount of phytoplankton rapidly diminishes, and from that time forward, as copepods, Sagittæ, and other animals form an increasing proportion of the catch, measurements of its volume become less and less instructive.

In Massachusetts Bay the phytoplankton attains its maximum abundance (as measured by volume) by the last half of April, diminishing again so suddenly that the amount taken among the copepods during the first week in May, 1920 (after the brief swarming of Phæocystis had come to an end), was hardly measurable. And while large volumes may be expected in the western basin until well into May (p. 338), the volume of phytoplankton taken there in the standard haul on June 26, 1915, after diatoms had practically disappeared, was less than 3 cubic centimeters (station 10299).

Near land, east of Penobscot Bay, where diatoms persist more or less throughout the summer (p. 396), we have occasionally made large catches in August, notably in 1912, when Asterionella (p. 431) occurred in such abundance that although the net came back aboard filled to the brim with several liters of slimy brown diatom soup (Bigelow, 1914, p. 133), its yield was only a part of what was actually present in the water through which it was drawn. In fact, this has been the richest haul of phytoplankton ever recorded for the Gulf of Maine.

In most parts of the gulf where the spring diatom flowering is a short-lived phenomenon, its dissipation leaves but little vegetable plankton in the water; nor does the augmentation of peridinians, characteristic of late spring and early summer,

[33] This has often been remarked by previous students.

produce a flora at all comparable in abundance to the diatoms which it succeeds. As a rule, indeed, the Ceratium plankton of midsummer has seldom yielded volumes much larger than 25 cubic centimeters, rarely as much as 40 cubic centimeters except when fortified by diatoms, or by Acanthurian radiolarians, as was the case off Cape Ann in August, 1914 (p. 460; Bigelow, 1917, p. 324). Occasionally, however, Ceratium occurs in greater abundance—for example, on August 13, 1912 (Bigelow, 1914, p. 131), when " we were struck by the slick, oily appearance of the water some 35 miles off Cape Elizabeth, and consequently stopped the vessel for a surface tow (station 10026b). The net, when brought aboard, was distinctly reddish, and its meshes clogged with what proved to be a mass of Ceratium, * * * and this phenomenon continued for several miles." It is not unlikely that a swarming of Ceratium was reponsible for a streak of white water 65 to 75 miles long and 30 to 40 miles wide reported off Monhegan Island in 1882 (Collins, 1883, p. 282). But such events as these are quite exceptional for the Gulf of Maine, our subsequent cruises having shown that 1912 was, generally speaking, a very "rich" summer for Ceratium as well as for diatoms. With our standard net and time of towing, 50 cubic centimeters would be a very rich catch of Ceratium for the gulf, whereas 10 times as much as this is nothing remarkable for diatoms during the period of their greatest abundance. Neither do the local swarms of Acanthometron, which are sometimes met with in the western part of the gulf in midsummer (p. 460), produce any such abundance of organic matter as do the diatoms; at the greatest, they have raised the volume of the catch to 70 or 80 cubic centimeters, as was the case off Cape Ann on August 12, 1914 (station 10253).

In summer, as a general rule, the greatest volumes of phytoplankton are to be expected in the coastal zone east of Penobscot Bay, especially over the small area near Mount Desert Island, where diatoms usually persist in numbers right through the season into autumn. But this productive area does not extend westward past Penobscot Bay, on the one hand, nor more than a few miles eastward past Mount Desert Island, on the other. July and August hauls near the coast off the mouth of the Grand Manan Channel and in the latter itself have been decidedly barren. Local swarms of diatoms may also produce an extremely abundant phytoplankton in July on Georges Bank (p. 391). In other parts of the gulf, where the abundance of the summer phytoplankton, or the reverse, depends on the numbers of Ceratium locally present, no division into "rich" and "barren" areas is yet possible, for our large hauls of peridinians have been at widely separated localities in different summers. Thus in 1912 our richest hauls of Ceratium (the largest we have ever made) were off Cape Elizabeth, as just noted; off Cape Cod in July, 1913, and July, 1916 (stations 10057 and 10058, Bigelow, 1915, p. 334; station 10345); and near Lurcher Shoal in August, 1914 (station 10245). On the whole, the deep offshore waters of the gulf have always proved decidedly barren of phytoplankton in midsummer, contrasted either with these Ceratium centers or, more markedly, with the diatom flowerings of the coastal waters.

In the Massachusetts Bay region the September flowering of Skeletonema is reflected in the amount of phytoplankton taken in the nets, as might be expected, raising the volume to some 25 to 30 cubic centimeters on September 29, 1915 (station 10320), when this diatom formed the bulk of the catch, contrasted with a volume of only 2 to 3 cubic centimeters at a neighboring locality on August 31 (station 10306). Though the eclipse of Skeletonema left the phytoplankton hardly richer at the mouth of the bay in that October (volume about 4 cubic centimeters on the 26th, in 1915, station 10338) than it had been at the end of August, it is probable that a general increase over its midsummer state takes place in the volumes of phytoplankton of Massachusetts Bay in late autumn, because peridinians, chiefly *Ceratium tripos*, were abundant enough there in November, 1916, to yield volumes of 18 to 20 cubic centimeters on the 8th (stations 10403 and 10404).

With the falling temperatures of winter the volume of phytoplankton as a whole shrinks to its annual minimum in all parts of the gulf which we have visited at that season; so much so that the greatest measured volume for the winter cruise of 1920–1921 (stations 10489 to 10502) was only 6.5 cubic centimeters (station 10488), and ranged down to less than 1 cubic centimeter per haul at the other stations, as follows:

Station	Approximate volume in cubic centimeters	Station	Approximate volume in cubic centimeters
10488	6.5	10495	3.5
10489	5	10496	3
10490	4.5	10498	2.5
10491	3.5	10499	2
10492	.5	10500	.5
10493	2	10502	4.5

Having made no vertical hauls for the phytoplankton in the Gulf of Maine, counting of diatoms or of peridinians has not seemed worth while. Fritz's (1921) counts of diatoms in the Bay of Fundy are likewise based on horizontal hauls, and hence do not represent the number present in any known volume of water; but Peck (1896) made a quantitative study of the diatoms of Woods Hole and Buzzards Bay based on the filtration of large samples (5 liters each) of sea water through a sand filter.[34]

Unfortunately, Peck's tables do not give the actual counts per sample, but are based on combinations of the several samples for a given level—surface, intermediate, and bottom—at all four stations and for all these levels combined for each station. On averaging them, however, it appears that the largest catches of diatoms were at least 420,000 per liter—that is, 420,000,000 per cubic meter of sea water.

To give the reader a more concrete idea of the numerical strength to which marine diatoms may attain when flowering actively, some of the oft-quoted counts for European waters will not be out of place here. One of the richest catches ever recorded, Johnstone (1908, p. 210) tells us, is Brandt's (1902, p. 71) of 3,173,000,000 diatoms, besides 500,000 peridinians and a few thousand copepods, in a net 1 square meter in mouth diameter, hauled up vertically from 30 meters, which, says Brandt, indicates an actual diatom flora of at least 6,000,000,000 per cubic meter of sea water after allowing for imperfect filtration by the net. To make these collossal numbers

[34] Essentially the Sedgewick-Rafter method, for an account of which see Whipple (1905, p. 15).

even more impressive, Johnstone (1908, p. 163) has calculated that on the basis of this haul "every drop of sea water from this part of Kiel Bay contained some 200 diatoms;" and though by Hensen's (1887) calculations less than one-tenth as many diatoms as this are present on the average in the West Baltic, their numbers are sufficiently appalling when extended to any considerable sea area.[35]

During the years that have passed since Hensen's pioneer studies in this field many similar counts have been made in the Baltic and in various parts of the North Sea, with the details of which it is unnecessary to delay here.[36] Lohmann, for instance (1908, Table B), has recorded some very large counts by the centrifuge method, including 7,800,000,000 Skeletonema per cubic meter in June, 1906, with another individual catch of about 2,000,000,000 diatoms in Kiel Bay on April 11, 1906. As still another example of the results of this modern method, the accuracy of which leaves little to be desired, though, as Gran (1915) himself points out, it is not of universal application, I may quote his own average of about 228,000,000 diatoms per cubic meter in the surface waters of the Skager-Rak for February, 1912.

The centrifuge, however, is not the "last word" in quantitative determination of the phytoplankton, for E. J. Allen (1919) has recently essayed the following totally novel procedure: To a small sample of sea water (0.5 cubic centimeters) he added a large amount (1,500 cubic centimeters) of a nutrient solution that had previously been found suited for the cultivation of marine diatoms (Allen and Nelson, 1910; E. J. Allen 1914). The culture was then examined after a period of incubation, whereupon he found a total of 232 different kinds of organisms. A second experiment yielded similar results. Since now it is obvious, to use his own words (E. J. Allen, 1919, p. 4), that each of these organisms "must have been represented by at least one individual or unit, either cell or spore, in the original ½ cubic centimeter of sea water from which the experiment was started," the latter must have contained at least 464 organisms (mostly diatoms) per cubic centimeter—that is, 464,000 per liter—and probably, as he calculates, as much as 1,000,000 per liter for the part of the English Channel whence his sea-water sample was taken. How much more effective this method is than centrifuging, even for such comparatively large organisms as diatoms (for which the culture method is particularly well adapted, as indicated by their great predominance in the final product), is illustrated by the fact that whereas the two culture experiments call, respectively, for 378,000 and 290,000 diatoms as the absolute minimum per liter, centrifuging a similar sea-water sample at the beginning of the experiment revealed only about one-thirtieth as many. Nor can even the method of the culture medium be relied on to give a total census of the phytoplankton, because it is by no means certain that the nutritive fluid employed was as suitable for the growth and reproduction of peridinians, infusorians, coccolithophorids, etc., as it was for diatoms. In short, as Herdman says (1920, p. 819), "every new method devised seems to multiply many times the probable total population of the sea."

[35] There has been much discussion as to the reliability of numerical results yielded by nets of the "Hensen" type, owing to uncertainty as to their coefficient of filtration. In the present connection it is enough to point out that in any case the ostensible results are always smaller, never larger, than they should be.

[36] For details of such I may refer the reader to Hensen (1887) himself, Driver (1908), Lohmann (1903 and 1908), and Gran (1915).

How closely the foregoing data, obtained in European waters, would apply to the Gulf of Maine is yet to be determined, but judging from Peck's results and from the large volumes of phytoplankton which we have ourselves obtained, there is no reason to suppose that its fecundity is lower than that of the North Sea or even than the still more prolific waters of the West Baltic. When such numbers as I have listed as examples are expanded from the trifling bulk of a cubic meter of water to cover the 36,000 square-mile area of the Gulf of Maine north of its offshore banks, and to a stratum at least 20 meters thick, they become too vast for the human mind to envisage. Peridinians never approach the diatoms in actual numbers so far as is known. For example, the largest count recorded by Gran (1915) in the North Sea (May 9, 1912) was 3,740 per liter for *Ceratium longipes*, a species with an April to June maximum, and hence to be expected in relatively large numbers at that particular season.

PERIDINIANS

The peridinian communities of the Gulf of Maine, like those of the North Sea, consist chiefly of one or other of two species (*longipes* and *tripos*) of the genus Ceratium,[37] with smaller numbers of *C. fusus* and at times *C. arctica*. The two predominant species alternate in dominance with the season of the year.

Ceratium

Judging from winter data for Massachusetts Bay (Bigelow, 1914a) and from our December and January stations of 1920–1921, *C. tripos* predominates everywhere in the gulf throughout the winter, though *C. longipes* likewise occurs in small numbers in most of the winter catches. *Tripos* was still the predominant member of the pair at every station in the western, central, and northern parts of the gulf and on Georges Bank as a whole during early March, 1920, except in the flowering centers for diatoms (p. 383; fig. 104), where so few Ceratium occurred that the relative numbers of the two species are not significant. *C. longipes* or intermediates between it and *C. arctica*, such as are reported by Paulsen (1908), occurred side by side with *C. tripos* at most of the March stations. Off the southeastern slope of Georges Bank *longipes* was at least as numerous as *tripos*, outnumbered it in the Eastern Channel, on Browns Bank, and over the slope farther east, and was the only member of the pair detected in tows made in the Northern Channel and over the shelf abreast of southern Nova Scotia, from March 17 to 20 (stations 20073 to 20076 and 20078).

Ceratium arctica, interesting because its occurrence is associated with low temperatures (Jørgensen, 1911), was likewise very generally distributed over the gulf in March, 1920, occurring only in very small numbers in the western half, but relatively more abundant in the Eastern Basin (though subordinate to *tripos* there); predominant, or at least as numerous as either *C. longipes* or *C. tripos*, at our several stations from Browns Bank to Cape Sable and off Shelburne; and more abundant, absolutely as well as relatively, in the eastern side of the gulf than in the western. The distribution of *C. arctica* at this season suggests an intrusion on its

[37] Identifications of peridinians follow Paulsen (1908) strictly. Being concerned here only with questions of distribution and relative abundance, not with systematics or genetic relationships, Paulsen's view that *C. longipes* and *C. arctica* are distinct (not varieties of one species as Meunier (1910) maintains) is accepted without comment.

part around the cape from the eastward. But if *C. arctica* occurs in the gulf chiefly as an immigrant from the north, as seems probable at present, its quantitative distribution within the gulf in early spring does not parallel the distribution of temperature, for at the time of the winter minimum the water is coldest next the western side of the gulf while *arctica* is most abundant in the eastern side.

The actual proportions in which the several species of Ceratium occurred during the early spring of 1920 appears from the following list of actual counts of samples at representative localities:

Relative numbers of species of Ceratium in samples, "Albatross" cruise, March 1 to 19, 1920

Locality	C. tripos	C. longipes	Intermediates between longipes and arctica	C. arctica	C. fusus
Massachusetts Bay, station 20050	22	1	0	1	0
Western Basin, station 20049	25	0	1	1	0
South center, station 20063	49	0	6	2	2
Eastern Basin, station 20054	12	0	1	4	1
Off Mount Desert, station 20056	9	3	0	2	0
Southeast Basin, station 20064	8	2	8	3	1
Georges Bank:					
Northwest, station 20047	20	0	0	0	0
Southwest, station 20045	22	5	5	4	1
East, station 20065	11	1	8	2	1
Southeast, station 20068	7	9	2	2	1
Southeastern slope, station 20069	5	7	×	3	0
Eastern Channel, station 20071	5	8	2	5	2
Browns Bank, station 20072	1	6	6	9	1
Off southern Nova Scotia:					
Station 20074	1	6	10	7	1
Station 20077	1	2	4	15	3

With the advance of the season and hand in hand with the augmentation of diatoms, peridinians of all species so diminish in numbers that in 1920 they had practically disappeared from the two productive centers for diatoms in the two sides of the gulf by mid-April and were so scarce elsewhere that counts of the relative numbers of the several species of Ceratium are no longer significant. But when they reappear in the Massachusetts Bay region late in April or early in May in the western side of the gulf, and in the Nova Scotian waters in the eastern, following the eclipse of the diatom flowerings, a complete reversal has taken place in the relative importance of the two leading species, for we have found *longipes* far more numerous than *tripos* during the first week in May at every station where the genus as a whole was sufficiently abundant for counts to be of value, only excepting the southwestern edge of Georges Bank, where the two species were about equally numerous (station 20129, May 18, 1920). In fact, *C. tripos* is then practically nonexistent within the gulf, or at best represented by occasional examples only. A slight recrudescence of *C. arctica* (or perhaps a fresh wave of immigration) apparently takes place during the first half of May, when occasional examples have been detected at most of our stations (except among the diatom swarms); and on the seventh of that month in 1915 *C. arctica* proved to be as abundant on German Bank (station 10271) as *C. longipes*, its area of abundance coinciding with the location of the cold water from the Nova Scotian current (then near its maximum flow for the year), which corresponds to a northern extralimital origin.

Relative abundance of species of Ceratium in samples, "Grampus" cruise, May 4 to 14, 1915, and "Albatross" cruise, May 1 to 17, 1920[1]

Locality	C. tripos	C. longipes	C. arctica	C. fusus
Off Cape Ann, 1920, station 20124	1	30	0	0
Off Cape Ann, 1915, staton 10266	1	39	8	4
Off Cape Cod, 1920, station 20125	2	12	1	1
Eastern Basin, 1915:				
Station 10269	0	30	5	1
Station 10270	0	20	1	1
German Bank, 1915, station 10271	0	100+	100+	0
Off Lurcher Shoal, 1915, station 10272	1	18	6	0
North of Cape Ann, 1915, station 10278	0	12	1	0
Southwestern Basin, 1920, station 20127	1	10	0	0
Western part of Georges Bank, 1920, station 20128	25±	25±	0	1
Southern edge of Georges Banks, 1920, Station 20129	0	25±	0	0

[1] In this table no account is taken of the intermediates between *C. arctica* and *C. longipes*, although occasional examples of this sort were noted at most stations, because it was usually possible to refer the specimens to one species or to the other.

C. longipes continues the dominant species in the Gulf during the last half of May and throughout the month of June, when peridinians play an increasingly important rôle in the phytoplankton, as illustrated by the following counts of samples for the year 1915:

Locality	C. tripos	C. longipes[1]	C. arctica	C. fusus
Off Cape Cod, May 26, station 10279	3	100+	0	1
Off Mount Desert, June 11, station 10284	0	9	0	0
Southeast Deep, June 25, station 10298	(2)	(3)	0	0
Western Basin, June 26, station 10299	4	19	0	0

[1] Including occasional intermediates between it and *arctica*.
[2] Occasional.
[3] Swarm.

During this period *C. arctica* practically vanishes from the gulf, where our only June record of it is in the extreme northeast corner (Bigelow, 1917, p. 328, stations 10283, 10284, and 10286), and off Petit Passage in the southern side of the Bay of Fundy (June 10, 1915). *C. arctica* has been detected only twice in the gulf in the later summer or in autumn—that is, off Mount Desert, August 13, 1914 (Bigelow, 1917, p. 323, station 10248), and off Cape Ann, August 31, 1915 (station 10306)—though it persists in some numbers along the southern coast of Nova Scotia at least as late in the season as August (Bigelow, 1917, p. 323).

C. tripos reappears in numbers in the Gulf of Maine tow nettings in July. During the first half of that month, when the surface temperature of the gulf is approaching its seasonal maximum and Ceratium its annual plurimum of abundance, *C. longipes* has still predominated over *C. tripos* (usually markedly so) at almost all the stations, both in the western half of the gulf generally,[38] over Georges Bank as a whole, and across the whole breadth of the shelf abreast of southern Nova Scotia (Bigelow, 1917, p. 323). Late in July, 1914, we found *C. tripos* dominating off the

[38] At one station (10301) off the mouth of the Grand Manan Channel, July 15, 1915, there were 16 *longipes* to 3 *tripos*.

southeast slope of Georges Bank (station 10220), where *longipes* slightly outnumbers it in March and April (p. 407), and local phenomena of the same sort noted on the western part of the bank and in the southwest corner of the basin of the gulf in July, 1913 and 1914 (station 10058, July 8, 1913; station 10215, July 20, 1914), fore-

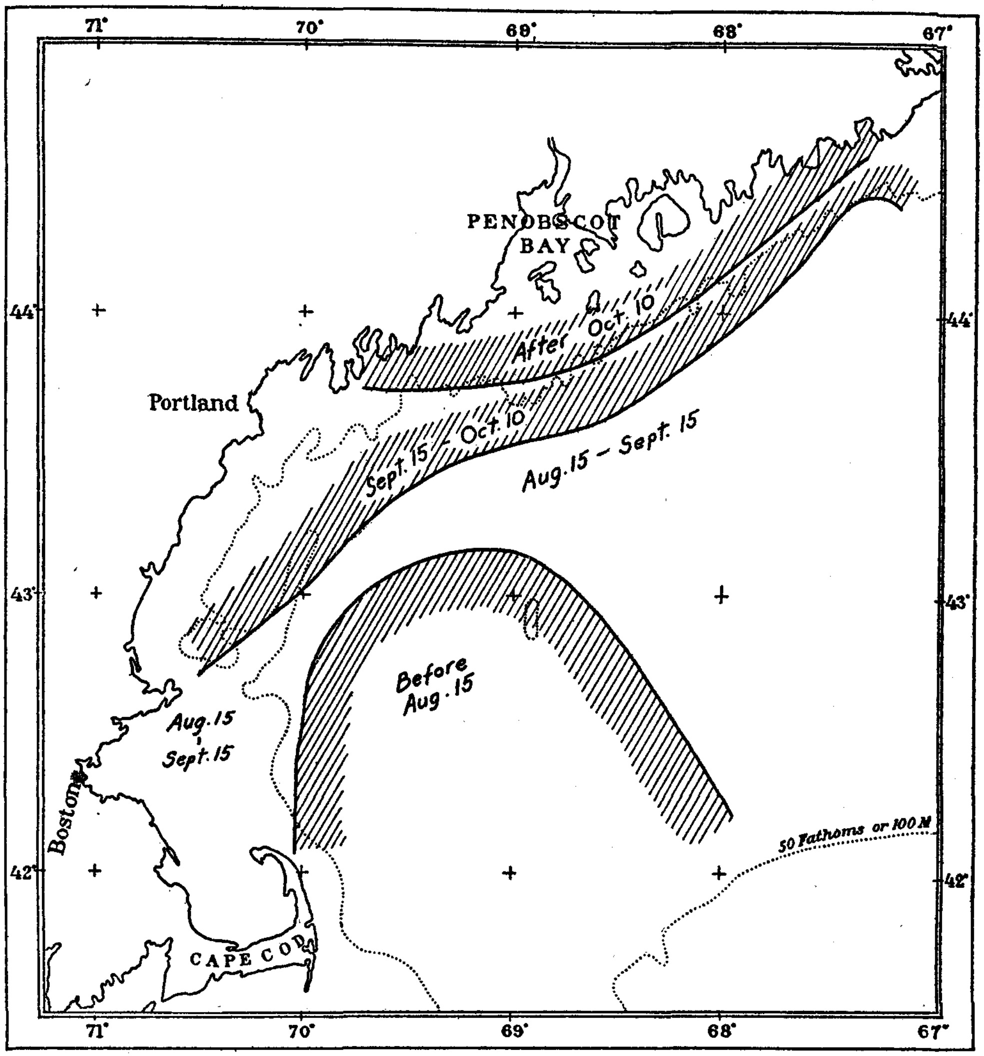

FIG. 110.—Approximate dates when *Ceratium tripos* may be expected to become dominant over *C. longipes* in different parts of the Gulf of Maine

shadow a second alteration in the mutual relationship of the two species during the latter part of the summer, which once more makes *C. tripos* the dominant member of the pair.

A detailed account of the augmentation of *C. tripos* in the gulf with the advance of the summer can not be given as yet, but the approximate dates when it may be expected to dominate the plankton in different regions, by our experience, are laid down on the chart (fig. 110). Our records show that it outnumbers or replaces *C. longipes* first in the offshore parts of the gulf, and that it may be expected to predominate over the latter in the western and central deeps and in the eastern branch of the basin north to latitude 43° or 43° 30′ N. by mid-August.

The following counts of samples from corresponding pairs of stations illustrate how completely the relative importance of the two species is reversed between June or the first half of July and the first days of August, and how nearly to the vanishing point *C. longipes* sinks in these particular parts of the gulf as *C. tripos* multiplies.

General locality	Relative numbers in samples	
	C. longipes	C. tripos
100-meter curve, off Cape Cod:		
July 8, 1913, station 10057	43	15
Aug. 5, 1913, station 10086	5	60
50-meter curve, northeast of Cape Cod:		
July 19, 1914, station 10213	50	1
Aug. 28, 1914, station 10264	1	23
Southwest part of deep basin:		
July 19, 1914, station 10214	63	3
Aug. 23, 1914, station 10256	5	76
Western Basin, off Cape Ann:		
June 26, 1915, station 10299	19	4
Aug. 31, 1915, station 10307	1	50+
Eastern Basin, lat. 43° 17′:		
Aug. 13, 1914, station 10249	13	47
Eastern Basin, lat. 43° 08′:		
Sept. 1, 1915, station 10309	4	28

A corresponding preponderance of *tripos* (32 to 2 *longipes*) likewise characterized a haul made by Capt. John McFarland off Chatham (Cape Cod) on August 26, 1913.[39]

The multiplication of or intrusion by *C. tripos* is apparently a slower process, and *C. longipes* persists correspondingly longer as an important factor in the plankton over the northeastern part of the basin. Thus in mid-August of 1914, when *tripos* already greatly predominated right across the gulf along a line from Cape Ann to Cape Sable, *C. longipes* still outnumbered it a few miles to the northward, as follows:

Locality	Number in samples	
	C. longipes	C. tripos
Off Lurcher Shoal Aug. 12, 1914, station 10245	105	1
Extreme northeast corner of basin, Aug. 12, 1914, station 10246	62	1
Off Mount Desert Rock, Aug. 13, 1914, station 10248	29	1
Off Penobscot Bay, Aug. 14, 1914, station 10250	32	2
Off Cape Elizabeth, Aug. 14, 1914, station 10251	115	1

In 1913 *longipes* still continued about as numerous as *tripos* in the deep hauls in the eastern side of the gulf (latitude about 43° 25′ N., stations 10092 and 10093) on August 11 and 12, by which date *tripos* was already predominant in the western basin (stations 10088 and 10089).

[39] In the report on the cruise of 1912 the two species were listed together as *tripos* (Bigelow, 1914).

Whether the summer augmentation of *C. tripos*, accompanied as it is by a decrease on the part of *C. longipes*, actual as well as relative, originates as the result of local propagation of the few specimens that survive the spring, or from immigration from the south and west, or of both processes, is not yet clear; but in either case the central deeps may be looked upon as its chief area of multiplication in the Gulf of Maine. From this center it gradually expands its area of abundance right in to the immediate vicinity of the land where *C. longipes* decreases in abundance as the numbers of *C. tripos* augment, just as happens offshore.

Relative abundance of the two predominant species of Ceratium, July and August, 1914

Station	C. longipes	C. tripos	Station	C. longipes	C. tripos
10213	50	1	10249	13	47
10216	38	14	10250	32	2
10223	21	1	10251	115	1
10225	9	4	10253	2	10
10227	34	1	10254	4	50
10229	21	1	10255	0	50
10230	60	0	10256	5	76
10245	105	2	10258	1	11
10246	62	4	10264	1	23
10248	29	1			

C. tripos usually predominates near Cape Cod and in the southern part of Massachusetts Bay by the last week in August. For example, we found 23 *tripos* to 1 *longipes* off the east side of Stellwagen Ledge on August 28, 1914 (station 10264), while the relationship between the two species was much the same near Provincetown on the 29th of the month in 1916 (station 10298). In some years, at least, this practical elimination of *C. longipes* from the catches happens equally early in the season near Cape Ann, where we found *C. tripos* much the more abundant of the two as early as August 22 in 1914 (station 10253, five times as many *tripos* as *longipes*), but in other summers *C. longipes* persists in numbers in the northeastern part of Massachusetts Bay long after *tripos* has taken its place off Cape Cod. This was the case in 1915, when the former predominated off Cape Ann on August 31 (station 10306, 17 *longipes* to 2 *tripos*) and about equaled *tripos* there as late as September 29 (station 10320), though the latter abounded, with almost no *longipes*, inside Stellwagen Ledge and near the tip of Cape Cod, only a few miles distant to the south, on the same day (stations 10221 and 10222). In fact, it was not until well into October that *tripos* finally replaced *longipes* at our standard station off Gloucester during that autumn (station 10330, October 18, 100+ *tripos* to 1 *longipes*). Probably the fact that *C. longipes* may persist in abundance in the northern side of Massachusetts Bay long after it has dwindled almost to the vanishing point in the southern, and such variations as I have just recorded in the precise date when *C. tripos* replaces it off Cape Ann from summer to summer, are due to variations in the drift flowing southward past Cape Ann, which may be expected to bring a constant supply of *C. longipes* with it throughout the summer, for the latter continues predominant over *C. tripos*, or at the least is a large factor in the peridinian plankton of the more northerly and easterly parts of the coastal belt of the gulf until well into the autumn as follows:

Relative numbers of C. tripos and C. longipes in samples

General locality and date	C. longipes	C. tripos	General locality and date	C. longipes	C. tripos
Off Isles of Shoals:			Near Mount Desert Island:		
Aug. 5, 1913, station 10105	(1)	(1)	Aug. 13, 1913, station 10099	(1)	(1)
Nov. 1, 1916, station 10400	1	3	Aug. 18, 1915, station 10305	20+	1
Off Cape Elizabeth:			Sept. 15, 1915, station 10317	13	3
Aug. 14, 1913, station 10103	40	18	Oct. 9, 1915, station 10328	(2)	(4)
Aug. 14, 1914, station 10251	115	1	Off Machias, Me.:		
Sept. 20, 1915, station 10319	(2)	(3)	Aug. 13, 1913, station 10098	26	7
Off Penobscot Bay:			Aug. 12, 1914, station 10247	42	3
Aug. 14, 1914, station 10250	32	2	Sept. 11, 1915, station 10316	9	25
Sept. 16, 1915, station 10318	13	5	Oct. 9, 1915, station 10327	(2)	(3)
Oct. 9, 1915, station 10329	8	5			

[1] Numbers about equal. [2] Predominant. [3] Fewer. [4] Not found.

Just how rapidly *C. tripos* may be expected to spread eastward toward Cape Sable from its offshore center of abundance in the center of the gulf is yet to be learned. It is established, however, that on August 12, 1913 (station 10095), and again on September 2, 1915 (station 10311), the two species were present in roughly equal numbers on German Bank, where *longipes* alone was found in June, 1915 (station 10290). *Tripos* greatly outnumbered *longipes* near Lurcher Shoal (station 10245) and in the neighboring part of the basin (station 10246) as early as August 12 in 1914. It is also probable that *tripos* will usually be found to dominate close in along the west Nova Scotian coast before the middle of September, for it outnumbered *longipes* near land off Shelburne (a few miles east of Cape Sable) on the 6th of that month in 1915 (station 10313, 30 *tripos* to 12 *longipes*), where we had found *longipes* predominant the previous June,[40] as well as during July and August of 1914.[41]

Ceratium tripos comes finally and definitely to dominate over *C. longipes* in all parts of the gulf by the middle or end of October, including even the coastal belt east of Penobscot Bay. McMurrich (1917) did not find *longipes* at all at St. Andrews after the 16th of that month, whereas *C. tripos* occurred there regularly from that date until March 2, when Ceratium disappeared with the inception of the vernal flowering of diatoms.

C. tripos has greatly outnumbered *C. longipes* in all the parts of the gulf we have visited in midwinter; in fact, the latter, if not wanting, was at least so rare that I failed to find it in several of the samples examined.

Relative abundance of the several species of Ceratium in winter, from samples

Locality	C. longipes	C. tripos	C. fusus	C. arcticum
Massachusetts Bay, Dec. 29, 1920, station 10488	1	19	2	2
Off Cape Ann, Dec. 29, 1920, station 10489	1	20	1	0
Western Basin, Dec. 29, 1920, station 10490	0	50	2	0
Off Cape Cod, Dec. 30, 1920, station 10491	2	30	3	0
Off Merrimac River, Dec. 30, 1920, station 10492	1	18	1	0
Off Isles of Shoals, Dec. 30, 1920, station 10493	0	15	3	1
Off Cape Elizabeth, Dec. 30, 1920, station 10494	0	15	3	1
Off Penobscot Bay, Jan. 1, 1921, station 10496	1	40	2	0
Off Mount Desert Island, Jan. 1, 1921, station 10497	2	35	4	3
Off Machias, Me., Jan. 4, 1921, station 10498	1	15	1	0
Fundy Deep, Jan. 4, 1921, station 10499	1	52	7	0
Eastern Basin, Jan. 4, 1921, station 10500	3	20	13	0
Eastern Basin, Jan. 5, 1921, station 10502	7	43	1	0
Off Yarmouth, Nova Scotia, Jan. 4, 1921, station 10501	1	19	2	0

[40] Station 10291, 19 *longipes*, 1 *tripos;* station 10294, many *longipes* and intermediates between it and *arctica*, no *tripos*.

[41] Station 10232, July 28, many *longipes*, no *tripos;* station 10233, July 28, 42 *longipes*, 3 *tripos;* station 10243, August 11, many *longipes*, no *tripos*.

The hauls listed above are further interesting as showing that *C. arcticum*, so widely distributed in spring (p. 407) but not detected in the gulf in late summer or autumn, reappears there in small numbers in midwinter, but curiously enough along its northern and western shores and not in the eastern side.

There is no reason to suppose that any notable alteration takes place in the relative numbers of the several species of Ceratium during the months of January and February; certainly not off Gloucester during the winter of 1913, where *C. tripos*

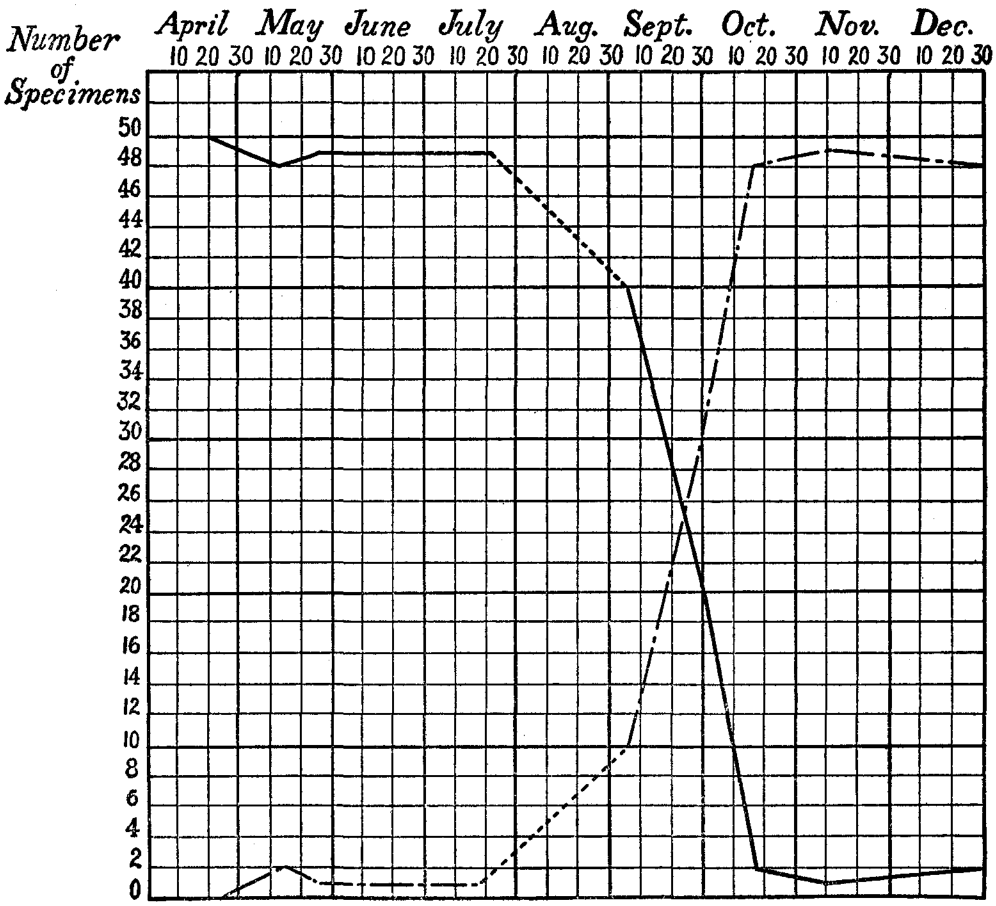

FIG. 111.—Proportionate numbers of *C. longipes* (solid curve) and *C. tripos* (broken curve) in samples of 100 Ceratium of all species in the Massachusetts Bay region at different seasons, 1913 to 1922

continued predominant until the diatom flowerings commenced in March. Doctor McMurrich's plankton lists also show this to have been the case at St. Andrews during 1916.

The mutual fluctuations of *C. tripos* and *C. longipes* in the northern part of Massachusetts Bay are represented in the accompanying diagram (fig. 111) based on the combined data for the years 1912, 1913, 1915, 1916, and 1920, which will serve equally for the offshore parts of the gulf if the reversal of dominance be imagined as taking place a month or so earlier in the season. With similar emendation in date in one direction or the other, it would apply to Massachusetts Bay equally in an "early" year, such as 1913, or in a late year.

The mutual fluctuations of *C. tripos* and *C. longipes* may be summarized as follows for the Gulf of Maine as a whole:

Early in spring when the vernal augmentation of diatoms is at its height, Ceratium (and indeed all peridinians) practically vanishes from the gulf, an event taking place first along the northwest coast, where the diatoms flower earliest, and soon afterwards in other parts of the gulf. After the flowerings of diatoms dwindle, *C. longipes* (fig. 112) multiplies until July, when all the gulf, except for a narrow zone along its northeast and east coasts, supports an abundant Ceratium plankton. During July *C. tripos* (figs. 113 and 114) multiplies in the central deeps. As the summer advances the area of abundance of *C. tripos* expands coastwise and the stock of *C. longipes* dwindles until *tripos* becomes predominant along the southwestern, the eastern, and finally along the northwestern and northern coasts of the gulf, with *C. longipes* persisting latest as an important factor in the plankton in the region between Cape Elizabeth and the Grand Manan Channel. *C. tripos* predominates throughout the winter, but even then, when *C. longipes* is at its lowest ebb, the latter has occurred in small numbers at most of our stations; nor does either species vanish wholly from the gulf at any season, though either may be so scarce when the other is at its peak of abundance, as well as during the flowering period of the diatoms, that careful search of considerable amounts of plankton may be required to reveal its presence.

The seasonal changes in the relative abundance of these two peridinians must not, of course, be understood to take place in as orderly a manner as they are represented here, for they are undoubtedly accompanied by temporary interruptions and even reversals, which would alter the smooth curves to a succession of zig-zags, were daily or weekly records available. In fact, such a reversal is known to have taken place in 1915 off Machias, Me., where *longipes* was predominant on July 15 (in the proportion of 16 *longipes* to 3 *tripos* at station 10301), was outnumbered by *tripos* on September 11 (station 10316), was again predominant on October 9 (station 10327), and would doubtless have been found outnumbered by *tripos* a month after that, had we visited that region again later in the season. Sporadic alternations of this sort do not weaken the general thesis that the succession, as here outlined, is a regular and characteristic feature of the planktonic cycle of the gulf, however, though its time table varies from year to year, as do all other seasonal changes in the sea.

In the foregoing account I have purposely refrained from alluding to the status of the two leading species of Ceratium on Georges Bank in late summer or autumn (*longipes* predominates there in spring and early summer (p. 408) as it does elsewhere in the gulf), because no collection of phytoplankton has yet been made on the bank during the half year, August to February.

A fourth species of Ceratium—*C. fusus*—has been taken so often in our tow nets that it deserves brief mention, though it is never predominant in the Gulf of Maine. *C. fusus* has been found at most of the stations where the genus as a whole occurs in any numbers, and at all seasons,[42] both in the inner parts of the gulf, on Georges Bank, on Browns Bank, and off southern Nova Scotia (Bigelow, 1917, p. 323). It has been lacking, or at least so rare as to be overlooked, whenever diatoms swarm, in which it parallels the more abundant species, *tripos* and *longipes*; occasionally, also, among catches of Ceratium plankton. However, no more definite seasonal fluctuation in abundance has been established for it in the Gulf of Maine, nor any regional concentration. Notwithstanding its nearly universal distribution in the gulf and almost constant occurrence there, it seldom rivals the tricornuate forms of Ceratium in abundance, the only instance of this sort so far recorded being that *C. tripos* and *C. fusus* were about equally numerous in the center of the gulf on August 10, 1913 (Bigelow, 1915, p. 334, station 10090).

The sporadic occurrence of the tropical species, *C. macroceras*, in the inner parts of the gulf has already been alluded to (p. 393). *C. bucephalum* (Paulsen, 1908, p. 77, fig. 100) has also been recognized once in early spring (mouth of the Bay of Fundy, station 20079, March 22, 1920); likewise off the southeast face of Georges Bank on February 22, 1920 (station 20044), and south of Marthas Vineyard, November 11, 1916 (station 10406).

OTHER PERIDINIANS

Only two other genera of peridinians have so far been definitely recognized in the Gulf of Maine—Peridinium and Dinophysis—though others doubtless occur. The former has been noted in practically every summer sample in which Ceratium occurs (Bigelow, 1915, p. 334); that is, it is practically universal in the gulf except in regions and at times where diatoms flower abundantly, (and even there it may be present but overshadowed by their masses) or when the plankton is so scanty that it may have been overlooked, though actually present, as, for example, at several of our stations in the early spring of 1920. Peridinium is usally a minor element in the phytoplankton; far less numerous than its companion genus Ceratium. In summer and early autumn the only exceptions to this rule have been on the western part of Georges Bank, July 20, 1914 (stations 10215 and 10216); near Mount Desert Island, September 15, 1915 (station 10317); and off Penobscot Bay, October 9 of that same year (station 10329), where the genus as a whole (represented by several species) was nearly as numerous as either species of Ceratium. Peridinium is relatively even less important in early spring, as exemplified by our cruises of March and April, 1920, when it was represented by few or occasional examples only, though it occurred at about half the stations, distributed over the gulf generally [43] except in the rich diatom centers. In May of 1915, however, Peridinium not only occurred at every station where Ceratium was detected, but rivaled the latter in abundance in the eastern side of the gulf (fig. 115, stations 10270, 10272, and 10273).

As it was again an important element in the plankton of the southwestern part of the basin and of the South Channel on May 17, 1920 (stations 20127, 20128, and

[42] For records of its occurrence in the summer hauls of 1913 and 1914 see Bigelow, 1915, p. 333, and 1917, p. 323. During the autumn of 1916 it was recognized at stations 10400 to 10406; during the spring of 1920 at stations 20044 to 20046, 20048, 20049, 20052 to 20055, 20057, 20063 to 20065, 20067, 20068, 20070 to 20074, 20077, 20080, 20086, 20087, 20093, 20096 to 20098, 20101, 20108, 20111, 20112, 200116, 20118, 20125, and 20128; and at all the stations during December, 1920, and January, 1921 (stations 10488 to 10502).

[43] Recorded for stations 20044, 20045, 20046, 20048, 20057, 20060, 20064, 20065, 20068, 20071, 20074, 20075, 20080, 20086, 20088, 20089, 20096, 20111, 20118, and 20119 for these months.

20129), it is probable that a considerable production of Peridinium takes place during that month. Doctor McMurrich likewise notes Peridinium as appearing in May at St. Andrews, and occurring in some numbers from June until September, while Willey (1913) describes it as sometimes abundant there in July and August.

Specific identification of the several members of this genus which occur in our tow nettings must await a specialist, but I may note that *P. depressum* [44] was the species chiefly responsible for the May maximum in the eastern half of the gulf in 1915, whereas most of the specimens so far identified in the rich catches from the other side of the gulf in the same month of 1920, especially station 20127, were *P. crassipes.* Inasmuch as the few Peridinium so far named from the summer and autumn catches likewise belong to *P. crassipes,* it is probable that that species occurs in the gulf throughout the year. *P. pallidum* is also recorded from the center of the gulf (Bigelow, 1915, p. 334, station 10090). The only species so far identified, in the estuarine waters off St. Andrews is *P. divergens,* typically a neritic form (Willey 1913; McMurrich, 1917).

The genus Dinophysis has been noted often enough in a preliminary examination of the catches to show that it may be expected anywhere in the gulf in summer, at which season its presence has been established in the central basin, off Lurcher Shoal, in the northeast corner of the gulf, in the coastal belt between Cape Elizabeth and Penobscot Bay, on the northwest part of Georges Bank, and off Shelburne, Nova Scotia; but only occasional specimens have been noticed among the Ceratium. Until its presence in the hauls has been fully listed, discussion of its seasonal and regional distribution would be idle; but its absence or at least rarity in the spring hauls for the years 1913, 1915, and 1920 suggests that it is at its lowest ebb at that season. Most of our records for Dinophysis are based on *D. norvegica,* a species widely distributed in northern waters (Paulsen, 1908). *D. homunculus,* native to warm seas and a valuable index for warm currents because it is easy to recognize, has not been found within the gulf although a lookout has been kept for it, but was noted south of Marthas Vineyard on October 1, 1915 (station 10332).

No doubt the plankton of the gulf will finally be found to include many if not most of the naked peridinians known from other seas.[45] So far, however, I can only record the presence of considerable numbers of an unidentified gymnodinid among the scanty plankton of the Eastern Basin on March 3, 1920 (station 20055).

DIATOMS

It is probable that with sufficient search all the diatom species that are pelagic in northern seas would be found in the Gulf of Maine at one season or another, but few species or groups of species, and fewer genera, are ever sufficiently abundant there to dominate the plankton.[46]

The following remarks apply chiefly to the open gulf. Quite different associations of diatoms are to be expected in its estuarine tributaries, especially a rich representation of brackish-water species that have been practically nonexistent at our *Grampus, Albatross,* and *Halcyon* stations. No study has yet been made of the plankton of

[44] Identifications follow Paulsen (1908).

[45] For descriptions of these, see Kofoid and Swezy's (1921) monograph and beautiful illustrations.

[46] On the identifications of the diatoms see p 382.

the various river mouths, bays, and harbors between Cape Cod and Grand Manan, but McMurrich (1917), Bailey (1917), and Fritz (1921) have published extensive lists of the diatoms occurring in the neighborhood of St. Andrews as well as at other localities in the Bay of Fundy and its tributaries, and Fish (1925) has done so for Woods Hole diatoms.

The survey of the diatoms, like that for the peridinians (p. 407), may commence at the end of the winter or first days of spring. At this season, as exemplified by the cruises of the *Albatross* during February and March, 1920, the diatom communities of the gulf fall naturally into three groups, according to locality—1, the sparse diatom flora of the whole deep basin and of the eastern half of the gulf from the mouth of the Bay of Fundy and the Nova Scotian coast on the one side to Cape Cod on the other, and from the 100-meter contour on the north to the shallows of Georges Bank on the south (p. 383); 2, the rich area on the western part of Georges Bank (p. 385); and 3, an even more productive zone along the western shore of the gulf (p. 383).

Over all the considerable expanse of the first area, noted on the chart (fig. 104) as "sparse mixed", Coscinodiscus (mingled with peridinians, as I have noted above) is the dominant diatom genus in March (dominant, however, not so much for its own numbers as for the scarcity of anything else), with the easily recognized *C. asteromphalus* (p. 437) its chief though not its only representative at that time. At most of the March stations offshore the three species of Chætoceras—*C. decipiens*, *C. atlanticum*, and *C. criophilum*—were likewise practically universal in the gulf in 1920.[47] These three are all oceanic in nature (Gran, 1908 and 1912; Ostenfeld, 1913); such, likewise, are *Chætoceras densum*, *Rhizosolenia semispina*, and *R. styliformis*, which have been detected at 5, 12, and 2 of the February and March stations in 1920. The offshore hauls likewise yielded an unmistakable if minor component of neritic origin, contributed by the coastal belt or by the offshore banks, including the following species: *Chætoceras debile*, *Ch. didymum*, *Ch. diadema*, *Ch. mitra*, *Ch. sociale*, *Ch. laciniosum*, *Ch. contortum*, *Biddulphia aurita*, *Eucampia zodiacus*, Licnophora, *Lauderia glacialis*,[48] *Thalassiothrix nitschioides*, Skeletonema, and Thalassiosira. *Thalassiothrix longissima*, which is partly oceanic and partly neritic on the other side of the Atlantic (Ostenfeld, 1913), was likewise detected just north of Georges Bank (station 20064) and on its eastern part (station 20066) on March 11.

When the occurrence of these several neritic forms is plotted for March, 1920 (fig. 116), it is evident (as might be expected) that they were most abundant around the periphery of the gulf, and especially in its western side between Massachusetts Bay and Portland, where diatoms were flowering actively at the time (p. 383); very rare, indeed, in the central deeps of the gulf, to whose diatom flora neither the coast line nor the shallow banks were contributing appreciably. It is interesting that this was equally true of the eastern part of Georges Bank in that March, though neritic diatoms swarm there at other seasons (p. 391).

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[47] These three species were detected side by side at 21 stations for February and March, 1920 (stations 20044 to 20046; 20048 to 20050, 20053, 20057, 20061 to 20069, 20071, 20082, 20086, 20088); *decipiens* and *criophyllum* at stations 20070, 20078, 20079, 20088; *atlanticum* and *criophyllum* at station 20052; *atlanticum* and *decipiens* at stations 20056 and 20083; *atlanticum* only at station 20054; and *decipiens* only at stations 20058, 20059, 20060, 20072, and 20084.

[48] This species is well described and figured by Gran (1908), but Dr. Albert Mann, in a letter, remarks that several other diatoms are confused under the synonyms there given.

I may add, for the sake of completeness, that much the same list of diatoms occurred over the whole breadth of the continental shelf off Shelburne, Nova Scotia, on March 19, 1920 (stations 20073 to 20076), though here the variety of species per

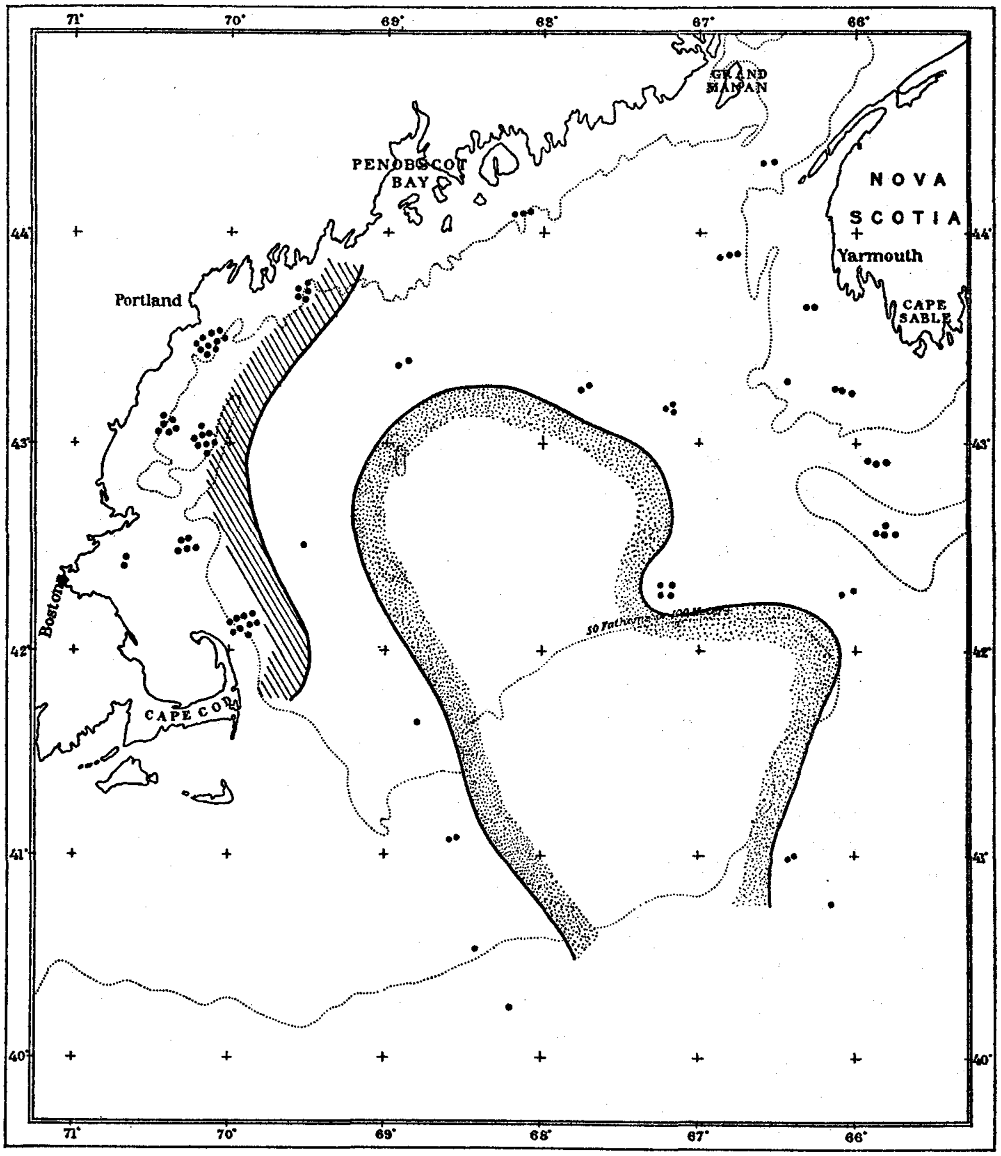

FIG. 116.—Occurrence of certain neritic diatoms in February and March, 1920, a dot for each locality record of the following species: *Biddulphia aurita, Chætoceras debile, Ch. contortum, Ch. diadema, Ch. didymum, Ch. laciniosum, Ch. mitra, Ch. sociale, Eucampia, Lauderia glacialis,* Licmophora, Skeletonema, *Thalassiothrix nitschioides,* and Thalassiosira. The hatched curve incloses the area where most of the stations yielded five or more of these species; the stippled curve where we found none of them

station averaged larger than in the neighboring parts of the Gulf of Maine, as, for example, in Browns Bank, in the Northern Channel, and along western Nova Scotia. The most interesting feature of the diatom communities along this line is that Coscinodiscus was most numerous over the inner half of the shelf where it, together with the oceanic species *Chætoceras criophilum* and *Ch. decipiens*, composed the bulk of the catch (stations 20073 to 20075), but occurred only sparsely at the outer stations (stations 20076 and 20077); whereas neritic species (notably *Ch. mitra, Ch. diadema, Ch. laciniosum, Ch. debile*, and *Thalassiothrix nitschioides*) were most plentiful over the outer half of the shelf (stations 10275 and 10276), not next the land as one might have expected, and even occurred outside the continental slope as well (station 20077).

Such a concentration of neritic forms at the outer stations off Shelburne instead of at the inner is intelligible when hydrographic conditions are taken into account, because the axis of the cold Nova Scotian current of low salinity, itself essentially neritic in its biologic aspect, occupied precisely the same location at the time.

The abundant diatom community already mentioned (p. 383) as characterizing the western part of Georges Bank on February 23, 1920, consisted chiefly of slimy masses of the tiny neritic species *Chætoceras sociale*, not of Coscinodiscus nor of the oceanic species of Chætoceras, though *Ch. decipiens, Ch. criophilum*, and *Ch. atlanticum* all occurred there, as did the neritic forms *Rhizosolenia shrubsolei, Eucampia zodiacus*, and Leptocylindrus. This flowering of *Ch. sociale* was very local, as seems usually to be the case when concentrations of diatoms occur on Georges Bank, and was confined strictly to the comparatively shoal waters of the bank (stations 20046 and 20047). *Ch. sociale* was sought in vain in the tow netting over the edge only 20-odd miles distant (station 20045), where *Thalassiothrix nitschioides* and an occasional cell of Guinardia and *Chætoceras diadema* were the only neritic diatoms recognized. The very sparse community of diatoms in the basin immediately to the north of the bank (station 20048) consisted of the same oceanic species of diatoms that characterize the central parts of the gulf generally in February and March—that is, Coscinodiscus, *Chætoceras atlanticum, Ch. criophilum, Ch. decipiens, Ch. boreale, Ch. densum, Rhizosolenia semispina*, and *Thalassiothrix longissima*.

No tropical phytoplankton was found at our stations outside the continental slope in February or March, 1920 (stations 20044, 20069, and 20077).

Our work for 1913 had already suggested that the diatoms that first commence rapid multiplication in the Cape Ann–Cape Elizabeth region in spring are the forerunners of the vernal flowerings that are the most spectacular event in the yearly planktonic cycle of the Gulf of Maine. These are the several species of Chætoceras that may rival the peridinians here and there along the coast even as early as the last of January or early February, especially in Ipswich Bay. Shortly thereafter the genus Thalassiosira begins flowering, a phenomenon which we have been able to follow through parts of the years 1913, 1915, and 1920.

In 1920 the tow at the mouth of Massachusetts Bay contained Thalassiosira, besides several other kinds of diatoms, on March 1 (station 20050; see list p. 423); and Thalassiosira and Chætoceras must both have commenced flowering actively even earlier than this alongshore between Cape Ann and Cape Elizabeth that year, the "rich" diatom area outlined on the chart (fig. 104) being dominated by these two genera on March 4 and 5.

The list given below (p. 425) for the station near Cape Elizabeth (20059), which was paralleled near the Isles of Shoals (station 20060), and the dominance by Thalassiosira may be taken as typical of this part of the coastwise belt during the first half of March. A few miles farther out at sea, however, on the same day, between the Isles of Shoals and Jeffrey's Ledge (station 20061), the several species of Chætoceras, combined, dominated instead of Thalassiosira, though there was also a considerable amount of the latter in the catch; in fact, practically a repetition of the list of species given for station 20059 (p. 425).

In the spring of 1921, when we found the vernal flowering just commencing along the western shores of the gulf during the first week of March, there was a typical though still only moderately plentiful Thalassiosira–Chætoceras plankton in Massachusetts Bay on the 4th (station 10505), dominated by the former, with *Chætoceras debile, Ch. didymum, Ch. diadema, Ch. decipiens, Biddulphia aurita, Ditylium brightwellii,* Coscinosira, Coscinodiscus, *Lauderia borealis,* and *Rhizosolenia semispina. Thalassiosira nordenskioldi,* with *Biddulphia aurita,* also dominated a very sparse diatom plankton in Ipswich Bay that same day (station 10506), with a strong sprinkling of *Ditylium brightwellii,* a few *Chætoceras criophilum,* Lauderia, and Coscinodiscus. North of this (stations 10507 and 10508) and farther offshore (stations 10509 and 10510) the water was still almost clear of diatoms except for Coscinodiscus.

In a tow near Seguin Island, March 4, 1920 (station 20058) *Lauderia glacialis,* not Thalassiosira or Chætoceras, dominated a moderately plentiful diatom plankton, which also included *Chætoceras decipiens, Ch. debile, Ch. diadema,* and other species not yet determined, *Rhizosolenia semispina* and *R. setigera, Thalassiosira nordenskioldi, Thalassiothrix nitschioides,* and Coscinodiscus. The assemblage of species was much the same near Mount Desert Island the day before, though the plankton was extremely scanty (station 20056; see list, p. 426). The inference from this is that Lauderia began flowering in this zone earlier in the season than either Thalassiosira or Chætoceras. We have found no evidence of such a sequence either between Cape Cod and Cape Elizabeth in the one side of the gulf or off western and southern Nova Scotia in the other (the latter marked "sparse diatom" on the chart, fig. 104), where tows during the second and third weeks of March, 1920, shortly antedating the local flowerings of Thalassiosira and Chætoceras, yielded no Lauderia at all but were dominated by Coscinodiscus, the diatom flora, as a whole, still being very sparse, though including a considerable list of species (see list, p. 427; stations 20072, 20078, and 20084).

In the coastal waters of the gulf the genera Thalassiosira and Chætoceras are the most characteristic members of the diatom flora of spring; it is unusual for any other to dominate there after the vernal flowerings are well underway.

Rapid multiplication of Thalassiosira and Chætoceras is responsible for the expansion of the extent of rich diatom plankton which takes place in the western side of the gulf from March on (p. 385). In 1920 *Thalassiosira nordenskioldi, Chætoceras debile,* and *C. decipiens* together dominated the plankton in Massachusetts Bay on April 6 (stations 20089 and 20090), with a considerable list of other species less numerous (see list, p. 424).

The swarms of diatoms off Cape Ann (station 20091), northward past Cape Elizabeth, across the mouth of Casco Bay, and seaward out to Platts Bank (stations 20091 to 20096) also consisted chiefly of Thalassiosira and of various species of

Chætoceras. The lists given below for station 20093 off the Isles of Shoals (p. 425) and station 20095 off Cape Elizabeth (p. 425) may serve as representative.

The two genera, Thalassiosira and Chætoceras, similarly dominated the plankton in the Isles of Shoals region during the April flowerings of the year 1913, as well as in Massachusetts Bay, where the tow on the 3d was chiefly *Thalassiosira nordenskioldi* and *Th. gravida*, with a scattering of *Chætoceras decipiens*, *Ch. densum*, *Ch. atlanticum*, *Ch. contortum*, *Biddulphia aurita*, *Coscinosira polychorda*, *Thalassiothrix nitschioides*, and *Rhizosolenia semispina* (Bigelow, 1914a, p. 405).

Much the same lists of species—chiefly Thalassiosira and Chætoceras—are responsible for the April flowerings of diatoms off western Nova Scotia, in the eastern side of the gulf, and out from Cape Sable across Browns Bank to the Eastern Channel (see lists for stations 20103, 20105, 20106, and 20107, pp. 428, 429. But whereas Thalassiosira is, on the whole, the dominant genus in the western side of the gulf in April and sometimes almost monopolizes the water there (p. 452), it has been entirely overshadowed by a great abundance of Chætoceras in all the hauls in the eastern side. This was also the case with the rich gathering of diatoms made off the southeast slope of Georges Bank on April 16 (station 20109; see list, p. 430). Douthart's tows in 1913 over the northern part of Georges Bank suggest that Chætoceras is also the most characteristic spring flowering diatom there (hence over the offshore banks as a whole), for on April 14 *Chætoceras densum*, *Ch. atlanticum*, and *Ch. decipiens* dominated on the central part of the bank, with smaller amounts of *Thalassiosira nordenskioldi* and *Th. gravida*, besides a scattering of *Ditylium brightwellii*, *Rhizosolenia obtusa*, *Rh. styliformis*, *Rh. semispina*, *Thalassiothrix nitschioides*, *Asterionella japonica*, Coscinodiscus, Coscinosira, and the neritic genus Pleurosigma. The fact that *Rhizosolenia styliformis* instead of Chætoceras dominated an equally productive gathering a few miles to the westward two weeks later illustrates the local fluctuations in the flowerings of different diatoms (Bigelow, 1914a, p. 415).

As the flowerings of diatoms expand eastward along the coast of Maine and offshore over the western half of the basin from April to May (p. 385), Thalassiosira continues to dominate in the coastwise belt (the seasonal expansions and contractions in the range of Thalassiosira are described below, p. 449), and Chætoceras offshore. The very rich gathering in the western side of the basin on May 5, 1915 (station 10267), consisting chiefly of three species of the latter, was one of the most monotonous we have made (see list, p. 429). The rich diatom plankton on the southwestern part of Georges Bank on May 17, 1920 (station 20128), was chiefly *Chætoceras sociale* (p. 430).

The status of the diatoms in summer, autumn, and early winter is discussed above (p. 391) and in the accounts of the several genera. The phenomena chiefly deserving attention are flowerings of Guinardia, Thalassiothrix, and Rhizosolenia on Georges Bank in July (p. 391), of Rhizosolenia in the shoalw ater off Marthas Vineyard in August (p. 431), the very productive flowering of *Asterionella japonica* along the coast of northern Maine in August, 1912 (p. 431), the persistence of an abundance of Thalassiosira and Chætoceras in the region of Mount Desert Island until into autumn (p. 426) and in the eastern side of the basin until late in the summer of 1912 (p. 392), and the flowerings of Skeletonema and *Rhizosolenia alata* in Massachusetts Bay and of the former in the Bay of Fundy late in summer and early in autumn (p. 394). Fish (1925) has already called attention to the interesting fact that these, which are summer forms in Massachusetts Bay to the north of Cape Cod, dominated the December catch at Woods Hole. The winter flowering of *Rh. alata* in Cape Cod Bay, described above (p. 396), is also interesting because suggesting a more southerly seasonal cycle there than for other parts of the gulf.

The accompanying photographs (figs. 117 to 126) illustrate the actual associations of the various species of diatoms in different parts of the Gulf of Maine from season to season. Several representative lists for standard stations also follow. The reader is cautioned, however, that in no case do these pretend to be complete, only the more numerous forms, such as would be found by examining a fair sample (but without exhaustive search), being enumerated. Whenever the genus Chætoceras forms any considerable part of the total plankton it has comprised specimens (listed as Chætoceras sp.) the identity of which has not been determined for one reason or another. But this limitation does not interfere seriously with the value of the lists, for it is precisely the more common and therefore ecologically more important species that are of interest to the student of broad oceanographic and biological problems. The samples for each station were examined independently by Dr. Albert Mann and by me unless otherwise noted. Species verified by Doctor Mann are starred. Since no attempt is made to contribute to the systematics of the group, the nomenclature follows Gran's (1908) convenient manual of the planktonic diatoms of northern seas, except in the genus Coscinodiscus, where Doctor Mann recognizes the older species, *asteromphalus* Ehrenberg and *oculus-iridis* Ehrenberg, as distinct from *subbulliens* Jörgensen.

Lists of diatoms at representative localities

[The most plentiful species for each station are so designated by being located above the dotted line. Species of which only odd examples were noted are marked S. The presence of the starred (*) species was verified by Dr. Albert Mann.]

1.—Massachusetts Bay

A. Southwest side Cape Cod Bay, November 12, 1925 (*Fish Hawk*, trip 1, station 9):

Diatoms scarce.[49]
Rhizosolenia alata dominant.

Chætoceras boreale.
Ch. decipiens.

B. Center of Cape Cod Bay, February 7, 1925 (*Fish Hawk*, trip 6, station 7):

Diatoms abundant.[49]
Rhizosolenia alata dominant.

Chætoceras decipiens.
Ch. boreale.
Coscinodiscus sp.
Thalassiosira nordenskioldi.
Thalassiothrix longissima.

C. West of Stellwagen Bank, February 28, 1925 (*Fish Hawk*, trip 7, station 2):

Diatoms very abundant.[49]
Thalassiosira nordenskioldi dominant.
Thalassiothrix longissima abundant.

Biddulphia aurita.
Chætoceras atlanticum.
Ch. decipiens.
Coscinodiscus sp. (?).
Rhizosolenia alata.
Rh. semispina.
Thalassiothrix nitschioides.

D. Off Gloucester, March 1, 1920, station 20050:

Diatoms scarce.
Chætoceras decipiens dominant.
*Thalassiosira nordenskioldi dominant.

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[49] Identified by Dr. C. J. Fish.

D. Off Gloucester, March 1, 1920—Continued.
*Chætoceras atlanticum.
*Ch. constrictum.
*Ch. criophilum.
Ch. debile.
Ch. diadema.
*Ch. didymum.
*Coscinodiscus concinnus.
*C. curvulatus.
*Lauderia glacialis.
*Nitschia seriata.

E. Off Gloucester, April 9, 1920, station 20090:[50]
Diatoms very abundant.
*Chætoceras debile dominant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum abundant.
*Ch. decipiens abundant.
*Ch. furcellatum abundant.

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*Biddulphia aurita.
*Chætoceras atlanticum **S.**
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.
*Ch. scolopendra.
*Ch. willei.
*Coscinodiscus asteromphalus.
*Fragilaria cylindrus.
*Navicula sp. (?) **S.**
*Rhizosolenia semispina.
R. setigera.

E. Off Gloucester, April 9, 1920—Continued.
*R. styliformis.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

F. August 24, 1922, station 10635:
Diatoms moderately abundant.
Skeletonema costatum dominant.
Rhizosolenia alata.
(Skeletonema costatum and Rhizosolenia alata together constituted nearly 100 per cent of the diatoms.)

Chætoceras decipiens **S.**
Chætoceras sp. (?) **S.**

G. August 24, 1922, station 10640:
Diatoms moderately abundant; many Ceratium.
Rhizosolenia alata nearly 100 per cent of the diatoms.

Skeletonema costatum.

H. October 1, 1915, station 10323 (near Cape Cod):
Diatoms in medium abundance.
*Skeletonema costatum nearly 100 per cent of the diatoms.

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*Chætoceras decipiens **S.**
*Coscinodiscus sp. (?) **S.**
*Rhizosolenia shrubsolei **S.**

2.—Neighborhood of the Isles of Shoals

A. March 4 and 5, 1920, stations 20060 and 20061 combined:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. diadema dominant.
*Thallassiosira gravida dominant.
*Th. nordenskioldi dominant.

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*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. debile.
*Ch. decipiens.
*Ch. didymum.
*Ch. laciniosum.
*Ch. sociale.
*Ch. teres.
*Coscinodiscus asteromphalus.

A. March 4 and 5, 1920—Continued.
*C. concinnus.
*C. curvulatus.
*C. excentricus.
*C. radiatus.
*C. subtilis.
*Detonula cystifera.
*Ditylium brightwellii.
*Lauderia glacialis.
*Melosira borreri **S.**
*Nitschia seriata.
*Pleurosigma stuxbergii.
*Rhizosolenia semispina.
*R. setigera.
*Stephanodiscus astrea **S.**
*Skeletonema costatum.
*Thalassiosira baltica.
*Thalassiothrix nitschioides **S.**

[50] The list of diatoms for a haul in the inner part of the bay on Apr. 6, 1920 (station 20089) is the same except that it includes **Chaetoceras laciniosum,* Ch. sociale,* and * *Ch. teres,* likewise *Rhizosolenia setigera* and **Thalassiosira subtilis,* but lacks *Ch. furcellatum,* Coscinodiscus, Fragilaria, and *Rhizosolenia styliformis.*

B. April 9, 1920, station 20093.[51]
Diatoms very abundant.
*Chætoceras decipiens dominant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras debile abundant.
*Rhizosolenia semispina abundant.

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*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. contortum.
*Ch. criophilum.
*Ch. diadema.
*Ch. furcellatum.
*Ch. scolopendra.
*Ch. sociale.
*Ch. teres.
*Ch. willei.
*Coscinodiscus asteromphalus.
*C. concinnus.
*Pleurosigma stuxbergii.
*Rhizosolenia setigera.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

C. Nearer the coast, in Ipswich Bay, April 9, 1920, station 20092:
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Thalassiosira gravida dominant.

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*Biddulphia aurita.
*Chætoceras atlanticum **S**.
Ch. contortum.
*Ch. decipiens.
*Ch. diadema.
*Ch. furcellatum.
*Ch. laciniosum.
*Ch. teres.
*Ch. wighami.
*Coscinodiscus concinnus.
*Rhizosolenia semispina.
*R. setigera.
Thalassiosira nordenskioldi.
*Thalassiothrix nitschioides.

3.—Off Cape Elizabeth

A. March 4, 1920, station 20059[52] (fig. 119):
Diatoms abundant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum abundant.

Biddulphia aurita.
Chætoceras debile.
*Ch. decipiens.
*Ch. diadema.
Ch. didymum.
Ch. sociale.
Ch. teres.
Ch. sp. ?
*Coscinodiscus curvulatus.
*C. excentricus.
*Ditylium brightwellii. **S**.
Lauderia glacialis
*Pleurosigma stuxbergii **S**.
*Rhizosolenia setigera.
*R. semispina.
Skeletonema costatum.
Thalassiothrix nitschioides.
*Thalassiosira gravida.

B. April 10, 1920, station 20095:
Diatoms very abundant.
*Chætoceras debile dominant.

B. April 10, 1920—Continued.
*Ch. contortum dominant.
*Thalassiosira nordenskioldi dominant.

Biddulphia aurita.
*Cerataulina bergonii **S**.
*Chætoceras atlanticum.
*Ch. decipiens.
*Ch. diadema.
Ch. didymum.
*Ch. laciniosum.
*Ch. scolopendra **S**.
*Ch. sociale.
*Ch. teres.
*Ch. willei.
*Coscinodiscus asteromphalus.
Coscinosira polychorda.
*Eunotia areus **S** (accidentally present).
*Nitschia closterium.
*N. seriata.
*Rhizosolenia semispina.
*R. setigera.
*Skeletonema costatum.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

[51] The list for Platts Bank the next day (station 20094) was the same, except that it included **Chætoceras densum* and *Ch. didymum*, **Coscinodiscus curvulatus*, **Nitschia seriata*, and *Skeletonema costatum*, but lacked *Chætoceras furcellatum*, *Ch. willei*, and *Thalassiothrix nitschioides*.

[52] The list was the same near Seguin Island on that day (station 20058, fig. 117), except that it lacked *Chætoceras diadema*, *Coscino discus excentricus*, and *Rhizosolenia semispina*, but included **Chætoceras atlanticum*, **Ch. criophilum*, **Ch. laciniosum*, **Ch. willei*, **Coscinodiscus asteromphalus*, **C. concinnus*, and *C. subtilis*.