C. May 13, 1915, station 10277: [53]
Diatoms very abundant.
Thalassiosira nordenskioldi dominant.
Thalassiothrix longissima abundant.

Chætoceras contortum.
Ch. debile.
Ch. decipiens.
Ch. didymum.
Ch. laciniosum.
Coscinosira polychorda.
Ditylium brightwellii.
Lauderia glacialis.
Rhizosolenia semispina.
R. setigera.
Thalassiosira gravida.
Thalassiothrix nitschioides.

4.—Near Mount Desert Island

A. March 3, 1920, station 20056: [54]
Diatoms scarce.
Lauderia glacialis dominant.
Coscinodiscus sp.?

Chætoceras decipiens.
Ch. didymum.
Ch. atlanticum.

B. May 11, 1915, station 10275:
Diatoms very abundant.
*Thalassiosira nordenskioldi nearly 100 per cent of the catch.

---

*Biddulphia aurita.
Chætoceras debile.
*Ch. decipiens.
*Ch. diadema.
*Rhizosolenia setigera.
*Thalassiosira gravida.
(A scattering of each.)

C. June 11, 1915, station 10285:
Diatoms abundant.
*Thalassiosira nordenskioldi dominant.
*Chætoceras contortum dominant.
*Ch. debile dominant.

Chætoceras constrictum.
Ch. decipiens.
*Ch. furcellatum.
*Ch. laciniosum.
*Ch. scolopendra **S.**
*Ch. teres.
Ch. sp.?.
*Coscinodiscus concinnus.
Coscinosira polychorda.
Lauderia glacialis.
*Rhizosolenia semispina.
*R. setigera.
*Thalassiosira gravida.

D. July 19, 1915, station 10302:
Diatoms in medium abundance.
*Thalassiosira gravida dominant.
*Chætoceras scolopendra abundant.
*Rhizosolenia setigera abundant.

---

*Chætoceras contortum.
Ch. debile.
*Ch. decipiens.
*Coscinodiscus asteromphalus.
*Nitschia seriata.
*Rhizosolenia alata.
*Thalassiosira decipiens.
*Thalassiothrix nitschioides.

E. August 14, 1914, at a locality off the mouth of Penobscot Bay, station 10250:
Diatoms abundant, with many Ceratium.
*Chætoceras criophilum dominant.
Ch. constrictum dominant.
*Ch. decipiens dominant.
*Ch. diadema dominant.
*Ch. scolopendra dominant.

---

*Chætoceras debile.
*Ch. densum.
*Ch. laciniosum.
*Ch. peruvianum.
*Corethron valdiviae.
*Licmophora jurgensii.
*Nitschia seriata.
*Rhabdonema arcuatum **S.**
*Rhizosolenia setigera.
*Skeletonema costatum.
*Thalassiosira gravida.
*Th. nordenskioldi.

F. September 15, 1915, station 10317: [55]
Diatoms in medium abundance.
*Thalassiosira gravida dominant.

[53] Not examined by Doctor Mann.
[54] Not examined by Doctor Mann.
[55] On Aug. 21, 1912, *Asterionella japonica* was nearly 100 per cent of the very abundant phytoplankton in this region (p. 431).

F. September 15, 1915—Continued.
*Coscinodiscus concinnus dominant.

Chætoceras constrictum.
Ch. decipiens.
*Ch. diadema.
*Coscinodiscus oculus-iridis.
*C. asteromphalus.
*Ditylium brightwellii.
*Melosira crenulata.
*Nitschia closterium.
*Paralia sulcata.
*Pleurosigma normanii.
*Rhizosolenia setigera.
*R. shrubsolei.
*Skeletonema costatum.
*Thalassiosira nordenskioldi.
*Thalassiothrix longissima.

G. October 9, 1915, station 10328:
Diatoms moderately abundant.
*Chætoceras decipiens numerous.
*Rhizosolenia setigera numerous.
*Thalassiosira decipiens numerous.
*Thalassiothrix longissima numerous.

---

*Actinoptychus undulatus.
*Chætoceras breve.
*Ch. didymum.
*Ch. constrictum.
Ch. danicum.
Ch. debile.
*Ch. difficile (with endocysts).
*Ch. laciniosum.
*Coscinodiscus concinnus.
*C. excentricus.
*C. asteromphalus.
*C. oculus-iridis.
Coscinosira polychorda.
*Ditylium brightwellii.
*Paralia sulcata.
*Rhabdonema arcuatum.
*Rhizosolenia shrubsolei.
*Thalassiosira hyalina.

5.—Bay of Fundy

A. Petit Passage, Nova Scotia, June 10, 1915:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. decipiens dominant.
*Ch. scolopendra dominant.
*Rhizosolenia semispina dominant.

---

*Actinoptychus undulatus **S.**
Chætoceras constrictum.
*Ch. criophilum.
*Ch. debile.
*Ch. diadema.

A. Nova Scotia, etc.—Continued.
*Ch. laciniosum.
*Ch. teres (with endocysts).
*Corethron valdiviæ.
*Coscinodiscus concinnus.
*Nitschia seriata.
*Paralia sulcata **S.**
*Rhabdonema arcuatum **S.**
*Rhizosolenia alata.
*Thalassiosira gravida.
*Thalassiosira nordenskioldi.

6.—Banks off Western Nova Scotia

A. Near Seal Island, Nova Scotia, March 23, 1920, station 20084:
Diatoms scarce.
*Actinoptychus undulatus dominant.
*Biddulphia aurita dominant.
*Coscinodiscus concinnus dominant.
*C. asteromphalus dominant.

Chætoceras decipiens.
*Paralia sulcata.
*Pleurosigma stuxbergii.
*Rhabdonema arcuatum.
*Rhaphoneis surirella.
*Rhizosolenia setigera.
*R. semispina.
Skeletonema costatum.
*Thalassiosira gravida.
*Thalassiothrix nitschioides.

B. South of Seal Island, Nova Scotia, April 15, 1920, station 20104:
Very abundant diatom plankton.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. diadema dominant.

---

*Actinoptychus undulatus **S.**
*Biddulphia aurita.
*Chætoceras criophilum.
*Ch. decipiens.
*Ch. laciniosum (with endocysts).
*Ch. seiracanthum.
*Paralia sulcata.
*Rhizosolenia semispina.
*Thalassiosira gravida.
Th. nordenskioldi.
*Th. decipiens.
*Thalassiothrix nitschioides.

C. Near Lurcher Shoal, April 12, 1920, station 20101 (fig. 120):
Diatoms moderately abundant.
*Chætoceras atlanticum dominant.
*Ch. criophilum dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant.

Chætoceras debile.
Ch. diadema.
*Ch. seiracanthum.
*Ch. scolopendra.
*Ch. sociale **S.**
*Coscinodiscus radiatus.
Lauderia glacialis.
*Rhizosolenia semispina.
*Thalassiosira decipiens.
Th. gravida.
*Th. hyalina.
*Thalassiothrix nitschioides.
Th. longissima **S.**

D. German Bank, April 15, 1920, station 20103.[56]
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant (with endocysts).
---
*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.

D. German Bank, April 15, 1920—Continued.
*Ch. didymum.
*Ch. scolopendra **S.**
*Coscinodiscus lineatus.
Coscinosira polychorda.
Lauderia glacialis.
*Pleurosigma longum **S.**
*Rhizosolenia semispina.
*R. setigera.
*Thalassiosira decipiens.
*Th. gravida.
Th. nordenskioldi.
*Thalassiothrix longissima.
*Th. nitschioides.

E. German Bank, June 9, 1915, station 10290:
Diatoms in medium abundance.
*Rhizosolenia semispina dominant.
*Chætoceras decipiens abundant.
---
*Actinoptychus undulatus.
Chætoceras contortum.
Ch. debile.
*Ch. diadema.
*Ch. laciniosum.
*Coscinodiscus asteromphalus.
*Navicula directa **S.**
*N. lata **S.**
*Nitschia seriata.
*Pleurosigma normanii **S.**,
*P. stuxbergii **S.**,
*Rhaphoneis surirella **S.**,
*Rhizosolenia alata.
*R. styliformis.
Thalassiosira sp.?

7.—Western Basin abreast of Massachusetts Bay

A. February 23, 1920, stations 20049 and 20058:
Diatoms very scarce.
Coscinodiscus sp. ? dominant.
Chætoceras decipiens.
Ch. atlanticum.
Ch. criophilum.

B. April 18, 1920, station 20115:[57]
Diatoms moderately abundant.
*Chætoceras atlanticum dominant.
*Ch. decipiens dominant.
*Rhizosolenia semispina dominant.

B. April 18, 1920—Continued.
*Thalassiosira nordenskioldi abundant.
---
*Biddulphia aurita.
Chætoceras densum.
Ch. contortum.
Ch. teres.
*Ch. scolopendra.
*Rhizosolenia setigera.
*Skeletonema costatum **S.**
*Thalassiothrix longissima.

[56] At a neighboring station (20104) Doctor Mann also lists **Actinoptychus undulatus*, **Chætoceras seiracanthum*, and **Paralia sulcata*.

[57] A station (20114) in the center of the basin that same day adds the following species, verified by Doctor Mann: *Chætoceras criophilum, Ch. didymum, Ch. furcellatum, Ch. teres; Rhizosolenia alata; Thalassiosira gravida, Thalassiothrix nitschioides;* also *Ch. densum* and *Ch. contortum* in another sample from station 20115.

C. May 5, 1915, station 10267 (fig. 121):
Diatoms very abundant.
*Chætoceras densum fully 50 per cent of the catch.

C. May 5, 1915—Continued.
Chætoceras criophilum.
*Ch. decipiens.
*Rhizosolenia semispina.
*Thalassiothrix longissima.

8. North Channel

A. March 20, 1920, station 20078:[58]
Very few diatoms.
Chætoceras contortum.
Ch. criophilum dominant.
Ch. didymum.
Coscinodiscus subbulliens.

Rhizosolenia semispina **S.**

B. April 15, 1920, station 20105:
Diatoms abundant.
*Chætoceras decipiens dominant.
*Ch. diadema dominant.
*Thalassiothrix nitschioides also abundant.

Bacteriosira fragilis **S.**
*Biddulphia aurita.

B. April 15, 1920—Continued.
Chætoceras contortum **S.**
*Ch. criophilum.
*Ch. debile.
*Ch. laciniosum.
*Ch. teres **S.**
*Coscinodiscus asteromphalus.
*C. denarius **S.**
*Nitschia seriata.
*Pleurosigma stuxbergii **S.**
*Rhizosolenia alata.
*R. semispina.
R. styliformis.
*Thalassiosira decipiens.
*Th. gravida.
*Th. hyalina.
Th. nordenskioldi.

9.—Brown's Bank

A. March 13, 1920, station 20072.[58]
Scanty diatom and Ceratium plankton.
Coscinodiscus asteromphalus dominant.
Coscinodiscus sp. dominant.

Chætoceras diadema.
Ch. debile.
Ch. mitra.
Thalassiothrix nitschioides.

B. April 16, 1920, station 20106:
Diatoms moderately abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.

B. April 16, 1920—Continued.
*Ch. diadema dominant.
*Thalassiosira gravida abundant.

---

*Chætoceras atlanticum.
Ch. criophilum.
*Ch. laciniosum.
*Coscinodiscus asteromphalus.
Coscinosira polychorda.
*Rhizosolenia semispina.
*R. setigera.
*Thalassiosira decipiens.
Th. hyalina.
*Th. nordenskioldi.
Thalassiothrix nitschioides.

10.—Eastern Channel

A. April 16, 1920, station 20107:
Diatoms very abundant.
*Chætoceras contortum dominant.
*Ch. debile dominant.
*Ch. decipiens dominant.
*Thalassiosira gravida dominant.
*Th. nordenskioldi.

---

*Biddulphia aurita.
*Chætoceras atlanticum.
*Ch. criophilum.
Ch. diadema.

A. April 16, 1920—Continued.
*Ch. laciniosum (with endocysts).
*Coscinodiscus oculus-iridis.
*Fragilaria oceanica.
*Navicula frigida **S.**
*N. vanhöffeni **S.**
*Rhizosolenia alata.
*R. semispina.
*Thalassiosira bioculata.
*Th. hyalina.
*Th. sp. ?
*Thalassiothrix nitschioides.

[58] Not examined by Doctor Mann.

11.—Georges Bank, east end

A. March 11, 1920, station 20066:
Diatoms not plentiful.
*Coscinodiscus asteromphalus dominant.
---
*Actinoptychus undulatus.
*Chætoceras atlanticum.
*Ch. criophilum.
*Ch. decipiens.
Ch. densum.
*Ch. didymum.
*Coscinodiscus concinnus.
*C. excentricus.
*C. oculus-iridis.
*C. radiatus.
*Melosira sulcata.
*Rhaphoneis surirella.
*Thalassiothrix nitschioides.

B. April 16, 1920, station 20109, southeast edge of bank.
Diatoms very abundant.
*Chætoceras debile dominant.
*Ch. decipiens dominant.
*Ch. laciniosum dominant.
---
*Chætoceras atlanticum.
*Ch. contortum.
*Ch. criophilum.
*Ch. densum.
*Ch. diadema.
*Ch. didymum.
*Coscinodiscus asteromphalus.
C. sp.?

B. April 16, 1920—Continued.
*Fragilaria oceanica.
Lauderia glacialis.
*Nitschia seriata.
*Pleurosigma stuxbergii.
*Rhizosolenia semispina.
*Skeletonema costatum.
*Thalassiosira gravida, abundant.
*Th. nordenskioldi, abundant.
*Th. hyalina.
*Thalassiothrix longissima.
*Th. nitschioides.

C. April 17, 1920, northeast part of bank, station 20111 (fig. 122):
Diatoms in medium abundance.
*Chætoceras atlanticum.
*Coscinodiscus [60] dominant.
*Chætoceras decipiens.
*Ch. densum.
*Coscinodiscus concinnus.
*C. heteroporus (?)

D. July 23, 1914, station 10224:
Diatoms abundant.
*Guinardia flaccida dominant.
*Rhizosolenia shrubsolei notably abundant.
---
*Actinoptychus undulatus.
*Cerataulina bergonii.
*Navicula gelida.
Rhizosolenia semispina.
*R. styliformis.

12.—Georges Bank, western end

A. February 22, 1920, station 20046:
Diatoms abundant.
*Chætoceras sociale dominant.
---
*Actinoptychus undulatus.
Chætoceras atlanticum.
*Ch. criophilum.
Ch. decipiens.
*Coscinodiscus crassus.
*C. subbulliens.
Eucampia zodiacus.
*Guinardia flaccida.
Leptocylindrus sp.?
*Navicula gelida.
*Nitschia sp.? abundant.
*Rhizosolenia imbricata.

B. May 17, 1920, station 20128:
Diatoms few on surface, abundant at 20 meters.
*Chætoceras sociale dominant.
---
*Chætoceras atlanticum.
*Ch. decipiens.
*Coscinodiscus concinnus.
*C. subtilis.
*Navicula gelida.
*Pleurosigma normanii.
*Thalassiosira decipiens.
*Thalassiothrix longissima.

[60] Doctor Mann states "fully 50 per cent of the diatoms are an intermediate form between *C. asteromphalus* and *C. oculus-iridis*, having the convexity and areolation of the former and the fineness and general delicacy of the latter. Indeed, Rattray and others look on *C. oculus-iridis* as not a valid species."

C. July 9, 1913, station 10059 (fig. 123):
Diatoms very abundant.
*Guinardia flaccida dominant.
*Eucampia zodiacus dominant.

---

*Biddulphia alternans.
*Coscinodiscus asteromphalus.
*Pleurosigma normanii.
*Rhizosolenia alata.
*R. shrubsolei.
*R. stolforthii.
*R. styliformis.
Skeletonema costatum.
*Stephanopyxis turris.

D. July 23, 1916, station 10347 (fig. 124):
Diatoms very abundant.
*Thalassiothrix longissima dominant.
*Rhizosolenia styliformis dominant.
(Both together constitute 90 per cent of the phytoplankton.)

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*Actinoptychus undulatus.
*Biddulphia alternans.
*Coscinodiscus concinnus
*C. oculus-iridis.
*C. woodwardii.
*Pleurosigma normanii.
*Rhaphoneis amphiceros.

13.—SHALLOW WATER SOUTH OF MARTHAS VINEYARD [61]

A. August 25, 1914, station 10258 (fig. 125):
Very abundant diatom plankton.
Rhizosolenia semispina 100 per cent of a large sample.

A. August 25, 1914—Continued.
Guinardia flaccida S.
No other diatoms noted.

NOTES ON THE DOMINANT GENERA OF DIATOMS

On the following pages such notes are given on the status of the more prominent genera as the preliminary examination of the tow nettings warrant. For convenient reference the genera are arranged alphabetically.

Asterionella

Asterionella japonica, as noted above (p. 392), occurred in extraordinary abundance in August, 1912. During that summer we first found it close to land in Ipswich Bay on July 8 (station 10008; it was not in Massachusetts Bay at that time), again in the coastal zone between Cape Elizabeth and Penobscot Bay the next week (stations 10016 to 10021), and near Lurcher Shoal off Yarmouth, Nova Scotia, on August 15 (station 10031); likewise in the basin near Mount Desert Rock (station 10032) and off the mouth of the Grand Manan Channel (station 10036) a few days later—captures so widely separated that its range must then have included the whole northern coastal belt of the gulf, though nowhere in any notable abundance. During the last half of August it flowered in such abundance that on the 21st, when "passing Great Duck Island, one of the small islands off Mount Desert, the appearance of the water was noticeably soupy, and immediately the vessel was hove to and a surface haul made with the No. 20 net. When brought on board, the net was filled with a brown slimy mass, which on examination proved to consist almost wholly of countless numbers of chains of *Asterionella japonica* * * *" (Bigelow, 1914 p. 133).

This swarm extended westward, though gradually diminishing in density, right across the mouth of Penobscot Bay to the neighborhood of Seguin Island, where there was such a sudden transition to clear water with very little phytoplankton that the

[61] Not examined by Doctor Mann.

change was plainly visible from the deck of the *Grampus*. Though occasional Asterionella were taken nearly as far west as Cape Elizabeth (station 10040), which seems to have been its southern and southwestern boundary at the time, we have never found Asterionella in the open gulf since then. But according to Bailey, Asterionella (his illustration (1915, pl. 2, fig. 18) identifies it as probably *A. japonica*) is not very uncommon in the St. Andrews' region. He has also reported it from Dead Man's Harbor and from the St. John's River in August, and Fritz (1921) found it occasionally—always in small numbers—in October, 1916, and from April until September, 1917, at St. Andrews. It was likewise noted in the northern part of Georges Bank on April 16, 1913, in the collections made by Douthart (Bigelow, 1914a, p. 415).

Herdman, Scott, and Lewis (1914) have described a similar swarming of *Asterionella japonica* near the Isle of Man in May as an event unprecedented for the Irish Channel. But the occasional presence of an abundance of this diatom at that locality is easily explained, for it is known to occur elsewhere in the waters between Ireland and England in February, May, August, and November, not far from the region covered by the plankton studies of the Liverpool Marine Biological Laboratory (Ostenfeld, 1913, pl. 57), while it flowers abundantly every spring in the English Channel (maximum in April) and throughout the whole southern part of the North Sea.

Whether *Asterionella japonica* is regularly abundant anywhere along the east coast of North America is still to be learned, but its presence in small numbers along the coastal zone between New York and Marthas Vineyard and in Long Island Sound during July and August, 1916 (stations 10360, 10361, and 10396), suggests that it may be more important south and west of Cape Cod than it is in the Gulf of Maine. Fish (1925) reports it at Woods Hole both winter and summer.

Biddulphia

Because of its dinstinctively neritic habit (it lives planktonic for only a short part of the year), locality records for *Biddulphia aurita* are valuable as indices of movements of water out from the coast. This diatom was found in small numbers among the swarms of Chætoceras and Thalassiosira all around the coastal zone of the gulf during March and April in the years 1913 (Bigelow 1914a, p. 405), 1920 (stations 20054, 20059, 20061, 20084, 20090, 20093, 20095, 20097, 20098, 20099, 20100, 20102, 20114, 20116, and 20117), and 1921 (stations 10505, 10506, and 10508). It is commonest close to the shore, as might be expected from its life history, rivalling Thalassiosira in abundance in a moderately plentiful diatom plankton off the Merrimac River on March 4, 1920 (station 10506), and occurs in some abundance at St. Andrews and elsewhere in the Bay of Fundy (Bailey, 1917, p. 104; McMurrich, 1917; and Fritz, 1921). It was also dominant in the deep off Mount Desert on April 11, 1920 (station 20098), and again off Yarmouth, Nova Scotia, on the 13th (station 20102), but on both these occasions all other planktonic forms were so scarce that the preponderance of Biddulphia was due less to abundance on its part than to an absence of other diatoms. The station off Mount Desert, just mentioned, is our only record for *B. aurita* outside the 100-meter contour; nor have we found it on Georges Bank. These scattered captures show that *B. aurita* is only a very minor

factor in the diatom flora of the offshore waters of the gulf, where it can safely be credited with a coastal origin.

Biddulphia is distinctly a spring species; in fact, we have never found it in the open gulf at any other season. At St. Andrews it occurs only irregularly and sparsely during the October–February period (McMurrich, 1917; Bailey, 1917), but Doctor McMurrich found it regularly, often in abundance, from February 26 until April 23, after which it is rare. Fritz (1921) likewise records an abundance of Biddulphia on April 20, but without naming the species concerned. The seasonal cycle is much the same for *B. aurita* in European seas, where Ostenfeld (1913, p. 500) describes it as living on the bottom for the greater part of the year, to invade the planktonic communities in great numbers during the spring months.

Biddulphia mobilensis, a true planktonic form though neritic in nature, has been noted in September and October, 1915 (stations 10316 and 10327), and in March, 1921 (station 10505), always in small numbers. Like *B. aurita*, it is more abundant in the estuarine tributaries of the Bay of Fundy, where Bailey (1917) records it for various dates in January and February and again from August to October, and where he found it very abundant and locally dominant in August.

Chætoceras

The relationship which the diverse genus Chætoceras bears to Thalassiosira during the spring flowerings of the latter, and the wide distribution of several of its members in the offshore and eastern coastal waters of our gulf at that time, have already been touched upon (p. 418). As a rule, the same species of Chætoceras that precede the Thalassiosira swarms in spring (p. 421) are to be found in some numbers among the masses of the latter later in the season, even when Thalassiosira is most abundant. To enumerate them, station by station, would be repeating entire the lists given above (p. 423), for practically all the species of the genus definitely known from the gulf have been found among the Thalassiosira plankton of April and May. Nor do the lists for the individual stations off the west and north coasts of the gulf for April (stations 20090 to 20096) differ seriously from the March lists (stations 20056 to 20062), *Ch. decipiens* being universal, with the oceanic species *Ch. criophilum* and *Ch. atlanticum*, on the one hand, and the neritic forms *Ch. diadema*, *Ch. laciniosa*, *Ch. contortum*, *Ch. scolopendra*, *Ch. didymum*, and *Ch. sociale* on the other, occurring often enough to show that though they may be overshadowed by Thalassiosira all of them may be expected anywhere along this zone. *Ch. debile* shows decided augmentation in April, when it not only occurred at every coastwise station in 1920 but dominated the phytoplankton locally on Platts Bank on the 10th (station 20094). *Ch. furcellatum*, easily recognized by its peculiar spine-bearing spores, which was not found at all in March, appeared in numbers near Cape Ann, off Cape Cod, and in Massachusetts Bay on April 9, 18, and 20, 1920 (stations 20090, 20116, 20117, and 20119).

Practically the same association of Chætoceras species, barring *Ch. furcellatum*, was likewise encountered off the west coast of Nova Scotia, on Browns Bank, and in the North Channel during April, 1920 (stations 20101 to 20106), and although

the oceanic species *criophilum, densum,* and *atlanticum* were more generally represented there than at the inshore stations, others as distinctively neritic—e. g., *diadema* and *debile*—were equally universal, and the latter was dominant at three out of these six stations (stations 20102, 20103, and 20106).

In the offshore deeps of the gulf, where Thalassiosira never dominates the plankton, the augmentation of diatoms characteristic of late spring is chiefly due to these same species of Chætoceras. Thus the April lists for these waters (stations 20097, 20098, 20112, 20113, 20114, 20115, and 20116) are much the same as those for March (p. 418), *Ch. criophilum, Ch. atlanticum,* and *Ch. decipiens* being practically universal even in the most oceanic parts of the gulf, with *Ch. diadema, Ch. laciniosum, Ch. contortum, Ch. didymum,* and *Ch. debile* less regular though widely distributed. The latter, in spite of its neritic affinities, dominated a very rich assemblage of diatoms in the Eastern Channel (p. 429, station 20107) and was abundant off the southern face of Georges Bank (station 20109) on April 16, 1920, although *Ch. decipiens, Ch. atlanticum, Ch. criophilum,* and *Ch. densum* were the only species of Chætoceras noted on the shallows of the bank itself at that time (stations 20110 and 20111). The fact that *Ch. densum,* which was apparently confined to Georges Bank during March, 1920, had spread to the southeast part of the basin by mid-April (stations 20112 and 20113), foreshadows the great abundance to which it attains in May (p. 429).

On the assumption that the status of the various diatoms was essentially the same in the gulf in 1913 and 1915 as in 1920, little change takes place in the general association of Chætoceras species from April until June. For example, the list for a station (10278) north of Cape Ann for May 14, 1915, includes *Ch. densum, Ch. decipiens, Ch. laciniosum,* and *Ch. debile,* with *Ch. contortum* and *Ch. didymum* nearby (station 10277). Even where *Ch. debile* is the only species of Chætoceras mingled in any abundance with the swarms of Thalassiosira, as is sometimes the case in April and May when Thalassiosira may practically monopolize the plankton, various other species of Chætoceras can usually be detected by sufficient search.

The vernal augmentation of *Ch. densum* just mentioned resulted in such an abundance of this diatom by the first week of May, 1915, that it either dominated the plankton or at least played that rôle jointly with *Ch. criophilum* over the western, central, and eastern deeps of the gulf generally (stations 10267 to 10269). In fact, these two, with smaller amounts of *Ch. decipiens,* were almost the sole components of the rich diatom plankton (fig. 121) at the first-named locality (station 10267); but few if any *Ch. densum* had reached the northeast corner of the gulf (station 10273) by that time, nor have we ever found this oceanic species an important factor in the phytoplankton near the land, where *Ch. decipiens, Ch. diadema, Ch. contortum, Ch. debile,* and *Ch. didymum* have proved the most plentiful representatives of their genus during May.

Chætoceras sociale in great abundance dominated the phytoplankton on the western part of Georges Bank in the last week of February (station 20046) and again on May 17 (station 20128) in 1920, suggesting that it continued flowering actively there throughout this period of more than two months. But apparently its season of reproduction was drawing to a close on our second visit to that general locality,

because the diatoms had then sunk from the surface (which was practically barren of them) to a depth of about 20 meters, where they were congregated in such numbers that even the coarse-meshed net came back clogged.

The same neritic species of Chætoceras—*laciniosum*, *contortum*, *debile*, and *diadema*—together with the more oceanic *decipiens*, besides occasional *Lauderia glacialis*, *Thalassiosira gravida*, and Coscinodiscus, were found over the coast banks west of Nova Scotia in June, 1915 (there were few diatoms there in May; p. 387) and dominated the much more abundant diatom plankton of that region in April, 1920 (stations 20103 to 21015).

I may also note that in 1915 the easily recognized cells of *Chætoceras constrictum*, which I have not detected during the spring, appeared in some numbers in the catches near Mount Desert Island on June 14 (station 10285) and in Petit Passage, Nova Scotia, on the south side of the Bay of Fundy on the 10th. Apparently this species reaches its plurimum in the gulf in mid-August, when we have found it dominant off Mount Desert (station 10250, August 14, 1914). On the other hand, the group of oceanic species that includes *Ch. atlanticum*, *Ch. criophilum*, and *Ch. densum* (subgenus Phæoceras of Gran, 1908), have as a rule been represented sparsely in our summer hauls. They were either wanting or at least very rare in all our tow nettings during July and August of 1913 and 1915, although several of the more neritic representatives of the genus (listed above, p. 418), with other diatoms, occurred abundantly along the coast east of Penobscot Bay during those months. In 1914 *criophilum* was an important though not the dominant element in the diatom plankton off Penobscot Bay on August 14 (station 10250), and at the more easterly stations the day before (stations 10247 and 10248), while *Ch. atlanticum* and *Ch. densum* were likewise detected in these hauls. More data are needed to show whether these oceanic species are to be expected regularly in the gulf in August but have been overlooked in the cruises made during that month in other summers.

If Chætoceras plankton is characteristic of the western part of Georges Bank in spring, as the abundance of *Ch. sociale* suggests, it must vanish before midsummer, because no Chætoceras were detected on the bank among the swarms of Guinardia (p. 391) in July, 1913 or 1914; only an occasional *Ch. densum* and *Ch. decipiens* on the southwest part of the bank on July 23, 1916 (station 10348); and no Chætoceras at all among the Thalassiothrix-Rhizosolenia community near by (station 10347, p. 391).

Chætoceras decipiens is the only species of the genus that has been detected consistently in the open gulf during the autumn months, and that only in the coastwise belt,[62] the only part of the gulf where diatoms of any kind occur in any number at that season. *Ch. debile*, *Ch. constrictum*, and *Ch. laciniosum* have been recorded locally along the coast of Maine in October (near Mount Desert Island, station 10328, October 9, 1915). *C. danicum* was also detected at this station—so far the only record for this brackish-water species in the gulf outside the Bay of Fundy.

The genus Chætoceras as a whole probably falls to its lowest ebb in the offshore waters of the gulf late in December and early in January, at which season *Ch. decipiens* and *Ch. criophilum* alone were detected at two stations (10488 and 10592)

[62] Stations 10310, 10316, 10317, 10318, 10322, 10323, 10327, and 10328, September and October, 1915.

on the *Halcyon* cruise in 1920 and 1921; but, as pointed out above (p. 396), a comparatively rich collection of Chætoceras was made in Ipswich Bay on January 30, 1913 (see also Bigelow, 1914a, p. 405).

According to McMurrich (1917, and unpublished notes), the genus Chætoceras as a whole is scarcest at St. Andrews during the winter and most abundant between mid-June and September. Fritz's (1921) more detailed counts of the several species of Chætoceras combined, at the same locality, show constantly increasing numbers from the middle of March through April and May, with very abundant flowerings in July and August followed by a decrease during the autumn to the midwinter minimum, when the genus was so scarce that on two occasions (December 27 and January 13) none at all were detected.

McMurrich's, Bailey's (1915 and 1917), and Fritz's lists for St. Andrews, combined, comprise the following species: *Ch. boreale*, *Ch. constrictum*, *Ch. contortum*, *Ch. convolutum*, *Ch. crinitum*, *Ch. criophilum*, *Ch. danicum*, *Ch. debile*, *Ch. decipiens*, *Ch. diadema*, *Ch. laciniosum*, *Ch. sociale*, *Ch. teres*, and *Ch. willei*. *Ch. debile* begins flowering actively there in April and May, is far the most important species numerically, and was chiefly responsible for the very rich Chætoceras flora of July and August recorded by Fritz. *Ch. sociale*, which yielded her next largest counts, was practically nonexistent in November, December, January, February, and March; appeared in April; flowered actively (207,500 per haul) in May; vanished in July; reappeared in August; and attained its maximum abundance (280,000 per haul) on September 6. *Ch. diadema* and *Ch. laciniosum* have been found at St. Andrews from late winter through spring, summer, and early autumn, both of them having their plurimum in July. *Ch. decipiens* has been found sparsely represented at St. Andrews in late June, July, August, September, October, and early November, and the various other species only between early July and the last week in October. The most notable difference between the status of the genus Chætoceras at St. Andrews, as contrasted with the open gulf, is the scarcity of oceanic species. *Ch. atlanticum* and *Ch. densum* have not been detected there at all. Fritz found *C. criophilum* in only one haul on October 12 at St. Andrews. It is also interesting that in 1917 *Ch. constrictum* did not appear in Fritz's lists at St. Andrews until July 17—i. e., about a month later in the season than on the other side of the Bay of Fundy in 1920 (p. 435). Fritz (1921, p. 53) has remarked that the greatest number of species of Chætoceras was recorded for September, though the plurimum for the genus as a whole and for its two most numerous species fell in August. Fish (1925) reports 20 species of Chætoceras at Woods Hole, but only two of them—*decipiens* and *didymum*—were plentiful enough in his catches ever to be classed as "abundant." These two showed a succession of maxima in winter, summer, and autumn; not, however, in spring.

Coscinodiscus

The genus Conscinodiscus is very widely distributed in the Gulf of Maine, both in time and space. In midwinter, on the whole, it is the dominant genus of diatoms, both at St. Andrews (McMurrich, 1917; Fritz, 1921) and along the northern and western shores of the gulf generally as off Cape Cod; for example, in Massa-

chusetts Bay and off the mouth of the Merrimac River,[63] and likewise out at sea, as exemplified by the western basin (p. 428). It seems that at this time of year Coscinodiscus is decidedly more numerous near land and on the offshore banks than in the deeper parts of the gulf or over the bank west of Nova Scotia, for during the *Halcyon* cruise of December and January, 1920–1921, our largest catches of Coscinodiscus were made in the Massachusetts Bay region (stations 10488 and 10489) and off the Merrimac (station 10492), whereas only a scattering was taken in our January hauls at sea off Penobscot Bay or in the eastern side of the gulf (stations 10496 and 10499 to 10502). Coscinodiscus was most numerous in the shallow waters over Georges and Browns Banks during the cruises of the *Albatross* in 1920 (stations 20066, 20072, 20110, and 20111); but although this genus may reach its highest development in the gulf in or near comparatively shoal water, its abundance in the Western Basin at the end of February, 1920, and again a month later (station 20049, February 23, 1920; station 20087, March 24, 1920), forbids the assumption that it is distinctively neritic. In fact, one of its commoner members—*C. asteromphalus*—has usually been described as oceanic in other seas.

Coscinodiscus does not exhibit as definite a flowering period in the gulf as do Thalassiosira or the more plentiful species of Chætoceras, nor does it ever rival the enormous numbers in which these latter genera so often appear there. None of our standard hauls has ever yielded more than a few cubic centimeters of Coscinodiscus, contrasted with hundreds of cubic centimeters of Thalassiosira and Chætoceras during their period of greatest abundance (p. 399).

In the open gulf we have made our richest catches of Coscinodiscus during midwinter, in February, March, and April. In fact, this genus has occurred in almost every offshore haul between the end of December and the middle of April, and Fritz (1921) found it constantly throughout the winter and early spring at St. Andrews. Coscinodiscus has been detected only occasionally in the western half of the gulf generally or on the offshore banks during the late spring or early summer. Thus it was found at only 1 out of 14 stations (station 10266) between May 4 and 30 in 1915, at 2 of the 12 June stations for that year, and not at all in the Massachusetts Bay region or off Cape Cod from May 4 to 17, 1920. If Coscinodiscus is not actually nonexistent in midsummer among the peridinian plankton of the basin of the gulf (likewise along the coastwise belt between Cape Ann and the Bay of Fundy) it is at least so overshadowed there by other more plentiful plant cells as to be overlooked easily. Fritz, too, records it as sometimes wanting and usually scarce at St. Andrews during June, July, and early August; but Coscinodiscus was a considerable element in the plankton near Lurcher Shoal, off Yarmouth, Nova Scotia, on August 12, 1914 (station 10245). Apparently this foreshadowed a widespread augmentation of it in the northeastern part of the gulf during the early autumn, for it occurred in considerable numbers at two stations off the eastern part of the Maine coast on September 11 and 15, 1915 (stations 10316 and 10317), again at these same localities on October 9 (stations 10327 and 10328), indicating that it is more

[63] At this locality we found Chætoceras far more numerous than Coscinodiscus as early in the winter as Jan. 16 in the year 1913.

plentiful and more generally distributed in the coastal belt east of Penobscot Bay in autumn than we have found it in August. McMurrich and Fritz have likewise found it comparatively plentiful at St. Andrews during the last half of October; in fact, Fritz's counts locate its plurimum for the year at that season.

We have no evidence that this autumnal augmentation of Coscinodiscus extends to the western part of the gulf, our October and November stations west and south of Penobscot Bay having yielded few or none during the seasons of 1912, 1915, and 1916. Its duration must be short even in the St. Andrews region, also, for both McMurrich (1917, p. 9) and Fritz (1921) found it considerably less plentiful there in November than in October, but it must multiply in early winter, being widespread from late December on.

The several species of Coscinodiscus are so closely allied to one another that the determination of them must await future critical study, wrong identifications being worse than none. The reader will find above (p. 423) lists of those so far determined by Doctor Mann for representative stations and seasons.

Coscinosira

Coscinosira polychorda, a neritic species, has occurred sparingly among the Thalassiosira and Chætoceras at the April and May stations in both sides of the gulf (stations 20090, 20093, 20095, 20096, 20103, 20104, 20106, and 20107 in April, 1920, and 10277 on May 14, 1915) and at one June station (10285, June 14, 1915), always near land. We have never found it an important factor in the spring phytoplankton, but it was relatively abundant, if not dominant, off Swan Island near Mount Desert Island on September 15, 1915 (station 10317), and occasional specimens were also noted at the same general region on the 9th of the following month (station 10328). One well-preserved chain was also noted in a haul off Machias, Me., January 4, 1921 (station 10498). The only Georges Bank record for Coscinosira is for April 15, 1913 (Bigelow, 1914a, p. 415). Bailey (1915, pl. 2, fig. 15; pl. 3, fig. 4) figures it from the Bay of Fundy, and Fritz (1921) includes it under the general heading "Thalassiosira" in her lists of diatoms for St. Andrews.

Ditylium

The genus Ditylium is never more than a minor factor in the plankton of the open Gulf of Maine, but it deserves a brief word here because it is an excellent indicator of waters of coastwise origin, being strictly neritic, but at the same time able to survive long sea journeys thanks to its powers of flotation, and so easily recognized that it is not apt to be confused with any other diatom.

The Gulf of Maine records for it are confined to the immediate vicinity of the western and northern coasts, mostly inshore from the 100-meter contour (fig. 127). Ditylium is not known either from Nova Scotian waters on the east or from the offshore banks on the south.

As a rule, the records of Ditylium outside the outer islands have been based on occasional specimens only among more plentiful diatoms of other genera. It was comparatively abundant in Massachusetts Bay on March 4, 1921 (station 10505), and Fritz (1921) found it plentiful at St. Andrews in October, with a scattering in November.

Wherever Ditylium is endemic in European seas it occurs throughout the year, though most commonly during the autumn and winter. McMurrich's and Fritz's (1921) data, combined, show it more seasonal at St. Andrews, occurring only from

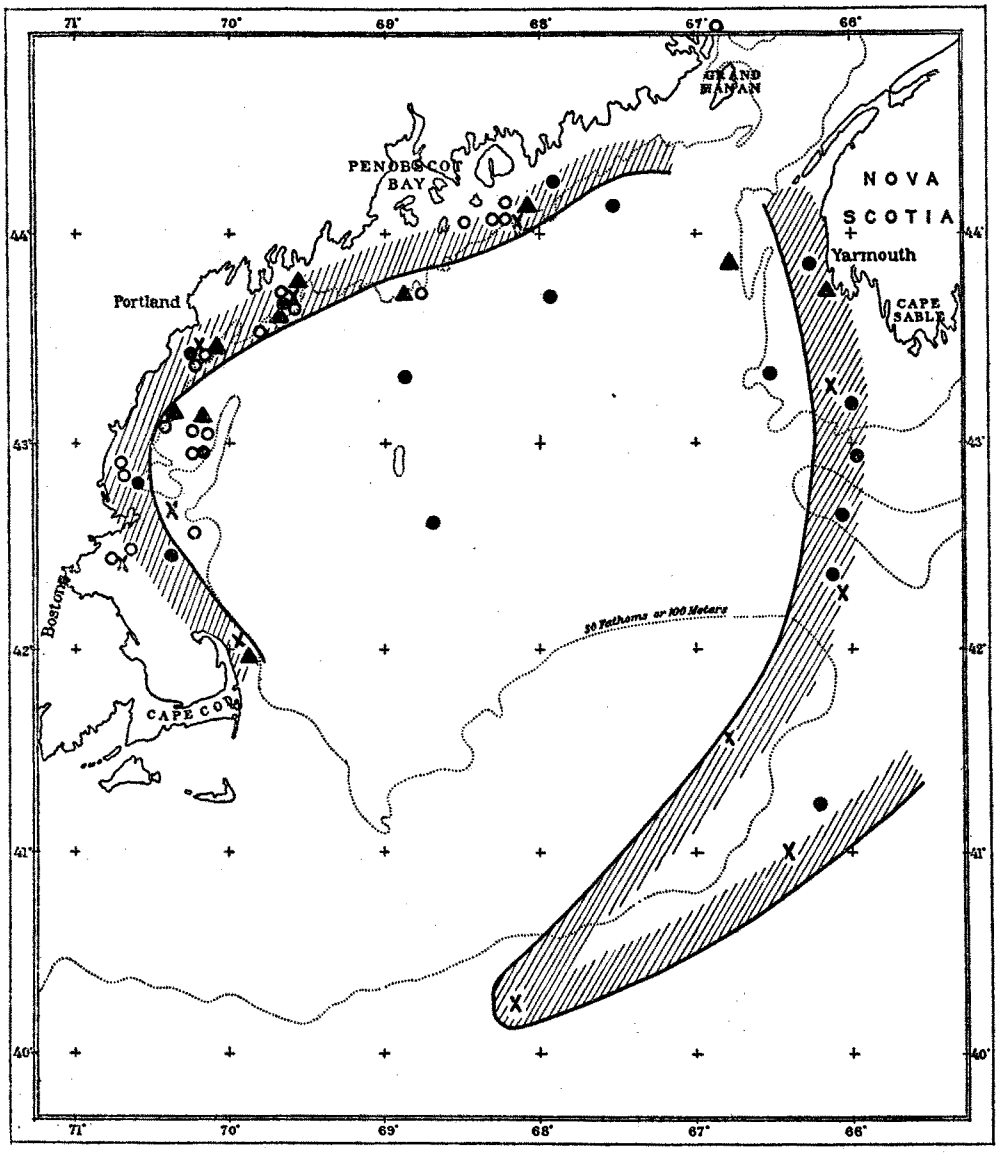

FIG. 127.—Occurrence of the diatoms Ditylium and *Thalassiothrix nitschioides*. ○, locality records for Ditylium; ×, for *Thalassiothrix nitschioides*, February and March, 1920; ●, for *Th. nitschioides*, April, 1920; ▲, for *Th. nitschioides*, other seasons and years. The hatched curve bounds the chief area of occurrence of *Th. nitschioides* in March

mid-August until mid-December, with its maximum in October. In the open gulf it has been recognized most often in December and January, when it occurred at about 50 per cent of the *Halcyon* stations in 1920 and 1921 (stations 10488, 10489,

and 10492 to 10497). We have occasional records of it in March (stations 10505, 10506, 20056, 20058, 20059, and 20061), none at all in April, one in May (station 10277), none for June, July, or August, and one each for September (station 10317) and October (station 10328).

Thus Ditylium is chiefly an autumn and early winter form in the coastal zone of the gulf, spreading offshore during the later winter and early spring. Fish (1925) likewise found it a winter diatom at Woods Hole.

Eucampia

Eucampia zodiacus, like Guinardia, has been strictly confined to Georges Bank in our towings, and to the coastal waters farther west and south, though Fritz (1921) found occasional specimens at St. Andrews in one July tow. It shared with Guinardia in the rich diatom flora that occupied the waters over the western part of the bank on July 9, 1913 (station 10059, fig. 123); was sparsely represented in that same general region in July, 1916 (station 10348), and again on February 22, 1920 (stations 20046 and 20047). The Arctic species, *Eucampia grœnlandica*, has not been identified from the Gulf of Maine, but specimens apparently intermediate between it and *E. zodiacus* (cf. Gran, 1908, p. 99, fig. 126b) occurred in some numbers among the Guianardia–Eucampia community just mentioned (station 10059).

Guinardia

G. flaccida, the unique member of this genus, has only once been detected within the Gulf of Maine (occasional specimens near Cape Ann, October 18, 1915, station 10330), and has not been reported at St. Andrews, but, as I have already noted (p. 391), it swarmed locally on the western part of Georges Bank in July, 1913 (station 10059); again on the northeast edge in the same month in 1914 (station 10224).

Guinardia is a summer, not a spring or autumn, diatom there, for it was only sparsely represented on our line across the western end of the bank on February 22 and 23, 1920 (stations 20044 to 20046), and not at all on the more easterly sections for the two months following, or in the collection which Mr. Douthart gathered on the bank during April, 1913. It is irregular in its occurrence on Georges Bank even in July, for in that month in 1914 it was wanting in the region where it swarmed in 1913, though abundant a few miles farther east at the time. It is a question whether Guinardia appears there in such numbers every summer, for it was not detected at all at our July stations on the western end of the bank in 1916 (stations 10347 and 10348), though the water was then full of other diatoms (*Thalassiothrix longissima* and *Rhizosolenia styliformis*). No towings have been made on the bank during autumn, but Guinardia probably occurs there at that season as well as in summer, the *Grampus* having found it flowering along shore west of Newport, R. I., as late as November in 1916 (stations 10405 and 10406). Fish (1925) found it regularly in winter at Woods Hole and only occasionally in summer.

It is not surprising that Guinardia should be at its maximum on Georges Bank during the July to September quarter, which is its flowering season in north European

waters as a whole (Ostenfeld, 1913), but its rarity or absence in the inner parts of the Gulf of Maine contrasts sharply with its status in European coastal waters, such as the English Channel and the North Sea generally, where it is one of the most dominant of diatoms. This difference in its distribution in the two sides of the North Atlantic can not be explained until its life history is better known for American waters, but it is at least suggestive that Guinardia flowers chiefly at a time of year when the Gulf of Maine offers the least favorable environment for the multiplication of diatoms of any sort.

Lauderia

The brief dominance of *Lauderia glacialis* off the coast of Maine in the very scanty pelagic flora of early March (stations 20056 and 20058) prior to the flowering of Thalassiosira has already been mentioned (p. 421), as has its occurrence near Cape Ann and in Massachusetts Bay at that same season (stations 20060 to 20062). In the western side of the gulf the flowering of Lauderia probably reaches its culmination by the end of March, at the latest, for it was not detected at any of the April stations west of Mount Desert in 1920. It is later in appearing in the eastern side of the gulf, for while none were detected at our several stations off western Nova Scotia on March 23, 1920, it was present there and out to the eastern channel and the southeast face of Georges Bank by April 15 and 16 (stations 20101, 20107, and 20109), accompanying the early flowerings of Chætoceras and Thalassiosira, though nowhere abundant.

Thus Lauderia appears just prior to the rich vernal flowerings of Thalassiosira and Chætoceras, reaches its maximum while these two genera are still in a state of active multiplication, and diminishes or vanishes after the brief period of a few weeks while they are still swarming. We have occasionally found Lauderia among other diatoms in May (station 10285 in 1915), but it is not recorded for later summer or autumn. Neither McMurrich (1917), Bailey (1917), nor Fritz (1921) have detected it at St. Andrews or in the Bay of Fundy. *L. glacialis* (fig. 117; Gran, 1908, p. 23, fig. 23) is the basis of all our records for the genus.

Nitschia

Nitschia seriata, like *Skeletonema costatum* (p. 448), is a summer species in the Gulf of Maine, where it has not been detected during the spring months. Our earliest seasonal record of it is for June 10, when it was represented by occasional examples among the more abundant Chætoceras and other genera off Petit Passage, Nova Scotia, in 1915. Fritz (1921) found it constantly at St. Andrews from July 3 onward throughout the summer; Bailey (1917) records it from the Bay of Fundy in August; and it has appeared with comparative regularity in our July and August tow nettings in those parts of the gulf where diatom plankton persists so late in the season, more especially in the coastal belt between Cape Elizabeth and Nova Scotia. For example, *N. seriata* was present in fair quantity on Jeffreys Bank off Penobscot Bay, as well as close in to the land nearby (stations 10016 to 10021 and 10025),

from July 26 to August 8, 1912; on German Bank, near Mount Desert Island, and off Penobscot Bay from August 12 to 14, 1913 (stations 10095, 10099, and 10101); and again off Penobscot Bay on August 14, 1914 (station 10250). Fritz (1921) found it throughout September and during the first week of October at St. Andrews; Bailey (1917) likewise lists it from the Bay of Fundy for September 18; but occasional specimens in the tow in Massachusetts Bay on October 1, 1915 (station 10322) constitute our only autumnal record for it in other parts of the gulf. *N. seriata* has not been detected in winter either at St. Andrews or in the open gulf, nor in the eastern channel, on Georges Bank, or over the continental slope at any season.

The seasonal fluctuations of *N. seriata* are essentially the same in the Gulf of Maine as in the English Channel, where it attains its maximum abundance in August (Ostenfeld, 1913); but it is described as most plentiful in spring in the northern part of the North Sea and over the northeastern Atlantic generally. Hence, if Ostenfeld's (1913, p. 415) suggestion that this species includes two biologic races—a northern, with maximum in spring, and a more southern, with maximum in August—be well founded, the Gulf of Maine *N. seriata* belongs to the latter. However this may be, *N. seriata* is one of the several diatoms that are summer forms in the gulf but which Fish (1925) found to be characteristic of the winter flora at Woods Hole (p. 423).

This species is of minor importance in the gulf, where it occurs only sparingly even at the time of its greatest abundance, and never, so far as known, in swarms such as have been recorded in European waters. Several other neritic species of the genus have been reported from the estuarine waters at St. Andrews and St. Marys Bay (Fritz, 1921; Bailey and Mackay, 1921), but they are not likely to be found out in the open sea in the gulf except as strays.

Rhizosolenia

The species of this genus that appears most frequently in the towings in the inner parts of the Gulf of Maine is the variety *semispina* of *Rh. hebetata* (Gran 1908, p. 55, fig. 671b), a form which fortunately is very easily recognized. In March *Rh. semispina* is widely distributed in the coastal belt from Cape Cod to Penobscot Bay on the western side of the gulf (stations 20058 to 20061 and 20088 in 1920; 10505 and 10506 in 1921), and in the shoal water along western Nova Scotia out to the Eastern Channel (stations 20072, 20078, 20079, and 20084) in the eastern; likewise over the outer part of the shelf off Shelburne (stations 20075 to 20077). As a rule Rhizosolenia has proved wanting among the sparse Coscinodiscus–Ceratium plankton that occupies all the central and deeper parts of the gulf during that month, but as a notable exception to this rule it dominated the diatom community of the western basin on March 5, 1921 (station 10510). A few *Rh. semispina* were also noted near the northern edge of Georges Bank on March 11, 1920 (station 20064), and over the slope to the southward on February 22 (station 20044). In April of that year *Rhizosolenia semispina* occurred at nearly all the stations in the gulf proper (stations 20089 to 20098, 20100 to 20107, 20109, 20112, and 20114 to 20117), dominating the plankton in the Western Basin on the 18th (station 20115). It was likewise recorded over the continental slope southeast of Georges Bank on the 16th

(station 20109), and in 1913 it was prominent in the rich diatom flora over the northwest part of the banks during the last few days of the month, as noted above (p. 422). In May, 1915, it was not uncommon among the more plentiful Chætoceras and Thalassiosira in the deeps of the gulf (stations 10267 to 10269) and was dominant locally there on the 10th (station 10273) and near the Isles of Shoals on the 14th (station 10278). It was also recorded in Ipswich Bay on the 8th in 1920 (station 20122), but it was not detected at all on the western part of Georges Bank and neighboring basin, in the Massachusetts Bay region, in the coastal belt north and east of Cape Elizabeth, nor off western Nova Scotia during that month, either in 1915 or 1920.

Rh. semispina was not found among the abundant diatom flora of the Mount Desert region in June, 1915 (e. g., station 10285), or in the offshore parts of the gulf during that month, but there was a scattering of it among the Thalassiosira and Chætoceras in Petit Passage on the 10th, and it might fairly be classed as dominant over German Bank on the 19th (station 10290).

Our midsummer records for this species are confined to Georges Bank (where occasional cells were noted in July, 1914, stations 10219 and 10223, but none at all among the *Rh. styliformis*, *Rh. shrubsolei*, and *Thalassiothrix longissima* that swarmed on July 23, 1916); to the Eastern Channel (station 10227), Browns Bank (station 10228), the neighborhood of Lurcher Shoal (station 10245), the northeast corner of the gulf (stations 10247 and 10248), the waters off the coast of Maine east of Cape Elizabeth (station 10258); and to the shelf off Marthas Vineyard, where it swarmed on August 25, 1914 (station 10258; fig. 125). Like diatoms generally, *Rh. semispina* practically vanishes from the central deeps of the gulf during the summer. Nor is there any reason to look for a considerable augmentation in its numbers there during the autumn, for it has appeared only sparingly in our September, October, and November hauls (station 10047, November 20, 1912; stations 10317 and 10336, September 15 and October 26, 1915; and stations 10400 and 10403, November 1 and November 8, 1916). It was widely distributed over the northern half of the gulf (always, however, in very small numbers) in the midwinter of 1920–21, when it occurred at about 50 per cent of the stations (stations 10490, 10491, 10494, 10495, 10496, 10497, 10500, and 10502). Fritz (1921a) records a scattering of "*Rh. hebetata*," which probably were this variety, at St. Andrews in every month except November.

The most notable feature of the occurrence of *Rh. semispina* in the Gulf of Maine, as outlined by our data, is its irregularity; no definite succession of flowerings is demonstrated. On the whole, however, it can be described as at its maximum during the spring and summer (this half of the year includes all the rich flowerings we have encountered), and at its minimum in autumn and winter. At Woods Hole, too, Fish (1925) reports the richest flowerings of this species as occurring in summer. This parallels its seasonal status in northern European seas, where it is most abundant from April until June, flowering earliest in the more southern and latest in more northern waters.[64] But no definite correlation between flowering periods and latitude or temperature is yet apparent for the Gulf of Maine.

[64] Flowers most abundantly in the North Sea in May, but not until August in Greenland waters and in Barents Sea.

Rh. semispina certainly is no more neritic in the Gulf of Maine than it is off north European coasts, where it is commonly regarded as oceanic, and I may hazard the guess that its occasional abundance in waters as shoal as those of German and Georges Banks and off Marthas Vineyard reflects local hydrographic conditions exceptionally favorable for its growth and reproduction, not any dependence on its part on the bottom below or on the neighboring coast line. Nevertheless, the presence of *Rh. semispina* is not a reliable index to offshore water, because it may be able to thrive in coastwise regions "several years after the inflow of oceanic water has taken place," as Ostenfeld (1913, p. 443) has remarked. In short, from the distributional standpoint *Rh. semispina* is intermediate between the typically oceanic *Rh. styliformis* and the strictly neritic *Rh. setigera* (p. 446), these three species bearing the same relationship to one another in the Gulf of Maine as on the other side of the North Atlantic. A fuller knowledge of the degree to which *Rh. semispina* is endemic within the limits of the gulf, or is immigrant thither from elsewhere, is much to be desired.

Only two other species of Rhizosolenia have so far been detected with any regularity in the collections from the open Gulf of Maine—*Rh. styliformis* and *Rh. setigera* (fig. 128). *Rh. styliformis* has been but sparsely represented in the tow nettings north of Georges Bank. In March, 1920, it was not found there at all; in April of that year it was noted (occasional specimens) off Cape Cod (station 20088). at the mouth of Massachusetts Bay (station 20090), and in the Northern Channel (station 20105). We did not detect it at all in the gulf north of the banks in May either in 1915 or in 1920, and only once in June, 1915 (station 10290), and have only one summer record of it in the inner parts of the gulf—viz, off Lurcher Shoal on August 12, 1914 (station 10245). It appeared in small numbers at three out of five stations near Massachusetts Bay from November 1 to 8 in 1916 (station 10400 north of Cape Ann and stations 10401 and 10403 off Massachusetts Bay), likewise off Cape Ann, off Cape Cod, and in the Western Basin on December 29 and 30, 1921 (stations 10489, 10490, and 10491), suggesting a period of augmentation in autumn and early winter either by propagation within the gulf or, as is more likely, by immigration from offshore. Similarly, Fish (1925) found it only in winter at Woods Hole, and very scarce even then. Evidently it is rare in the Bay of Fundy, for while Bailey (1915) notes it for St. Andrews, McMurrich found it on one occasion only, and Fritz (1921) does not list it there at all.

Rh. styliformis is far more important in the plankton over the offshore banks than it is in the inner parts of the gulf, as might be expected from its typically oceanic nature. For example, the *Grampus* found it in abundance on the western part of Georges Bank in July, 1913 (station 10059), and again in July, 1916 (stations 10347 and 10348), and likewise over the northeast part of the bank in that same month in 1914 (station 20223). It also occurred generally from off Nantucket out to the continental slope of Georges Bank in July, 1916 (stations 10349, 10351, and 10354 to 10356). Although we did not detect *Rh. styliformis* anywhere on the bank (or on Browns Bank either, for that matter) in March, April, or May of 1920, it dominated the pelagic flora over the northern part of Georges Bank on the 27th of April in 1913, when "many of the specimens were so large (1.1 millimeters) as to be easily

visible with the naked eye" (Bigelow, 1914a, p. 415). Curiously enough, this species has not been detected in our tows over the offshore slope of the bank in summer, though represented there in March, 1920 (station 20069).

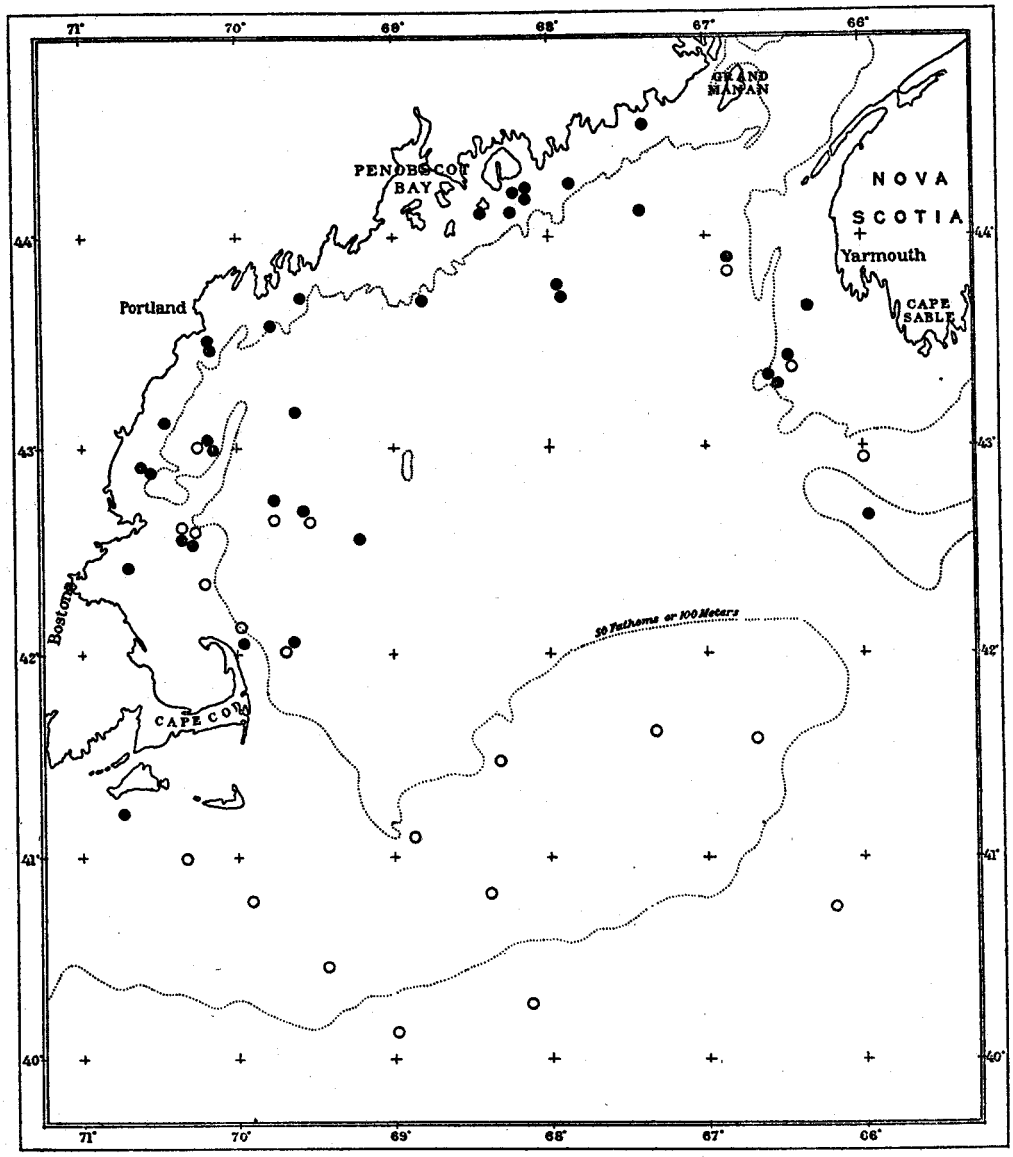

FIG. 128.—Locality records for *Rhizosolenia setigera* (●) and *Rh. styliformis* (○)

The comparative scarcity of *Rh. styliformis* in the inner parts of the Gulf of Maine, contrasted with its abundance over large areas of the open north Atlantic in summer (Cleve, 1897; Ostenfeld, 1913), suggests that the optimum salinity for

it is high (over 35 per mille, as Ostenfeld suggests) and that water less saline, say, than 33 per mille operates as an actual bar to its dispersal and propagation. Otherwise it would be hard to explain its failure more completely to colonize the Gulf of Maine, which is fully as accessible to it, both by temperature, by the influx of offshore water, and by its geographic location, as the northern part of the North Sea is, where *Rh. styliformis* occurs in abundance throughout the half year from May to November.

Inasmuch as *Rh. styliformis* occurs chiefly as an immigrant in the Gulf of Maine, where its presence is indicative of ocean water, it is one of the diatoms for which a sharp lookout should be kept, a lookout facilitated by its large size and precise structural characters.

Rhizosolenia setigera is the antithesis of *Rh. styliformis* in its relation to the coast line, for it is neritic instead of oceanic and produces resting spores, corresponding to which difference it occurs more regularly in the Gulf of Maine. Its period of greatest abundance falls in spring. Its richest flowerings roughly correspond with those of the abundant Thalassiosira–Chætoceras flora in their geographic locations, having been limited in 1920 to the Cape Ann–Cape Elizabeth belt (stations 20058, 20059, and 20061) and to one locality off Yarmouth (station 20083) in March, spreading to Massachusetts Bay on the one side of the gulf (stations 20089, 20116, and 20117) and to the banks off Nova Scotia, to Browns Bank, and to the northeast corner of the gulf on the other (stations 20098 and 20099) by the last week of April. McMurrich (1917), too, found this species attaining its maximum abundance in the St. Andrews region in April, though Fritz (1921) does not list it at all from that locality. At Woods Hole, however, Fish (1925) found rich flowerings in late summer as well as during the winter and early in spring.

Rh. setigera either diminishes in numbers in the open gulf during May and June or has been overlooked there among the more numerous diatoms of other genera, for we have only one definite record of it for each of these months (station 10277 on May 13, 1915, and station 10299 on June 26, 1915). But it occurs occasionally throughout the summer and at least until early October in coastal areas wherever diatoms persist so late in the season in any quantity; off Penobscot Bay and in the Mount Desert region, for example; near Machias, Me.; and on German Bank (stations 10029 and 10030 in 1912; 10248 and 10250 in 1914; and 10301, 10305, 10317, and 10318 in 1915). In the Bay of Fundy this species apparently passes through a period of abundance in September and October (Bailey, 1917), an interesting phenomenon paralleling its occurrence on the other side of the Atlantic, where it has two maxima—one in spring and the other in autumn (Ostenfeld, 1913). We have found nothing to suggest this in other parts of the Gulf of Maine, however, or in Massachusetts Bay.

Rh. setigera was recognized at only two stations during the December to January cruise of 1920–1921 (stations 10490 and 10502), and not at all in Massachusetts Bay during the winter of 1912–13. *Rh. setigera* has not been found on Georges Bank, on Browns Bank, in the Eastern Channel, or over the continental slope to the south. The chart (fig. 128) illustrates the sharp contrast between the distribution of the neritic species, *Rh. setigera*, and that of its oceanic relative, *Rh. styliformis*.

Rhizosolenia shrubsolei was sparsely represented off Cape Cod and near Mount Desert Island early in October, 1915 (stations 10323 and 10328), and on the northeast and southeast parts of Georges Bank in July, 1914 (stations 10220 and 10224); it swarmed on the western end of the bank on July 23, 1916 (station 10348), and likewise in Nantucket Sound on October 25, 1915 (station 10335). Fritz (1921) lists it regularly from St. Andrews through October and November, occasionally in December, and not at all during the other months of the year, but Fish (1925) found it flowering in midsummer at Woods Hole, as well as in winter. *Rh. imbricata*, if it be actually separable from *shrubsolei*, which Gran (1908) doubts, was detected by Doctor Mann at one station on the western part of Georges Bank on February 22, 1920 (station 20046).

We have found Rhizosolenias of the *alata–obtusa* group (critical examination of them is needed before they can be referred definitely to one or the other species or variety) in small numbers on and south of Georges Bank in July (stations 10215 and 10220 in 1914, and 10348 in 1916), and once in abundance in the deep water a few miles to the north of the bank during that month (station 10058, July 8, 1913). There are no other summer records for them in the basin of the gulf, but they dominated the moderately abundant diatom plankton at most of the stations occupied by the *Halcyon* in the outer part of Massachusetts Bay from August 22 to 24 in 1922 (stations 10631 to 10642), though not in Cape Cod Bay (stations 10643 and 10645); likewise off Mount Desert Island on July 19, 1915 (station 10302). Fritz (1921) noted them (occasional cells) at St. Andrews on August 28, regularly during the last half of September, October, and November, but not in any other month. We have no autumnal record for the *alata–obtusa* group in the open gulf but they were detected at three stations (10493, 10496, and 10497) along the coast between Cape Ann and Mount Desert from December 30, 1920, to January 1, 1921. In 1925 they were flowering in great abundance in the eastern side of Cape Cod Bay and in the channel between Cape Cod and Stellwagen Bank from December 16 to February 6 to 7 (*Fish Hawk* stations 2, 4, 6, and 7, trips 3, 5, 6, and 7, p. 396), after which date they were only occasional, being succeeded by Thalassiosira (p. 396). We also have record of them in the North Channel (station 20105), in the Eastern Channel (station 20107), and in the center of the gulf (station 20113) in April, 1920.

This completes the list of Rhizosolenias so far recognized in the towings from the outer waters of the Gulf of Maine. Fritz (1921), however, also lists *Rh. faroensis* occasionally in August and October at St. Andrews. In general, the genus Rhizosolenia is far less important a factor in the phytoplankton of the offshore waters of the Gulf of Maine than in the open North Atlantic, where, as Cleve (1900) long ago pointed out and as Ostenfeld (1913, p. 444) has recently remarked afresh, this genus may be its most abundant member, a difference to be expected because most of the species of Rhizosolenia, and especially *Rh. styliformis* (p. 444), are oceanic in nature. As noted above (p. 396), however, rich flowerings of the genus (*Rh. alata*) in the inner parts of Massachusetts Bay during the winter of 1924–25 suggest greater importance for its neritic members close to the coast.

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Skeletonema

Skelteonema costatum is an interesting species because it reaches its maximum abundance in the Gulf of Maine during the summer and early autumn, not in spring, as most other diatoms do, whereas Fish (1925) found it a winter form at Woods Hole and occurring only occasionally during the warm months. Skeletonema is typically neritic and has been found flowering actively in Massachusetts Bay, the Bay of Fundy, and on Georges Bank, but not in the deeper parts of the Gulf of Maine. Bailey (1917) found it occasionally in estuarine situations on the north shore of the Bay of Fundy in January and February and again in July and August, but not at all during March, April, May, June, or October. In the open bay near Grand Manan he describes it as abundant on September 18. Fritz's (1921) more extensive lists note Skeletonema as occurring irregularly (always in small numbers) at St. Andrews during the winter and early spring of 1917, multiplying in April, and reaching its maximum in July and early August. In Massachusetts Bay we have not detected it at all at any October, November, winter, spring, or early summer station, nor in any of the hauls made in this region in 1916—July, August, October, or November. In 1915 it appeared at the mouth of the bay, near Provincetown, and off Cape Cod from September 29 to October 1 (stations 10320 to 10323) in sufficient abundance to give a characteristic aspect to the phytoplankton (p. 394), though the period of reproduction must have been brief, for no Skeletonema were found at three stations across the mouth of the bay on October 26 and 27 (stations 10337 to 10339).

It would be interesting to know how far offshore this autumnal flowering extended, but unfortunately we have no data bearing on this. In 1922, however, when it again dominated the phytoplankton at six stations around the shore of Massachusetts Bay from Gloucester to the neighborhood of the Cape Cod Canal on August 24 (stations 10634, 10635 to 10637, 10639, 10642, and 10643), the belt that it occupied extended only 4 to 5 miles out from land, none having been detected at the eight other stations in the outer parts of the bay which the *Halcyon* occupied on that day and two days previous. Unfortunately no plankton hauls were made later in the season during that year.

Skeletonema was also abundant on the western part of Georges Bank on July 9, 1913 (station 10059)—our only record of it on the offshore banks—among the Guinardia and Eucampia, which at the time dominated the local phytoplankton. The only other records for it in the open gulf, outside the outer headlands, are for occasional chains off Cape Sable, off Cape Cod, near Cape Ann, off Mount Desert Rock, and in the northeastern corner of the basin in March and April, 1920 (stations 20084, 20088, 20091, 20098, and 20100).

Evidently the flowerings of this genus are closely confined to the immediate vicinity of the land in the Gulf of Maine and to the shallow water of the banks, where it flowers irregularly during summer and early autumn; and probably it will be found to occur as abundantly along the coasts of Maine and Nova Scotia as it does in Massachusetts Bay and at St. Andrews, when the diatoms of the other harbors and bays are studied.

Skeletonema costatum, a form of wide distribution, mainly northern, but, as Ostenfeld (1913) remarks, including the coasts of almost all countries, is similarly

neritic in other seas and usually confined to the neighborhood of the coast. In north European waters it has its maximum in spring but has been found flowering in autumn as well at many localities.

Thalassiosira [65]

The spring flowerings of Thalassiosira (fig. 129) are perhaps the most notable event in the phytoplanktonic cycle of the coastal belt of the Gulf of Maine. In 1920 these commenced first in the coastal belt between Cape Elizabeth and Cape Ann, probably during the last week of February, and they progressed so rapidly that by March 5 (stations 20059 and 20060) a tow of a few minutes clogged the nets with brownish masses of *Thalassiosira nordenskioldi* (*Th. gravida* only occasionally appears in these catches, and *Th. decipiens* still more rarely), with smaller amounts of *Chætoceras criophilum, Ch. decipiens, Ch. didymum, Ch. diadema, Ch. atlanticum, Ch. laciniosum, Ch. debile, Rhizosolenia semispina, Rh. setigera, Thalassiothrix nitschioides, Coscinodiscus,* and *Lauderia glacialis.* Thalassiosira also commenced to flower at about this same date in the Massachusetts Bay region in 1925, when it was not detected in Cape Cod Bay in December or January, but was extremely abundant near Stellwagen Bank on February 24, in Cape Cod Bay and near the tip of Cape Cod during the first week of April, and still plentiful in the northern side of Massachusetts Bay during the last week of the month.

Thalassiosira is a characteristically neritic genus, and at first its flowerings are closely confined to the immediate vicinity of the land. Thus it was overshadowed by Chætoceras 22 miles out at sea on March 5, 1920 (station 20061), though diatoms were in as great volume there as close inshore, with practically the same list of species plus the more oceanic *Chætoceras atlanticum* but lacking the neritic *Thalassiothrix nitschioides.*[66] During the first week of March in 1920, Jeffreys Ledge marked roughly the offshore boundary for the flowerings of Thalassiosira in the western side of the gulf; in fact, it did not spread out over the western basin until some time between March 24 and April 18 in that spring.

Thalassiosira may be expected to commence multiplying one or two weeks later in the season in Massachusetts Bay than it does just north of Cape Ann, for only occasional specimens were noted off Gloucester on March 1 and at the head of Massachusetts Bay on the 5th in 1920;[67] but it was extremely abundant at both these localities from April 6 to 9 (stations 20089 and 20090).

In the northern side of the gulf the first flowerings of Thalassiosira hardly spread beyond Cape Elizabeth, it being only sparsely represented near Seguin Island on March 4, 1920 (station 20057), though other diatoms were moderately abundant there (p. 425), and it was not found at all off Mount Desert Island the day before (station 20056). On April 10 (station 20096), however, it dominated a moderately abundant assemblage of diatoms at the first of these localities, evidence

[65] For records of Thalassiosira during the spring of 1913 see Bigelow, 1914a. It has since been recognized at station 10250 in August, 1914; stations 10275 to 10278, 10280, 10281, 10285, 10287, 10290, 10301, 10302, 10322, 10328, 10329 and off Schoodic Head on June 3 and Petit Passage on June 10, 1915; stations 20050, 20058 to 20061, 20072, 20088 to 20107, 20109, 20114 to 20117, and 20122 in 1920; and stations 10505 to 10507 in 1921.

[66] Halosphæra was likewise detected at this station (p. 459).

[67] At this station (20062) no peridinians were detected and but few diatoms, chiefly *Th. nordenskioldi* with occasional cells of *Chætoceras decipiens, Ch. atlanticum, Ch. criophilum,* and *Lauderia glacialis.*

of an eastward expansion of its flowering area; and although the waters farther east along the coast supported only a scattering of Thalassiosira on the 12th (station 20099, April 12), it is probable that this genus is flowering actively all along the northern

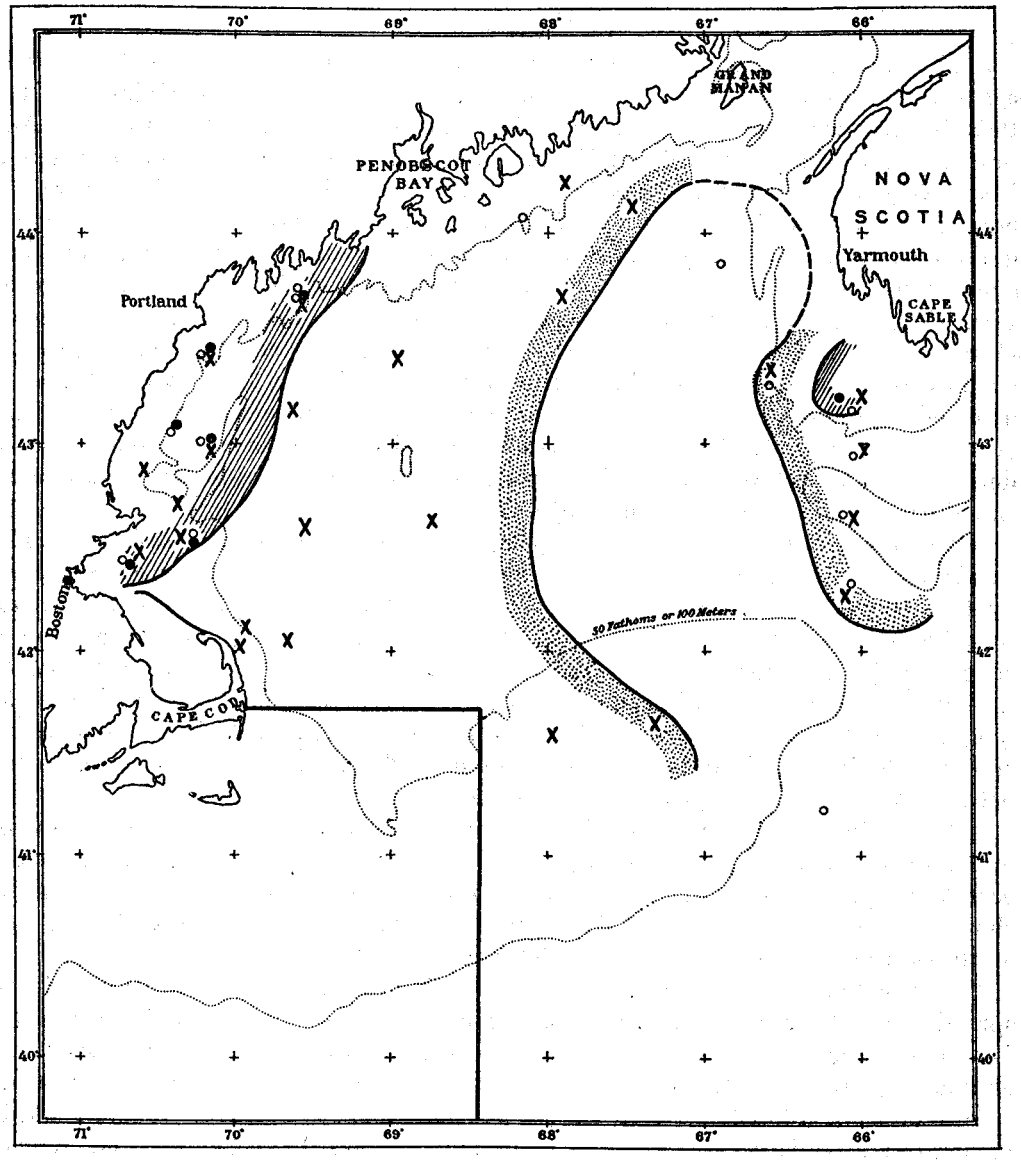

FIG. 129.—Distribution of the diatom genera Thalassiosira and *Lauderia glacialis*. ●, locality records for Thalassiosira for March; ✕, for April; ○, for *Lauderia glacialis*. The hatched curve marks the offshore boundary to the abundant flowerings of Thalassiosira up to mid-March; the stippled curve incloses its flowerings up to the last week of April for the years 1913 and 1920

shores of the gulf by the middle of the month in most years. It is also likely that the harbors and bays along this part of the coast see a great production of Thalassiosira commencing a week or two earlier, judging from conditions at St. Andrews.

Thus Fritz (1921) found no Thalassiosira during November, December, or January, but a scattering appeared in her tows in February and early March; it was flowering actively by the end of that month, reaching its plurimum during the last half of April and first half of May. Similarly, McMurrich (1917) did not detect it at St. Andrews until March nor regularly until April in 1916.

Thalassiosira likewise spreads seaward over the whole western half of the gulf from mid March to mid April (fig. 129). And while we found no Thalassiosira on Georges Bank in February, March, or April of 1920, except for occasional examples at one station on the southeastern slope (station 20109) on the 16th of the latter month (flotsam, perhaps, from the Thalassiosira flowerings then under way from Cape Sable out to the Eastern Channel), this genus is to be expected to appear over the western half of the bank during the last half of April, Douthart having collected masses of it over the north central part on the 14th of the month in 1913 and in less abundance at various locations in that same general region on the 27th (Bigelow, 1914a, p. 415).

It is not clear whether this Georges Bank flora is primarily driftage from the inner parts of the gulf which multiplies actively in the shoal waters over the bank, or whether it represents the local flowerings of Thalassiosira that have survived there since the last preceding period of multiplication as resting spores on the bottom. In any case the result is that the range of Thalassiosira extends from the north shore of the gulf right out across the western side of the basin to Georges Bank by the last week in April, and Douthart's rich gatherings point to the northwestern part of the latter as the site of very productive flowerings.

The flowerings of Thalassiosira that take place in the shoal waters off Cape Sable and out to Browns Bank arise entirely independent of those in the western side of the gulf. They do not commence until later in the season, for only an occasional specimen was found off the Cape on March 23 in 1920 (station 20084), and none on Browns Bank or in the northern channel a few days earlier (stations 20072 and 20078). However, production must have been under full headway there soon after that, because the genus occurred in abundance at all the stations off Cape Sable, on German Bank, and right out to the Eastern Channel by April 15 and 16 (stations 20103 to 20107).

At this time the Eastern Channel marked the extreme limit of the shoals of Thalassiosira in this direction, there being none in our towings on the neighboring parts of Georges Bank on April 16 and 17 (stations 20108 to 20111), although there was a very abundant community of Chætoceras over the seaward slope (station 20109). But what is known of the expansion of the Nova Scotian current during the later spring makes it probable that Thalassiosira would have been found generally dispersed over the eastern half of Georges Bank a week or two later, thus making its range continuous over the whole of the latter at some time late in April.

It is at about this date that Thalassiosira attains its widest distribution as an important factor in the plankton of the gulf, as outlined on the chart (fig. 129). It is doubtful whether it ever spreads in any abundance over the western side of the basin, for we found a belt of considerable breadth entirely free from it there

from April 12 to 17 in 1920; nor did we find it at all in the eastern side of the gulf in the first half of May in 1915.

Considering the gulf as a whole, Thalassiosira attains its plurimum abundance as well as its widest range during the last half of April, but it remains so typically neritic throughout its vernal flowering period that it is always most plentiful close in to the land, where it may monopolize the surface waters locally. Such, for example, was the case off Gloucester on April 3, 1913 (station 10055), when the mass of diatoms taken in a short tow was almost exclusively composed of two species of Thalassiosira—*T. gravida* and *T. nordenskioldi*—with only occasional examples of *Chætoceras densum, Ch. atlanticum, Ch. contortum, Biddulphia aurita, Coscinosira polychorda, Thalassiothrix nitschioides*, and *Rhizosolenia semispina*. Even more monotonous and equally abundant catches of Thalassiosira were made by Welsh between Cape Ann and Cape Elizabeth early in May, 1913. On the 2d he wrote:[68] "The water yesterday and to-day full of green slime," and on the 3d, "the water is full of greenish-brown algæ," which on examination proved to consist almost altogether of Thalassiosira (in Bigelow 1914a, p. 406). This genus was equally predominant, and in great abundance, off Penobscot Bay on May 12, 1915 (station 10276), and at St. Andrews Fritz found it far outnumbering all other diatoms combined on April 20 and May 1, 1917, the dates of its maximum abundance.

Even in the centers of greatest abundance for Thalassiosira along the western and northern shores of the gulf we have usually found a considerable mixture of the several species of Chætoceras in the catches of the tow nets, especially of *Ch. debile, Ch. decipiens, Ch. diadema*, and of various other diatoms as well. Farther out at sea, in the basin of the gulf, Thalassiosira has never been notably abundant and has been both outnumbered and outbulked by Chætoceras at most of the stations. This was the case on Platts Bank (station 20094) on April 10 and in the western side of the basin (station 20115) on the 18th in 1920. Near Cashes Bank, however, Thalassiosira was a large element in the plankton—though hardly to be described as dominant—the day previous (station 20114). Possibly this shoal ground is a local flowering center.

These observations suggest that Thalassiosira first spreads to the basin of the gulf as flotsam from the coastal zone and to some extent from Georges Bank, but that it continues to multiply as long as the physical state of the water with which it drifts continues favorable for its existence and reproduction.

Thalassiosira did not dominate the diatom community at any of our stations off western and southern Nova Scotia during the spring of 1920, though it was both plentiful and widespread there in April, as I have just remarked.

It is probable that the geographic range of Thalassiosira in the Gulf of Maine begins to contract, from the sea shoreward and from south to north along the western shore, about the 20th to the 25th of April in most years. Our stations for 1915 and 1920 combined show that it entirely vanished from the Cape Cod–Massachusetts Bay region by the first week of May. It was confined to the northern coastal zone, from Cape Ann to the Bay of Fundy, by the second week of the month in 1915. In the zone between Cape Ann and Cape Elizabeth, where it was so

[68] In his field notes.

abundant during the first days of May, 1913, that the streaks in which it occurred were dense enough to discolor the water, the proportion of living cells and chains rapidly diminished and dead débris increased after the 1st of May.

In 1915 Thalassiosira, like most other diatoms, had likewise entirely disappeared from the banks off western Nova Scotia by May 7 to 10 (stations 10271 and 10272), where our tows for the spring of 1920 proved it plentiful in April, though it may persist until later close in to the coasts. It is also probable that it vanished by May from the parts of Georges Bank where it flowers in April, none having been found on the western end on May 16 and 17 in 1920 (stations 20127 to 20129), nor in any of our summer tows on the bank.

As the spring draws to a close the range of Thalassiosira continues to contract, until by the middle of June it is confined to the immediate vicinity of the land from Cape Elizabeth on the west to the northern shores of Nova Scotia on the east[69]; but notwithstanding this shrinkage in the area occupied by it, it continues flowering actively along the northern shore of the gulf. Thus we made almost pure catches of *Thalassiosira nordenskioldi* and *Th. gravida* and in great abundance near Mount Desert Island, off Penobscot Bay, and off Casco Bay on May 10 to 13 in 1915 (stations 10275 to 10277), and again off Schoodic Head, a few miles east of Mount Desert Island, on June 3. It was also fairly plentiful off the mouth of Penobscot Bay on June 14 (station 10287), and in 1912 *Th. gravida* was a considerable element in the plankton at two stations between Casco Bay and Penobscot Bay as late in the season as July 26 to August 2 (stations 10016 and 10022).

In 1915 it was not uncommon near Mount Desert Island and off Machias, Me., as late as July 15 and 19 (stations 10301 and 10302), while Bailey (1917, p. 98) records it from Eastport on July 29 and locally along the shores of the Bay of Fundy during the first half of August.

Thalassiosira was not detected at any station outside the 100-meter contour in the northern and eastern deeps of the gulf in August, 1913, 1914, or 1915, but in 1912 we found it at two stations and in some numbers in the Eastern Basin as late as the 14th of that month (stations 10027 and 10028). Evidently its summer status varies from year to year in this part of the gulf. This is also the case at St. Andrews and probably in all estuarine situations generally along the coast line east of Mount Desert Island. Thus Doctor McMurrich's notes give it as dominant only until about June 8 at St. Andrews in 1916 and scattering until July 6, but in 1917, when Fritz (1921, p. 53) found its flowering culminating early in May, with "the enormous total of 8,750,000 frustules" in her tow on the 1st, it persisted in moderate numbers throughout June. She noted a second maximum (1,760,000 in the tow) on July 3, and while only small numbers of Thalassiosira were taken after that date, the genus persisted, among more numerous diatoms of other genera, right through the late summer and early autumn until October 24, which was her latest date for it. Thus there is a marked contrast between the seasonal periodicity of Thalassiosira at St. Andrews on the one side of the gulf and in Massachusetts Bay in the other, where,

[69] During June, 1915, Thalassiosira was detected at stations 10281, 10284, 10285, 10287, 10290; also half a mile off Schoodic Head on the 3d, where it was extremely abundant, and off the entrance of Petit Passage, Nova Scotia, on the 10th.

though dominant and extremely plentiful in April, it practically vanishes by the first week of May.

Neither of the two most abundant species of Thalassiosira (*Th. nordenskioldi* or *Th. gravida*) exists planktonic in the surface waters of the open gulf in any numbers after August, nor are they recorded for the outer parts of the Bay of Fundy after August 10 by Bailey (1917). The fact that we found a scattering of *Th. nordenskioldi* close to Swan's Island off the mouth of Penobscot Bay on September 15 (station 10317), and again in Massachusetts Bay on October 1 (station 10322), during the autumn of 1915, shows that they may persist in small numbers here and there along the coast until well into the autumn; but the genus has not been detected in any haul in any part of the open gulf between the last week of October and the first week of February.[70]

The seasonal lists of Thalassiosira in northern seas generally (especially the well-marked periodicity in its appearances and disappearances), and the certainty that its abundance in the Gulf of Maine results from local flowering and not from immigration, makes it probable that is passes the balance of the year, from the close of the summer flowerings until its reappearance in the plankton in early spring, on the bottom as resting spores. But so far as I am aware these have not actually been seen in this genus.

The relative numerical proportions in which the two commoner species of Thalassiosira—*Th. nordenskioldi* and *Th. gravida*—occur in our spring and summer samples have not been worked out fully, but the preliminary examination suggests that on the whole *Th. nordenskioldi* is the more important in March, April, and May (as might be expected from the experience of European students), and that *Th. gravida* increases in relative abundance as the season advances. A third species of Thalassiosira, *Th. decipiens*, which has been rare in the spring tow nettings (stations 20059, 20101, and 20104 to 20106), appeared in numbers near Mount Desert Island (station 10328) and off Penobscot Bay (station 10329) on October 9, 1915. *Th. hyalina* has been detected at several widely separated localities during the spring of 1920 (occasional specimens only)—viz., off Cape Cod on March 24 (station 20088), in the Northern Channel (station 20105), over Browns Bank on April 16 (station 20106), off the southeast face of Georges Bank on April 16 (station 20109), and in the Eastern Channel (station 20107). *Thalassiosira baltica* is recorded from one station (20061) and may well have been overlooked elsewhere among the swarms of *Th. nordenskioldi*. There is also one locality record each for *Th. clevei* (station 10328), *Th. subtiles* (station 20089), and *Th. bioculata* [71] (station 20107).

Thalassiothrix

This genus is represented in the Gulf of Maine hauls by two species—*longissima* and *nitschioides*. The records for *Th. longissima* are too scattered to outline its seasonal fluctuations in our waters in a satisfactory way. It appeared only twice in the catches for March, 1920—that is, in the southeast corner of the basin (station 20064) and on Georges Bank (station 20066). McMurrich (1917), too, found it only once at St. Andrews during that month (March 4); then, however, in abundance. It was not detected among the Thalassiosira–Chætoceras flowerings in the north-

[70] Fritz (1921) records it on Feb. 9.

[71] Identified by Dr. Albert Mann.

western side of the gulf during April, 1920, nor did Fritz find it at St. Andrews at any time during the spring or until the end of August. But it occurred sparingly at two of our April stations in the northeast corner of the gulf and off the Nova Scotian coast (stations 20101 and 20103), likewise locally off Georges Bank (station 20109), in the basin (stations 20114 and 20115), and off Cape Cod (station 20116) during that month in 1920. We have twice made rich catches of Thalassiothrix between Cape Elizabeth and Penobscot Bay in May (station 10277, May 13, and station 10280, May 31, 1915). It likewise dominated the diatom plankton on the western end of Georges Bank and southeast of Nantucket Shoals on July 23, 1916 (stations 10347, 10348, and 10354), but we have not found it elsewhere in the open gulf during June, July, or the first half of August, though Fritz (1921) records it at St. Andrews on August 28.

Th. longissima was present in small numbers off Penobscot Bay on September 15, 1915 (station 10317), and irregularly at St. Andrews during that month in 1917, according to Fritz. It flowers abundantly in the Bay of Fundy and along the coast of Maine in October, for Fritz counted over half a million in her standard haul at St. Andrews on October 6, 1917. It was abundant near Mount Desert Island on October 9, 1915 (station 10328), and a corresponding augmentation of this species extended southward at least as far as Cape Ann during the last 10 days of that month (stations 10329 and 10330).

Fritz found few *Th. longissima* at St. Andrews after the middle of October and none in January or February. Neither have we found it anywhere in the open gulf during the winter. McMurrich (1917) describes it as present in great numbers at St. Andrews on February 26, 1915.

On the whole these data suggest two maxima for *Th. longissima*—one late in the spring and the other in October,[72] paralleling its seasonal history in the North Sea region, where its chief flowering time is May, though it may also occur in great quantities around Scotland in August and November (Ostenfeld, 1913, p. 408). At Woods Hole Fish (1925) found it regularly in late winter and spring but only occasionally at other seasons. The flowerings of Thalassiothrix observed by McMurrich in February and March show that its seasonal cycle is less regular than that of Thalassiosira, Biddulphia, etc.

Th. longissima is usually a minor element in the phytoplankton of the inner parts of the gulf, where its flowerings are not only local but brief in duration. But it was extremely plentiful on the western end of Georges Bank on July 23, 1916, at the stations just mentioned, where with fewer *Rhizosolenia styliformis* it formed a very rich and monotonous diatom community (fig. 124), and when its center of abundance extended over a considerable area, out to the continental slope on the south and to Nantucket Shoals on the west.

We have never seen this flowering of Thalassiothrix rivaled within the gulf, and a single occurrence of this sort does not necessarily establish Georges Bank as a major center of production for it. This species is so large and so easily recognized that it may finally prove of great value for the study of ocean currents, as Ostenfeld

[72] Probably the "Thalassema" mentioned by Bailey (1917, p. 107) as dominating some of the October gatherings in Passamaquoddy Bay were actually *Thalassiothrix longissima*.

(1913) points out, but before it can be used in this way for American waters a far clearer insight must be gained into its hydrographic and geographic relationships. In fact, it is still an open question whether *Th. longissima* is oceanic or neritic in the western Atlantic, or as indifferent to the proximity of coasts or shallows as it is on the European side.

Thalassiothrix nitschioides, although one of the most characteristically neritic of all pelagic diatoms, has occurred far more often in our tow nettings than has its relative, *Th. longissima*. Fritz (1921) found *Th. nitschioides* at St. Andrews throughout the year except between October 15 and December 13, and the numbers counted were usually so small that its absence from the hauls made during that period is perhaps not significant. Probably it occurs irregularly the year round in similar situations all along the coast line of the gulf, and its presence or absence and its relative abundance out at sea may depend more on the currents sweeping it out from these sources of supply around the coast line than on local flowerings.

It seems that few drift out to sea during the winter, for it was detected at only one station—off the mouth of the Merrimac River (station 10492)—during the midwinter cruise of the *Halcyon* in 1920 and 1921, and not at all in our tows off Gloucester from November, 1912, to February, 1913. But we had it off the western part of Georges Bank on February 22, 1920 (station 20045), and during that March it was found at four stations in the coastal belt between Cape Cod and the Bay of Fundy; also in the Eastern Channel, on the southeastern slope of Georges Bank, and at two stations off Shelburne, Nova Scotia (stations 20056, 20058, 20059, 20064, 20066, 20068, 20071, 20075, 20076, 20084, and 20088; fig. 127). *Th. nitschioides* attains its widest distribution in the gulf in April, during which month in 1920 it not only occurred more regularly in the coastal belt than in March (in fact, at almost every inshore station where diatoms of any sort were plentiful), and off Nova Scotia out to the southeastern slope of Georges Bank, but likewise at four localities in the central basin of the gulf (stations 20089 to 20093; 20095 to 20098; 20100, 20102 to 20107, 20109, 20114, and 20117).

Our records suggest that *Th. nitschioides* practically disappears again from the offshore parts of the gulf after the end of April, for it was detected at only one station off Cape Elizabeth (10277) during the May cruise of the *Grampus* in 1915, not at all at the 10 stations occupied by the *Albatross* on the western side of the gulf and on Georges Bank from May 4 to 17, 1920 (stations 20120 to 20129). We have not found it at sea in the gulf during the summer and only once during the autumn, viz, off Penobscot Bay on October 9, 1915 (station 10329).

Th. nitschioides follows much the same seasonal cycle in north European waters, where it flowers most abundantly from February until April, according to locality, diminishing in abundance during May, and with its annual minimum in August. It is far less important as a member of the plankton in the Gulf of Maine, where we have never found it abundant, than it is in the North Sea region, where it occurs at all times of the year (Ostenfeld, 1913, p. 409), very generally over the entire area, and at times in great numbers.

The occurrence of *Th. nitschioides* so far offshore off Nova Scotia and over the southeastern slope of Georges Bank, contrasted with our failure to find it in any of

our other towings on the bank irrespective of season, is best explained as due to a drift of the Nova Scotian current moving southwestward in spring from the Scotian banks across Browns Bank and the eastern channel and along the outer part of Georges Bank. This is corroborated by sundry other lines of evidence, planktonic as well as hydrographic.

As there is some confusion between this species and the closely related *Th. frauenfeldi* in the European lists published by the International Committee for the Exploration of the Sea (Ostenfeld, 1913), I may note that only such cells as were attached to one another in their characteristic zigzag chains are recorded here as *nitschioides*, these being quite different in appearance from the chains of *frauenfeldi*. The latter species has not been identified in any of the Gulf of Maine tow nettings.

Other diatoms

The genera so far discussed include all that we have found important in the plankton of the outer waters of the Gulf of Maine, and while the station lists (p. 423) include various others, none of them occur regularly or abundantly enough to color the plankton. I may emphasize especially the universal rarity of brackish-water, littoral, and bottom-dwelling diatoms out at sea. Pleurosigma, for example, is never represented by more than occasional examples, though detected at many localities far and wide. Under estuarine conditions, however, as in the tributaries of the Bay of Fundy, littoral diatoms of many genera are much more abundant (Bailey, 1917; Fritz, 1921; Bailey and Mackay, 1921).

Finally, I may emphasize our failure to find any diatoms in the gulf to which it is safe to ascribe either a Tropic or an Arctic origin, except, perhaps, for *Fragilaria oceanica*, occasional examples of which were detected in the tows in the Eastern Channel and over the southeast slope of Georges Bank on April 16, 1920 (stations 20107 and 20109). The absence of other arctic diatoms in the Gulf of Maine is the more striking if contrasted with their abundance and frequent dominance in the Gulf of St. Lawrence in spring, as is illustrated by the following table based on Gran's (1919) list for May 11, 1915. This Arctic community proved so shortlived there, however, that it had entirely disappeared in June, to be replaced by a typically boreal assemblage, most of whose members—*Rhizosolenia setigera*, *Nitschia seriata*, Coscinodiscus, and *Chætoceras laciniosum*—are equally characteristic of the spring plankton of the Gulf of Maine.

St. Lawrence diatoms, May 11, 1915	Arctic[1]	Gulf of Maine	St. Lawrence diatoms, May 11, 1915	Arctic[1]	Gulf of Maine
Acnanthes tæniata	×		Fragilaria cyclindrus	×	
Amphiprora hyperborea	×		Fragilaria oceanica	×	×
Bacteriosira fragilis	×		Navicula pelagica	×	
Biddulphia aurita		×	Navicula septentrionalis	×	
Chætoceras atlanticum		×	Navicula vanhöffeni	×	
Chætoceras compressum		×	Nitschia closterium		×
Chætoceras criophilum		×	Nitschia frigida	×	
Chætoceras debile		×	Pleurosigma stuxbergi		×
Chætoceras decipiens		×	Rhizosolenia hebetata		×
Chætoceras diadema		×	Thalassiosira bioculata		
Chætoceras scolopendra		×	Thalassiosira gravida		×
Chætoceras teres	×	×	Thalassiosira hyalina	×	×
Detonula confervacea	×		Thalassiosira nordenskioldi		×
Eucampia grœnlandica	×		Thalassiothrix longissima		×

[1] Species that are endemic in the Polar seas, where ice forms in winter, and in the Gulf of St. Lawrence, but which occur only as immigrants farther south.

NOTES ON OTHER UNICELLULAR PLANTS AND ANIMALS

The flagellates Phæocystis and Halosphæra and the tintinnid infusorians and acantharian radiolarians are secondary in importance to the peridinians and diatoms in the plankton of the Gulf of Maine, but are still sufficiently abundant there at times to call for brief notice. The last two are grouped here with the phytoplankton for convenience sake, though they are animals and consequently consumers and not producers.

PHÆOCYSTIS

The brown unicellular alga Phæocystis is the only organism that we have ever found rivaling the vernal flowerings of diatoms in the Gulf of Maine either in abundance of floating vegetable matter produced or in actual numbers. Its identity is established by the simple structure of its cells, together with their green color and association into slimy colonies. But whether we have to do with *Ph. pouchetii, Ph. globosa,* or with both these species, has not been determined, the precise character by which the two are separable—i. e., the form of the colonies, whether lobate (*pouchetii*) or globose as in *globosa* (Lemmermann, 1908)—having been destroyed either by preservation or by the churning which they underwent in the nets. This is unfortunate, because *pouchetii,* with a range hardly extending south of 55° N. latitude in European waters, is decidedly a more northern form than *globosa,* which occurs in maximum abundance in the southern part of the North Sea and in the English Channel (Ostenfeld, 1910).

The Gulf of Maine records for Phæocystis have been confined to April 18 to 20, 1920, when it was sparsely represented in the western basin (station 20115) but so plentiful off Cape Cod and in the southern part of Massachusetts Bay (stations 20116 to 20118) that the fine-meshed silk nets used on the surface were clogged with its slimy masses after a few minutes towing, making it impossible to obtain a representative catch of diatoms or of other members of the phytoplankton. The Phæocystis colored the water brown; in fact, the appearance of the nets as they are lifted dripping with brown slime of offensive odor betrays the presence of this alga at once.

Plentiful though Phæocystis was at this time, its flowering period must have been brief, because it was not found in the region in question three weeks earlier (stations 20087 to 20090) or off Massachusetts Bay and Cape Cod two weeks later (stations 20120 to 20125), and it was not found anywhere in the gulf during the first weeks of May, 1915.

These few records show that Phæocystis fills much the same biologic niche in American as in north European waters. The region of its occurrence in the gulf is reconcilable, without discussion, with the neritic habit with which Gran (1902 and 1912) and Ostenfeld (1910) have credited it, and which its European distribution as a whole demands, though it is not confined to the immediate neighborhood of the coast in either side of the North Atlantic. It seems a regular event for Phæocystis to appear suddenly in tremendous quantities, and while its maximum flowering falls later in the northern than in the southern part of its range, it is characteristic of it to dominate the plankton for only a short time at any given region. Off the Norwegian

coast, according to Gran (1902, p. 17), Phæocystis reaches its maximum after the diatoms have passed their apex of abundance, with a monotonous Phæocystis plankton succeeding them for a very short period. Apparently it bears much the same temporal relationship to the vernal diatom flowerings in Massachusetts Bay, but in the western basin farther offshore it seems that Phæocystis precedes instead of succeeds the greatest seasonal abundance of diatoms.

The records of the International Committee point to May as the month in which Phæocystis is at its maximum in the North Sea—that is, about the same season as in the Gulf of Maine. Judging from the general geographic distribution of Phæocystis, the latter is probably its most southerly center of abundance in the western side of the North Atlantic, but the optima of temperature and salinity for this alga can not be established for American waters until more records are available. It may, however, be of interest to note that the Gulf of Maine collections (being from water of 3 to 4.5°) have been well within the temperature limits of *Ph. pouchetii* in European waters. But the salinity in which we have found it (31.43 to 32.45 per mille) is far less than the mean of the European records, which is given by Ostenfeld (1910) as about 34.8 per mille for *pouchetii* and as 34.89 per mille for *globosa*, though the former also occurs at the mouth of the Baltic in waters less saline than those of the Gulf of Maine.

HALOSPHÆRA

The unicellular pelagic alga *Halosphæra viridis* Schmidt[73] has been found at many of our stations, sometimes in considerable numbers, though it is not sufficiently prominent in the Gulf of Maine to have received a local vernacular name as it has in the Mediterranean (Steuer, 1910, p. 2). Halosphæra was first detected in the gulf in 1915, when it was widely distributed over the eastern basin of the gulf in May (stations 10269, 10270, 10271, 10272, and 10273), though nowhere abundant, and occurred locally off Mount Desert in June (stations 10284 and 10286); also at one station (10310) in August. It was likewise found across the whole breadth of the continental shelf south of Nova Scotia in June (stations 10291, 10293, 10294, and 10296), and off Shelburne in September (station 10313); likewise on German Bank on September 2 of that year (station 10310) and in the Massachusetts Bay region early and late in October (stations 10322, 10336, and 10337). During the spring cruises of the *Albatross* in 1920 Halosphæra was detected at some thirty stations in the gulf widely distributed both in time and space (stations 20044, 20045, 20048, 20054, 20057, 20064, 20067, 20069, 20070, 20072, 20073, 20074 to 20076, 20078 to 20080, 20086, 20097, 20098, 20100, 20105, 20112, 20120, 20123, 20124, 20126, and 20129). These records, combined, suggest that Halosphæra attains its maximum in the gulf late in the spring, practically disappearing again in midsummer,[74] though it has been described as plentiful at that season in the colder waters about Cape Breton, Nova Scotia (Wright, 1907). Doctor McMurrich found Halosphæra in late spring and early summer (April 17 to July 6) at St. Andrews, which corresponds to the May–June maximum in the open Gulf of Maine.

[73] Identification according to Lemmermann, 1908, p. 21.

[74] Our failure to find Halosphæra previous to 1915 was probably due to the fact that most of our stations in previous years were in late July and August when Halosphæra is rare in the Gulf of Maine.

We have never found Halosphæra dominant in the plankton of the gulf. The richest catches have been over the outer part of the shelf off Nova Scotia (fig. 130; stations 10293 to 10295) and off Mount Desert Island (station 10284) in June, 1915. Most of our records are based on the vegetative stage and on stages in division of the protoplasm (Lemmermann, 1908, p. 21, figs. 71 and 72). Cells with aplanospores have been detected only once in our towings—that is, near Shelburne, Nova Scotia, June 23, 1915 (station 10293), and no attempt has been made to trace the life history of Halosphæra in American waters, as Gran (1902, p. 12) has done so carefully for the Norwegian Sea.

The seasonal fluctuations of Halosphæra in the Gulf of Maine generally parallel its occurrence in the North Sea, where it is at its maximum in May and its minimum in August. But east of Cape Sable it evidently reaches its greatest abundance later in the season, for Wright (1907) describes it as an important factor in the plankton at Canso, eastern Nova Scotia, in June and July.[75]

It is now well established that Halosphæra is not endemic in the North Sea but occurs there only as an immigrant from the Atlantic via the northern route around Scotland; and it is primarily of southern—Atlantic—origin in the Norwegian Sea, though it may also be endemic there to some degree. Whether it is equally an immigrant in the Gulf of Maine is yet to be determined, but the facts that our largest catches of it have been made over the outer part of the continental shelf and that we have never found it in any great numbers in the inner part of the Gulf point in this direction.

ACANTHARIAN RADIOLARIANS[76]

The swarming of radiolarians, represented by the genus Acanthometron, is a decidedly sporadic event in the Gulf of Maine, as it is in North European waters also (Mielk, 1913), but on such occasions they are extremely conspicuous among the plankton, thanks to their large size, distinctive appearance, and reddish color. Up to the present time we have only once found Acanthometron dominant—that is, on August 22, 1914 (station 10253, fig. 131), when it swarmed off Cape Ann and in the western basin. We have never found Acanthometron before or since in midsummer in the gulf. Apparently it occurs more regularly in early autumn and is more generally distributed then, for it was comparatively plentiful in the center of the gulf (station 10309), in the northeast corner (station 10316), off Penobscot Bay (station 10318), and off Shelburne, Nova Scotia (station 10313), during the first and second weeks of September in the year 1915. It was a conspicuous element in the plankton of Massachusetts Bay during the last week of that month (stations 10320 and 10321; fig. 132), but its presence there was short-lived, for none were found a month later (stations 10337, 10338, and 10339, October 26 and 27). Acanthometron has been detected in only one October tow elsewhere in the gulf (a few miles off Penobscot Bay, October 9, 1915, station 10329). It was not found at any of the stations in the western part of the gulf in the late autumn, winter, or spring, but a few specimens were noted on German Bank and in the North Channel on April 15, 1920 (stations 20103 and 20105).

[75] For notes on the temporal occurrence of Halosphæra in the open Atlantic, the Norwegian Sea, and in the Mediterranean see Cleve (1900), Gran (1902), Steuer (1910), and Ostenfeld (1910).

[76] For an excellent account of the northern acantharians see Popofsky, 1905.

These scattered records point to late summer and early autumn as its season of greatest abundance in the Gulf of Maine, and they suggest, though hardly prove, that its chief center of distribution lies in the western part of the gulf with a second-

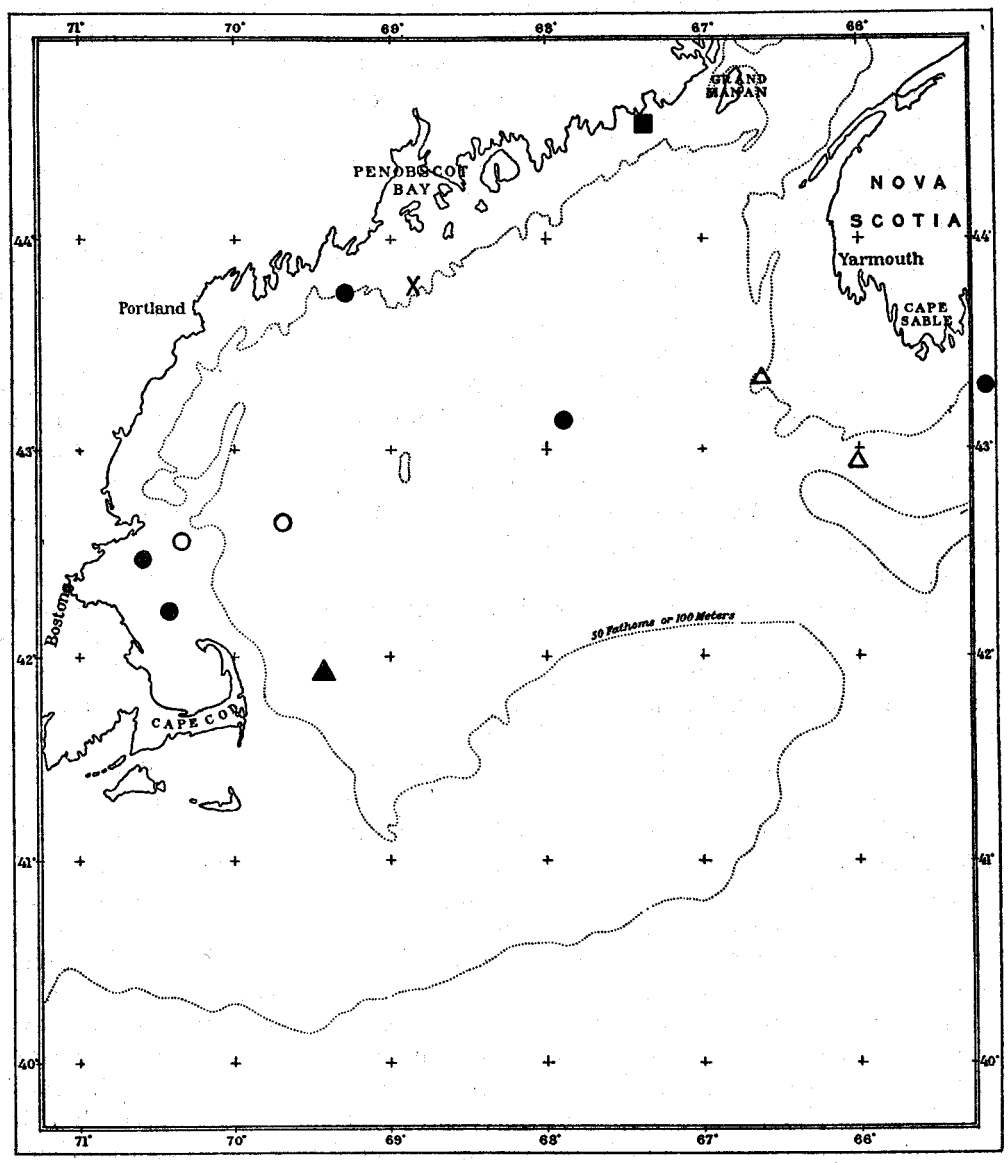

FIG. 132.—Locality records for Acanthometron, 1914 to 1920. ○, August, many; ▲ August, few; ●, September, many; ■, September, few; X, October, few; △, April, occasional

ary center somewhere off southern Nova Scotia, for which its presence off Shelburne on September 6, 1915, is evidence. Furthermore, the areas of abundance for Acanthometron have been small in extent, with neighboring stations yielding

few or none even on the same day. The August swarm just mentioned was so concentrated that only odd specimens appeared in the tow at the station next to the south (station 10256) and none at all at those to the east or north. On September 1, 1915, when it was abundant at station 10309, none were taken 40 miles to the southwest (station 10308), 35 miles to the east (station 10310), or 60 miles to the northeast (station 10315). Similarly, none were taken off Cape Elizabeth on September 20, 1915 (station 10319), nor off Mount Desert Island on the 15th (station 10317), though it was plentiful at an intervening station (10318) on the 16th, with no notable hydrographic difference in the state of the water. There is no apparent correlation between the presence or absence of Acanthometron in the gulf and the precise temperature, for while the August swarms of 1914 were living in water of about 18 to 20° off Cape Ann, the Nova Scotian collections for September, 1915, were from a temperature colder—and perhaps very much colder—than 15°. We have one record of Acanthometron from water of only about 4° (German Bank, station 20103, April 15, 1920).

Its occurrence is equally independent of salinity within broad limits, for it was most abundant in the Western Basin and off southern Nova Scotia when the water was near its freshest for the year, but we have not detected it in Massachusetts Bay until salinity has increased considerably from its seasonal minimum. Broadly speaking, however, Acanthometron is plentiful in the gulf only while the temperature is comparatively high and the salinity comparatively low.

Acanthometron likewise attains its seasonal maximum in late summer and autumn off north European coasts, with a general increase from August on, and its minimum in May. On both sides of the Atlantic the richest catches of this radiolarian have been from the eddies of cyclonic currents—that is, from the southern Norwegian Sea (May), Irminger Sea (July), middle of the North Sea (November), and in our gulf from the Western Basin (August).

Although Acanthometron occurs at times and locally in even greater abundance in the shallow coastal waters of the eastern side of the Atlantic than in the Gulf of Maine, it is essentially an immigrant there from the open ocean. The records of the International Committee for the Exploration of the Sea prove that although it is independent of actual temperature and salinity for its ability to exist, its abundance in the North Sea depends more or less on the amount of warm, highly saline ocean water entering around the north of Scotland (Mielk, 1913). Its chief centers of abundance in the Gulf of Maine have been in the regions farthest removed from such oceanic influence—that is, close in to land and in the semistagnant Western Basin. Furthermore, we have never found it in the zone of mixture between cool coast waters and warmer ocean waters along the continental slope, and its absence there is particularly significant because Acanthrometron centers have often been encountered in the contact zone between Atlantic and Arctic waters on the other side of the North Atlantic.

Here we must leave the question of the distribution of Acanthrometron for the present; but in passing I may point out that more data on this point are particularly desirable, not so much for the sake of mere completeness of local information as because of a very interesting phenomenon exhibited by this form, namely, the sharply

circumscribed areas in which it occurs when it does swarm and the suddenness of its appearances and disappearances, the causes of which are totally unknown.

TINTINNIDS

The tintinnids of the Gulf of Maine offer an interesting field for study because the several members of Cyttarocylis—the chief genus—have rather precise geographic characteristics (Jørgensen, 1899; Brandt, 1906). The records for 1914, 1915, 1916, and 1920 show that tintinnids may be expected anywhere in the gulf; only rarely, however, have they formed any considerable part of our catches of phytoplankton. As a rule, they are decidedly scarce, often absent, or at least so rare as to be overlooked, though they are conspicuous objects in the field of the microscope. In1920 they were found at most of the March stations in the eastern side of the gulf from the coast of Nova Scotia out to the Eastern Channel and across the continental slope off Cape Sable (fig. 133; tintinnids sufficiently numerous to be recorded at stations 20071, 20072, 20074 to 20079, 20083, 20084, and 20086); but none were detected on Georges Bank or in the western half of the gulf during that month. By mid-April [77] the tintinnids, like the peridinians, had practically disappeared from the waters where they occurred in March, with no compensating augmentation elsewhere in the gulf. In 1915 we found tintinnids in some numbers on German Bank and off Lurcher Shoal on the 7th and 10th of May (stations 10271 and 10272), as well off as Penobscot Bay two days later (station 10276). Apparently (though our records are insufficient) they gradually spread westward from May on, with the advance of the season, for we took them in large numbers off Cape Cod on July 22, 1916 (station 10346).

In August and September, 1915, tintinnids were recognized in the Eastern Basin, in the center of the gulf, and alongshore from Penobscot Bay to Cape Elizabeth (stations 10304 to 10306, 10310, 10311, and 10316 to 10319). In October of that year they occurred in localities as widely separated as the Massachusetts Bay region (stations 10320, 10323, and 10336), the neighborhood of Mount Desert Island (station 10328), and off the Grand Manan Channel (stations 10316 and 10327). McMurrich found them at St. Andrews from late August until October 9, in 1916. In short, they may be expected anywhere in the gulf in summer and early autumn.

Only three times have we found tintinnids an important factor in the plankton of the gulf—that is, at the Cape Cod station just mentioned, July 22, 1916, where there were about half as many Cyttarocylis as Ceratium in a sample taken at random; off Cape Elizabeth on September 20, 1915 (station 10319); and off the southeast slope of Georges Bank on July 22, 1914 (station 10220). But the group is evidently more important east of Cape Sable, for they appear at times in great numbers in the cold water along the outer coast of Nova Scotia, this being the case at several of our stations in July and August, 1914 (Bigelow, 1917, p. 329). Wright (1907) records both Tintinopsis and Cyttarocylis as common at Canso, Nova Scotia, during the summer.

[77] There are only two April records for the group in the gulf—stations 20098 and 20101. Elsewhere during that month they were at least so rare as to be overlooked.

I can give only the briefest of notes on the species of tintinnids concerned, though these are not hard to identify, thanks to Jørgensen's (1899) and Brandt's (1906) beautiful figures. Most of the Gulf of Maine records listed above are based

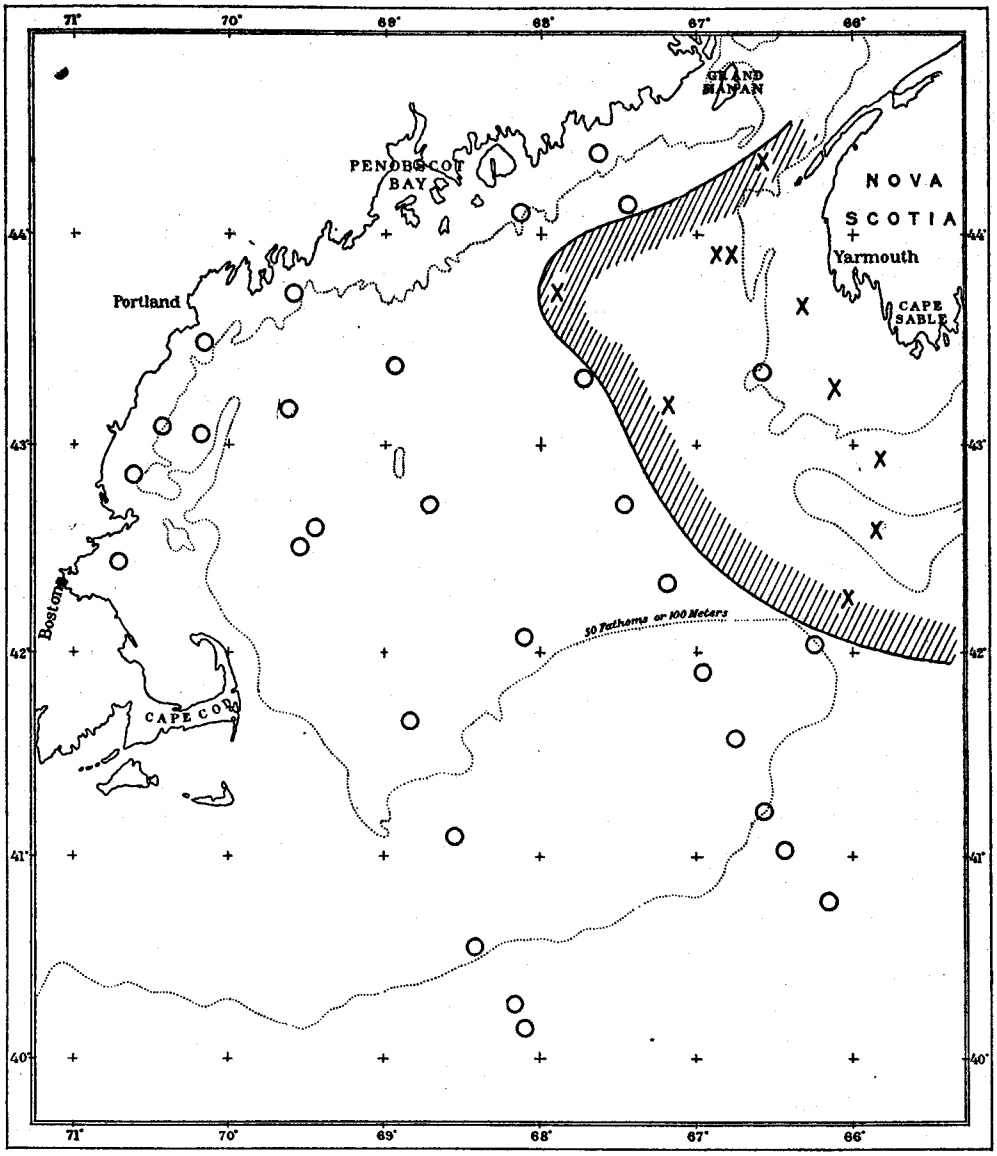

FIG. 133.—Distribution of the tintinnid genus Cyttarocylis in February and March, 1920. X, localities where it was, and O, where it was not found. The hatched curve marks its approximate western boundary at the time

on one form or another of the highly variable *Cyttarocylis denticulata*. This was notably the case for the rich haul off Cape Cod and for the towings off southern Nova Scotia in July and August, 1914, just mentioned, but the rich catch off Cape

Elizabeth (station 10319) was chiefly *C. serrata* (Brandt, 1906, Taf. 39, figs. 4 and 6). McMurrich (1917) records *C. ehrenbergi* and two species of Tintinopsis—*T. campanula* and *T. ventricosa*—from St. Andrews, while his unpublished plankton lists note *Cyttarocylis denticulata* and *C. subulata.*

According to Brandt (1910) the limits of *C. denticulata* in the North Sea area are chiefly determined by temperature, its upper optimum being about 12°. In a general way this is true also of the Gulf of Maine and of Nova Scotian waters, for it is more numerous in the cold Nova Scotian current than in the higher temperatures of the gulf, but the data are not sufficiently extensive to show whether its distribution within the gulf reflects the slight regional differences in temperature that prevail there.

OTHER UNICELLULAR ORGANISMS

The reader must not assume that the foregoing notes exhaust the major groups of unicellular organisms in the Gulf of Maine. On the contrary, such important divisions as the coccolithophorids, the silicoflagellates, and the infurosia (apart from the tintinnids) have not been mentioned at all, not because they do not occur but because they have not been detected so far in our offshore hauls, or only on the rarest occasions. Infusoria, in particular, may be expected to prove of considerable ecologic importance when tow-net catches, preserved by methods suitable for these minute and very delicate organisms, are intensively studied. Such, at least, is the case in June in the Gulf of St. Lawrence, where the infusorian genera Mesodinium and Labœa occur in abundance, as they do also in the waters off Halifax in May. (Gran, 1919, p. 493.) The silicoflagellate genus Distephanus occurs at times in some numbers at St. Andrews. (McMurrich, 1917, p. 4.)

We have not detected Notiluca in any of the Gulf of Maine towings, though its wide distribution in general and its seasonal abundance in the Irish Sea and coastal regions of the North Sea region in particular, where it is one of the most frequent sources of phosphorescence (Ostenfeld, 1910; Herdman, Scott, and Dakin, 1910), point to its presence in the gulf as probable.

Globigerina is likewise to be expected in the gulf as an occasional immigrant from the ocean waters of the open Atlantic, but is never likely to prove of any importance in the Gulf of Maine plankton.

NOTES ON THE BIOLOGY OF THE PHYTOPLANKTON

Perhaps no phenomenon in the natural economy of the gulf so arrests attention (certainly none is so spectacular) as the sudden appearance of enormous numbers of diatoms in early spring, and their equally sudden disappearance from most of its area after a brief flowering period. As precisely this same phenomenon takes place in north European waters, where biologists have long occupied themselves with the marine plankton, no wonder the possible factors, hydrographic and seasonal, or the physiology of the diatoms themselves, which first permit and then estop their almost inconceivably rapid multiplication and finally even prohibit their further existence, have been the subject of much study and discussion. Nevertheless, as Herdman (1920, p. 817) has recently declared, the factors governing this phenomenon still remain imperfectly understood.

The obstacle to the advance of knowledge along this line has not been any lack of plausible explanations; on the contrary, various changes take place in spring in the physical medium in which the plankton exists, any or all of which might, *à priori*, be assumed to control the life history of the planktonic plants. Such, for example, are the seasonal variations in the temperature of the water; in its salinity; in its density, viscosity, and vertical stability; in the activity of its vertical circulation; in its alkalinity; in the supply of dissolved foodstuffs; and in the strength of the sun; every one of which, directly or indirectly, affects the viability and reproduction of the phytoplankton, and which, in unfavorable combination, may make existence impossible for them.

It has been observed repeatedly, and in widely separated seas, that the vernal augmentation of the diatoms synchronizes with the first vernal warming of the water. But, as Moore, Prideaux, and Herdman (1915, p. 247) have emphasized, "it is to be remembered that the physical cause must have a latent period ahead of the biological effect." It may be stated as a general rule that the vernal flowerings of diatoms follow so closely after the commencement of vernal warming (if not antedating it) that the latter can not be the cause of the former. This is certainly the case in the waters between Cape Ann and the Isles of Shoals, where diatoms commence to multiply actively in March, the temperature still being at its winter minimum (p. 383), while in 1925 winter flowering of *Rhizosolenia alata* commenced in the falling temperature of December (p. 396). Furthermore, marine diatoms as a class have been found tolerant of such wide variations of temperature and of salinity, both over the geographic and seasonal ranges in nature, and in cultural experiments (Allen and Nelson, 1910; Fritz, 1921a), as to make it in the highest degree unlikely that slight changes in either of these environmental features, within the limits of both obtaining in the Gulf of Maine, are themselves of prime importance in the economy of these pelagic plants. But temperature and salinity in combination determine the viscosity, the density, and the vertical stability of the water, which in turn tend to control the activity of its vertical circulation and thus indirectly to favor or hinder the flotation and food supply of marine diatoms as the seasons change.

Herdman (1920) believes the increasing intensity of the sunlight is the chief stimulant for the spring flowering of diatoms, and certainly without sufficient sunlight the reproduction and even the continued existence of diatoms—for that matter, of all chlorophyllous plants—would become impossible. This may well be the case in the higher latitudes of northern Europe, likewise in Canadian waters, during the short winter days. And while terrestrial experience in the latitudes of the Gulf of Maine (40 to 45° N.) shows that the sun rises high enough in the sky for active photosynthesis at all seasons, the increasing percentage of hours of sunlight per day, and its greater intensity consequent on the increasing declination of the sun, no doubt help to make the spring a more favorable season for the flowering of diatoms than late autumn or winter. But this factor can not by itself explain the seasonal cycle of diatom flowerings as they actually occur, for if increasing light be a factor inducing their commencement it should equally favor their continuance throughout the summer, instead of the culmination and disappearance after a few weeks that characterizes most parts of the Gulf of Maine (p. 396).

On the whole, with successive observations and experiments it grows more and more probable from year to year that, given temperatures, salinities, and alkalinities (p. 486) in which diatoms can exist, with sunlight sufficient for active photosynthesis, their regional and seasonal abundance depends chiefly on the richness of the water in dissolved food substances, organic and inorganic, and to a less extent on the activity of vertical circulation of the water and its viscosity.[78]

The suddenness with which diatoms commence flowering in spring tends to corroborate this generalization, for if the gulf were abundantly supplied with nutrients the year round we might expect to find their numbers steadily augmenting throughout the coastal waters of the gulf during the late winter, as vertical circulation grows more and more active and as the sun rises higher and higher; but as a matter of fact (and this is true not only of the Gulf of Maine but of other northern coastal waters) the tremendous flowerings of diatoms so characteristic of early spring culminate almost between one week and the next.

The most reasonable explanation for this is that at least one of the nutritive substances on which they depend, whether it be nitrogen, phosphoric acid, silica, or some other, occurs in less than the minimum required for their active growth and reproduction during the winter and until the first days of spring, when the increasing outflow from the rivers, combined with an increasingly active vertical circulation of the sea water, raises the supply above this critical point, whereupon a rapid multiplication of diatoms at once ensues. Conversely, an exhaustion of one or other foodstuff is now generally accepted as the cause of the sudden disappearance of diatoms after their vernal flowering period. The diminishing viscosity, also, and the increasing vertical stability of the water, which characterize the advancing summer owing to the rising temperature, likewise militate against the continued multiplication of diatoms. The former renders flotation difficult, as explained below (p. 482), and the latter so effectively isolates the surface stratum of water (where diatoms find their optimum light conditions) from the underlying layers that replenishment with nutrients from below is effectively hindered.

Although our Gulf of Maine studies touch only the outer edge of this very complex subject, it is of such fundamental importance in the economy of the sea that a brief discussion here needs no apology.

Diatoms being producers, not consumers, it is, of course, from what Johnstone (1908, p. 212) has called the "ultimate foodstuffs in the sea" that they derive their nourishment, chief of which are carbonic acid, the nitrogen compounds, phosphoric acid, silica (because of their habit of secreting silicious skeletons), and various other mineral salts in minimal quantities; also oxygen (not, of course, a food substance but necessary for life). Except under very special circumstances it is hardly conceivable that the phytoplankton of the open sea ever suffers a shortage of oxygen or of the available sources of carbonic acid. But as all the other nutrients occur only in minute quantities in sea water we can readily understand that the supply of one or the other might fall temporarily below the minimal amount[79] required for diatom

[78] See Johnstone (1908), Herdman (1923), and Johnstone, Scott, and Chadwick (1924) for general discussions of the nutrition of the phytoplankton.

[79] For discussions of Liebig's "Law of the Minimum" in its relation to marine plants, see Johnstone, 1908, p. 234; Gran, 1912, p. 367.

growth, and in the long run probably the supply of nitrogenous compounds chiefly determines the regional richness and poverty of the phytoplankton as a whole.

Allen and Nelson's (1910) experiments on rearing marine diatoms corroborate this, for they found it necessary to increase the concentration of nitrates, and apparently also of phosphates, above that of normal sea water in order to produce active multiplication. Fritz's (1921a) work along this line is especially pertinent here, for she experimented at St. Andrews on the culture of planktonic marine diatoms of Gulf of Maine species with similar results, being unable to obtain any considerable and persistent growth without the addition to the normal sea water of the nutrient salts—nitrates and phosphoric acid—employed by Allen and Nelson. With these, however, she obtained flourishing cultures of *Thalassiosira nordenskioldi, Skeletonema costatum, Asterionella japonica, Nitschia closterium, Melosira hyperborea,* and various other planktonic species.

NITROGEN

It has long been known that sea water absorbs nitrogen so readily from the air that the surface strata are usually saturated with this element, but it is still questionable whether any of the planktonic plants are able to utilize elemental nitrogen first hand. It has long been the commonly-accepted belief, also, supported by experiments on land, that no chlorophyllous plants can do so, unless, like the Leguminosæ, in symbiosis with nitrogen-fixing bacteria; but that all others—terrestrial or marine, unicellular or multicellular—are dependent on nitrogen compounds elaborated by some other means for their food supply of this essential element.

In 1920, however, Moore and Webster (1920) published the results of experiments which seemed to demonstrate that certain green unicellular algæ do possess the ability to obtain, and to fix by a process of photosynthesis, elemental nitrogen dissolved by the water from the air. A year later Moore, Whitley, and Webster (1921) carried out further experiments on a marine green alga, which they grew in measured volumes of sea water, finding that at the end of the experiment the amount of fixed nitrogen in plant and water combined exceeded the nitrite present at the beginning. From this they concluded that the excess must have come from the elemental nitrogen dissolved in the water, and so, in turn, from the air. These experiments, however, were not conclusive, no precaution having been taken to exclude the nitrogen-fixing bacteria which Reinke (1904) and Keding (1906) found on the fronds of several species of fixed algæ at Helgoland, and which, therefore, were probably present on the algal fronds used by Moore, Whitley, and Webster in their experiments, or to determine their presence or absence. And although Moore and his associates adduce several reasons why they think it improbable that the value of their experiments is detracted from by this "loophole" in technique, it remains an open question whether the increase in the amount of fixed nitrogen, which they demonstrated, did actually result from photosynthesis by the algal fronds experimented upon or from activity on the part of bacteria living symbiotic upon them.

So far as I am aware, the ability of marine phytoplankton to synthesize elemental nitrogen has not actually been tested by critical experiment directed to this definite end. But it has repeatedly been found that very much richer cultures of

planktonic diatoms may be grown with the aid of appropriate nutriants (including ammonium sulphate) than in normal sea water, and that exhausted cultures of diatoms may be temporarily revived by adding nitrogen in appropriate combination, which would hardly be the case were the diatoms able to avail themselves directly of the nitrogen gas dissolved in the water.[80] Therefore it may be assumed that diatoms, probably also peridinians, Phæocystis, Halosphæra, etc., require a supply of ready combined nitrogen for their existence.

The elemental nitrogen absorbed by the water from the air may serve as the source of this combined nitrogen through the medium of the bacteria just mentioned. These nitrogen-fixing bacteria have been found in the Baltic and in the North Sea, in bottom muds from many localities; also on the surfaces of a great variety of fixed algæ, including Fucus and Laminaria, and on the surfaces of planktonic organisms; likewise in the Indian Ocean (Keutner, 1905; Keding, 1906). Hence, they are probably cosmopolitan in such situations and may be expected to prove as widespread in the Gulf of Maine as they are in the North Sea region, though they have not been actually detected there as yet. The two genera, Clostridium and Azotobacter, have been found to exist under the most diverse physical conditions, and they may well prove of prime importance in the economy of life in the narrow coastwise belt where fixed algæ flourish, though this is still a matter of conjecture, as is the extent to which their activities depend on symbiosis with other bacteria or with algæ. But since they have never been detected free in the sea water it is not likely that their activities contribute much directly to the supply of nitrogen available for the use of planktonic plants on the high seas.

However this may be, normal sea water is extremely poor in nitrogen in combinations utilizable by plants—that is, as ammonia, nitrates, or nitrites—the chief sources for the latter in coastwise seas such as the Gulf of Maine being the drainage from the land and the decomposition of organic matter in the sea.

It has long been appreciated by biologists that northern rivers, especially those that flow from countries with heavy rainfall and much cultivated land and those that are polluted with organic wastes, do bring down to the sea vast amounts of this dissolved nitrogenous nourishment (Gran, 1915). It has been calculated from the nitrogen content of the Rhine (averaging 2 to 3 milligrams of nitrogen, in the form of dissolved compounds, per liter) that the North Sea receives annually not less than 390,000,000 kilograms (383,000 tons) of combined nitrogen in this way (Brandt, 1899, p. 230; Johnstone, 1908, p. 282).

The greater part of the watershed of the Gulf of Maine being timbered, not cultivated, and less densely settled than the countries bordering the North Sea, its river waters might be expected to prove less rich in nitrogen than the Rhine water; and the many analyses made by the United States Geological Survey prove such to be the case, with the rivers of Massachusetts richer in nitrogen than those of Maine. Thus the Charles River, a short distance above Boston, has been found to average about 0.879 part of nitrogen—as ammonia, nitrates, and nitrites—per million of water,[81] the Merrimac 0.524 part per million in its lower course above Haverhill, and

[80] Allen and Nelson (1910) give an extended discussion of this subject.
[81] Massachusetts Board of Health, 1890, examination of water supplies.

the Kennebec only about 0.3 part of combined nitrogen per million at Augusta (Whipple, 1907, p. 182). Perhaps 0.5 part per million would be a fair average for all the rivers emptying into the gulf—that is, only about one-fourth to one-fifth as rich as Rhine water. Nevertheless, this is a considerably higher concentration of total nitrogen than Raben (1905a and 1910) found in the sea water of the North Sea, where it ranged from 0.110 to 0.378 part per million, or in the Baltic (0.105 to 0.247 part per million). With a total annual runoff of not less than twenty-five hundred billion cubic feet of water from the rivers and streams that drain the watershed of the gulf, the latter must yearly receive at least 39,857 tons of nitrogen fixed in combinations readily assimilable by plants. This, roughly, is one-tenth the amount (383,000 tons) given by Johnstone (1908, p. 282) for the North Sea from Brandt's (1899) oft-quoted calculation of the nitrogen discharged by the Rhine. But the area of the Gulf of Maine, as inclosed by a line Cape Cod–Cape Sable, is only about one-fifth that of the North Sea, hence its river waters contribute at least half as much of nitrogen compounds yearly per unit of sea area as do those of the North Sea, and very likely more than half, for the other rivers that drain into the North Sea may not carry as heavy a load of nitrogen as does the Rhine.

Whipple's (1907) analyses of the water of the Kennebec, which may be taken as typical of the rivers tributary to the gulf, may not prove a definite seasonal periodicity in the concentration of dissolved total nitrogen, the range being from 0.24 to 0.49 part per million of water for the months of January, March, April, May, June, and August; but the highest concentrations (0.487 and 0.327) were in March and April, just when the total outflow is swelling with the spring freshets. Therefore it is safe to assume that the land drainage that empties into the gulf is at least as rich in nitrogen in spring, when the discharge from the rivers is at its maximum, as it is during the rest of the year, if not actually richer, as the analyses suggest. With the concentration of dissolved nitrogen compounds probably at least twice as high in river water as in the sea water of the gulf, the freshening of the latter, which is caused in spring by river freshets, is probably accompanied by a considerable increase in the concentration of nitrogen in the coastal zone over the values obtaining there in winter, with the alteration greatest near the mouths of the larger rivers and along the zones where their discharges have the greatest effect on salinity.

Although the decomposition of dead animals and plants in the sea does not actually add anything to the store of nitrogen preexisting in the water, simply transforming it from one form to another, it must constantly be making available for the use of the phytoplankton large amounts of this foodstuff that was previously bound up in other organic forms [82]—that is, in the bodies of animals and in attached plants, such as eelgrass (Zostera) and the larger algæ; and great though the amount of nitrogenous fertilizer brought down to the Gulf of Maine by its affluent rivers is, this source may rival it.

As every seaside farmer knows, eelgrass (Zostera) rots much more slowly than do the various algæ such as the "rock weeds" (Fucaceæ) and "kelps" (Laminariæ)

[82] Johnstone (1908) gives an interesting chapter on the circulation of nitrogen.

and the many smaller forms, but even for Zostera time brings progressive decomposition. After it has disintegrated to a fine dustlike state, further oxidization probably takes place more rapidly, particularly when it is suspended in the upper, more illuminated water layers. Is it not reasonable, then, to think of such organic particles or aggregates of particles as foci around which diatoms can multiply, being nourished by the nitrogenous substances as these constantly go into solution, just as the weeds in our gardens thrive around the particles of manure or of nitrogenous fertilizers that are similarly disintegrating or dissolving in the soil? At any rate, whether or not this particular picture be correct, a vast supply of organic matter is derived from the Zostera, the constituents of which must eventually join the general nutritive store of the sea water in which it decays and from which it was taken in the first instance. Even such of it as passes through the digestive tracts of bottom-dwelling mollusks must also travel the same path in the end, either as excreta or by the final death and decay of the endless chain of animals that feed one on another. What is true of Zostera is equally true of the more rapidly decaying marine algæ.

Qualitatively, at least, all this applies as well to the Gulf of Maine as it does to the other side of the North Atlantic, Zostera, with the "rock weeds," "kelps," etc., being abundant, with the general conditions of temperature, etc., under which they live, die, and decay, much the same. And since Zostera forms dense fields in the sandy and muddy bottoms of sheltered bays, estuaries, etc., all around the coast from Cape Cod to Nova Scotia, with beds of "rock weeds" (Fucaceæ), Laminariæ, etc., along the rocky or stony shores where it fails, the organic débris produced by the annual decay of submerged marine vegetation along the coast, spermophyle and algal, must reach very large proportions.

The decay of the dead bodies of the members of the animal communities that thrive so abundantly in the gulf, both on the bottom and planktonic, are also constantly making nitrogenous compounds available in the first instance as detritus, finally to find their way into solution. The importance of the rain of dead bodies of planktonic organisms, which is constantly descending through the water, as providing pastures for animals living on the bottom below, has long been realized. Some are devoured by other animals en route; others, like the medusæ and ctenophores, may entirely decompose and go into solution as they sink; but it is probable that in moderate depths, such as those of the Gulf of Maine, fragments at least of most of them reach the bottom before they entirely disintegrate. Naturally a larger amount of plant detritus accumulates on bottom in shoal water near land than out at sea because nearer the source of supply, and animal débris may also be expected to be most abundant in moderate depths. Think, for instance, of the product of the death rate in an extensive mussel (Mytilus) bed. But the following analyses prove that there is some nitrogenous débris (derived from plants and animals combined) everywhere in the uppermost layer of mud, silt, or sand on the bottom of the gulf, in deep water as well as in shoal.

Analyses of nitrogen (as N_2) in sea sediments from the Gulf of Maine and vicinity, performed by the chemical laboratory, United States Geological Survey

Station	Locality	Depth in meters	Per cent N_2
10288	Latitude 48° 28′, longitude 67° 30′	227	0.09
10291	Latitude 43° 24′, longitude 66° 22′	64	.12
10292	Latitude 43° 19′, longitude 64° 59′	157	.11
10294	Latitude 42° 36′, longitude 64° 27′	176	.06
10295	Latitude 42° 22′, longitude 64° 16′	500+	.24
10301	Latitude 44° 31′, longitude 67° 24′	73	.01
10513	Latitude 43° 47′, longitude 69° 08′	80	.13
10518	Latitude 43° 07′, longitude 69° 19′	194	.24
10522	Latitude 43° 00′, longitude 69° 35′	157	.32
10523	Latitude 42° 58′, longitude 69° 55′	219	.32
10525	Latitude 43° 04′, longitude 70° 23′	110	.20
10526	Latitude 43° 05′, longitude 70° 33′	44	.19
10530	Latitude 43° 38′, longitude 69° 46′	77	.12
10534	Latitude 43° 27′, longitude 69° 42′	137	.17
10540	Latitude 43° 03′, longitude 68° 51′	185	.19
10541	Latitude 42° 00′, longitude 68° 20′	201	.27
10548	Latitude 43° 30′, longitude 68° 38′	122	.19
10550	Latitude 43° 13′, longitude 68° 30′	198	.19
10551	Latitude 43° 09′, longitude 68° 05′	192	.07
10552	Latitude 43° 18′, longitude 67° 11′	201	.11
10553	Latitude 43° 09′, longitude 66° 53′	186	.19
10556	Latitude 42° 57′, longitude 66° 42′	218	.05
10575	Latitude 44° 06′, longitude 67° 04′	117	.13
10577	Latitude 44° 20′, longitude 67° 26′	110	.16
10595	Latitude 43° 58′, longitude 68° 16′	101	.13
10608	Latitude 41° 58′, longitude 69° 40′	174	.13
10617	Latitude 42° 04′, longitude 69° 57′	64	.09
10623	Latitude 42° 14′, longitude 70° 15′	24	.17
20064	Latitude 42° 20′, longitude 67° 13′	320	.19

Owing to technically unsatisfactory preservation of the specimens, these determinations can be regarded only as approximations of the amounts of nitrogen actually present in the muds; but recognizing this possible source of error, the average is about 0.16 per cent of nitrogen (as N_2), for the whole series (otherwise expressed, about 3.2 pounds per ton of mud or sand).

As long as this store of nitrogenous detritus remains mingled with the mineral deposits that cover the sea floor, it remains unavailable for the use of the planktonic vegetation, though it supports many mud-eating animals that live on the bottom. It must be constantly going into solution, however, as the breaking down by decomposition proceeds, a process hastened in regions of strong tides where vertical currents keep much of this flocculent material in suspension, as is proved by the considerable amounts of fine organic débris often taken in the tow nets. Its availability for the support of diatoms and of the other planktonic plants thus depends largely on the state of circulation of the water, a question discussed below (p. 479).

The gradual impoverishment of the animal plankton, which takes place from autumn on, with the dying of the large medusæ, copepods, and other groups, has been commented on (pp. 47, 88). Its natural result is to cause a more rapid accumulation of animal débris during the cold half of the year than in summer. Generally the death rate among the animals living on bottom along the littoral zone is also higher in winter than in summer. Everyone who frequents the shores of the gulf knows that this is true of the algæ, vast quantities of rockweed and kelp being torn adrift from the rocks by the autumnal gales and piled up along the beaches, where they are soon ground up

into fine fragments. The largest amounts of eelgrass (Zostera) leaves are also thrown off around the shores of the gulf during the autumn and early winter; but these are so tough and decay so slowly that great accumulations of their fragments are still to be found the following spring, especially in the deeper channels that cut the mud flats where fields of this plant flourish, and it may be several years before they are reduced to the state of fine silt. Thus, the amount of nitrogen in solution in the sea water tends to increase during the winter, while conversely the denitrifying bacteria (which are known to exist in the sea) are less active at low than at high temperatures.

Rain and snow falling on the surface of the gulf likewise add nitrogenous compounds to its waters, for they wash out ammonia from the air and nitric acid formed during electrical discharges. But the amount of nitrogen dissolved in rain is much less in temperate than in tropical climates, Muntz and Marcano's (1889 and 1891) analyses showing larger amounts (an average of 2.23 milligrams nitric acid and 1.55 milligrams ammonia per liter) in the rain water at Carracas, Venezuela, than have been found in Continental Europe or in England. No nitrogen analyses have been made of the rain water that falls on the Gulf of Maine, or, so far as I can learn, for any neighboring part of North America, but probably it does not differ much from European analyses—that is, is in the neighborhood of 0.2 milligram nitric acid and 0.5 to 0.9 of ammonia per liter.

SILICA

The obvious dependence of diatoms on silica (which is present in only very minute quantities in sea water) for the construction of their shells has naturally tended to focus attention on the fluctuations in concentration of that substance as probably governing the abundance of marine diatoms, and several recent authors, among them Michael (1921), have definitely accepted it as the chief determinant.

Diatoms require much more silica than nitrogen, the disparity between these two substances being much greater in the dry matter of these plants than in the sea water in which they live. Evidently it would be impossible for diatoms to form their silicious frustules without a sufficient supply of silica; in fact such a failure, with resultant abnormal forms, has actually been recorded by Allen and Nelson (1910) for experimental cultures, while these were undergoing rapid multiplication.

Sources for dissolved silica.—We might naturally expect to find the land drainage from an area as largely composed of felspathic rocks and of glacial débris as is the watershed of the Gulf of Maine, much richer in dissolved silica than the sea water, an expectation confirmed by several analyses of the waters of several New England rivers and springs made by the United States Geological Survey, as well as for river waters in other parts of the world. Thus, according to Fuller (1905, p. 53), 12 representative springs in various parts of the State of Maine carry from 5.1 to 15.1 parts of silica (as SiO_2) per million, the average for all 12 being about 10 parts per million, which is about five times as much as the sea water off Gloucester at the season of its highest concentration (p. 476). Spring waters, of course, undergo various and rapid modifications on their way first to the rivers and then to the sea, a river being "the average of all its tributaries plus rain and ground water, and many rivers show also the effects of contamination from towns and factories" (Clark, 1916, p. 64). Nevertheless, Clark's (1916, p. 71) analyses of the water of the Androscoggin a few miles above tide water [83]

[83] Average of 38 analyses of weekly samples taken between Apr. 25, 1905, and Jan. 16, 1906.

show as much as nine parts silica (as SiO_2) per million. Androscoggin water is, therefore, almost as rich in silica as the spring water average just quoted (Clark's exact figures are SiO_2, 18.63 per cent of total solids, salinity 48.3 per million). According to one analysis the upper waters of the Merrimac are even richer in silica than this (SiO_2, about 31 parts per million), but since the Merrimac flows for many miles through an alluvial valley in its lower course, and at the same time receives several important affluents from swampy areas, it probably reaches the sea with a much smaller percentage of silica in its water.

If we can take the Androscoggin as fairly typical of the rivers of northern New England (including the St. John River, of which no analyses are available), which is justified by the nature of its watershed, it appears that, on the whole, the river water emptying into the Gulf of Maine is 7 to 8 times as rich in dissolved silica (SiO_2) as our analyses off Gloucester suggest as a fair average for the latter. A discrepancy of this sort obtains between the silica contents of river and sea water in temperate zones generally, and its effects are probably accentuated in the Gulf of Maine, just as the effect of land drainage is in reducing surface salinity by the concentration of the run-off from a large watershed into a comparatively small and topographically circumscribed area of sea. It would therefore be reasonable to expect the waters of the Gulf of Maine to average high in silica when sufficient analyses are made to plot the distribution of silica in boreal seas generally.

In addition to the silica brought down by the rivers in the dissolved state, probably much larger amounts are carried to the sea, suspended in the form of the finely divided clay which is derived from the disintegration of felspars, etc. Though most of this clay is precipitated to the bottom on mixture with the salt water, part of it is carried to great distances. Murray and Irvine (1892, p. 240) suspected from their cultural experiments "that the pelagic silicious organisms might, in part at least, obtain the silica for their frustules and skeletons" from this clayey matter. So far as I know these experiments have been neither confirmed nor refuted, nor is it clear whether they were sufficiently precise to eliminate other possible causes for the abundant growth of diatoms which ensued on the introduction of clay into the artificial culture solution. But we must reckon with the possibility that diatoms not only make use of the dissolved silica but also of the insoluble silicates, given vertical circulation strong enough to keep the latter in suspension in the water.

A third possible source of silica is the slow solution of the rocks that form part of the coast line of the Gulf, and of its submarine boulders, sands, and clays. Silicious deposits of this sort have commonly been regarded as so nearly insoluble in sea water as to be negligible biologically; but as Clark (1916, p. 132) points out (geologists generally recognize this), sea water does attack and in the end dissolve the most refractory silicates, even if very slowly. In fact, Joly (1901) found that sea water dissolves more silica (SiO_2) from felspar than does distilled water.[84] But there are two reasons for hesitancy in applying Joly's generalizations to conditions as they occur in nature. First, I am unable to judge from his brief account whether his analyses took due account of the small amount of dissolved silica which we must

[84] Earlier tests by Thoulet (1889) gave the opposite result.

suppose to have been present originally in the sea water employed in his tests, and second, because distilled water exercises much less solvent action than do the land waters with their load of dissolved organic compounds, humus acids, and Co_2, which actually do the work of erosion on their way to the rivers and so to the sea; but, however slowly rock silicates are degraded in the sea, they are so degraded in the end. Indeed, all minerals, given time, finally succumb to the combined action of water, oxygen, and carbonic acid. Where a constant and rapid interchange of water between the bottom and the upper layers is kept up by vertical circulation (water, too, of low alkalinity—that is, of comparatively high carbonic acid tension—as is the case on Georges Bank (p. 481) and in the Bay of Fundy) degradation of silicates will be more rapid than in the deeps, where, as Murray (1912, p. 187) points out, "the soluble by-products are removed and the supply of oxygen and carbonic acid maintained by diffusion only."

Furthermore, we must bear in mind that in the case of the degree of concentration of silica we are dealing with solutions so attenuated that although the destructive action of sea water on felspathic rock fragments is almost inconceivably slow, it may be sufficient under hydrographic conditions as favorable as Georges Bank offers to yield the very small extra amount of silica needed to favor the active growth and multiplication of diatoms when added to what is in all sea water. Finally, the frustules of dead diatoms are themselves a potential store of this element and in one of its less insoluble forms.

It is still to be proved that there is not always a sufficient supply of silica at all times and in all parts of the sea for the growth and multiplication of diatoms. But stress has often been laid on the apparent parallelism between the seasonal fluctuations in the concentration of dissolved silica which Raben (1905) reported for the waters of the North Sea and of the Baltic (Murray and Irvine's earlier analyses are open to criticism) and the ebb and flow of the diatoms. Indeed, the correspondence between the two sets of phenomena, as it appears on Johnstone's diagram (1908, fig. 30), is striking enough. Subsequent analyses made by Raben himself during the years 1904 to 1912 (Raben, 1905a to 1914), both for the central and eastern North Sea and for the western part of the Baltic, show that the seasonal fluctuations in the amount of silica are less regular than his earlier work suggested. But he again found maxima in February and November over the periods of years covered by the tests, the silica (SiO_2) content varying in the Baltic from 0.53 to 1.76 milligrams per liter in February, to 0.40 to 0.93 in May, 0.20 to 1.49 in August, and 0.93 to 1.36 in November, averaging as follows:

Average silica (SiO_2) content in the western Baltic, 1902 to 1912

Month	Silica, milligrams per liter	Number of analyses	Month	Silica, milligrams per liter	Number of analyses
February	0.97	19	June	0.80	2
March	.83	5	August	.86	14
April	.65	4	November	1.17	23
May	.69	17			

Diatoms are at their maxima in this part of the sea in spring. Hence, the general correspondence between the silica curve and the fluctuations of the diatoms is at least suggestive. Furthermore, only a very slight difference in the concentration of silica dissolved in the sea water may be needed to control the multiplication of diatoms—perhaps less than one part in two million of water.

To test whether a similar parallel between seasonal concentration of dissolved silica and abundance of diatoms would be found in the Gulf of Maine, samples of sea water of about 8 liters each were collected monthly off Gloucester from December 28, 1920, to October 26, 1921, and shipped in 2-gallon tinned-iron cans to the chemical laboratory of the United States Geological Survey for analysis. The determinations for silica were made by Dr. R. C. Wells, who has described his methods (Wells, 1922), the results being as follows:

Soluble silica in sea water collected at the surface about 1 mile south of Eastern Point Light, Gloucester, Mass.

Date of collection	Silica as SiO_2 in milligrams per liter of water = parts per million	Date of collection	Silica as SiO_2 in milligrams per liter of water = parts per million
Dec. 28, 1920	1.5	June 27, 1921	[1] 1.9
Jan. 26, 1921	2.5		1.9
Mar. 2, 1921	2.9	July 27, 1921	.6
Mar. 25, 1921	1.4	Aug. 26, 1921	.3
Apr. 25, 1921	.3	Oct. 26, 1921	[2] .4
May 26, 1921	.4		[2] .7

[1] Average, 1.4.

[2] Average, 0.55.

These are the first analyses for silica for sea water off the North American coast. Unfortunately, the samples of water were not large enough to allow duplicate determinations except in two instances.[85] As the diagram (fig. 134) illustrates, the seasonal fluctuations proved much wider than Raben's work would have suggested, with a pronounced maximum early in March, perhaps a second maximum in June and July, and something like six or seven times as much silica per liter at the beginning of March as in May or in autumn. That is to say, in the particular year in question (1921) the sea water near Gloucester was richest in silica a week or two prior to the time when we have usually found diatoms commencing to flower actively, became rapidly impoverished during the month when we have found diatoms most plentiful there in other springs, and poorest in silica at about the time the rich diatom flowerings come to a close. During June the supply of silica accumulated somewhat, and correspondingly we have twice found diatoms flowering in the bay late in summer or early in autumn (September in the year 1915, August in 1922; pp. 394 and 391). With the seasonal fluctuations so notable for diatoms and fairly demonstrated for the concentration of silica, with the maxima for the former

[85] Doctor Wells writes me that although the iron of several of the containers was somewhat rusted, in most cases careful analysis of the sediment showed practically no silica; and by analysis the iron of the cans was found to contain not more than 0.0002 gram silica per gram, so that measurable contamination of such large volumes of water by that agency is ruled out of consideration.

preceding those of the latter, and with the dependence of flowerings of diatoms on an adequate supply of silica obvious, the parallelism between the curves for this substance and for abundance of diatoms can not reasonably be regarded as accidental.

PHOSPHORIC ACID

Recent analyses of seasonal fluctuations in the amount of phosphoric acid in north European seas make it probable that exhaustion of the supply of this essential foodstuff operates, widespread, to check the vernal flowerings of diatoms. Phosphoric acid (P_2O_5) exists in such weak solution in sea water (usually less than one part per million), and its analysis is attended with such difficulty that none of the earlier determinations can be depended on; but recent tests[86] have shown a definite seasonal periodicity in the silica content of the English Channel, the North Sea, and the Baltic. Atkins's (1923a and 1925a) data for the neighborhood of Plymouth (espe-

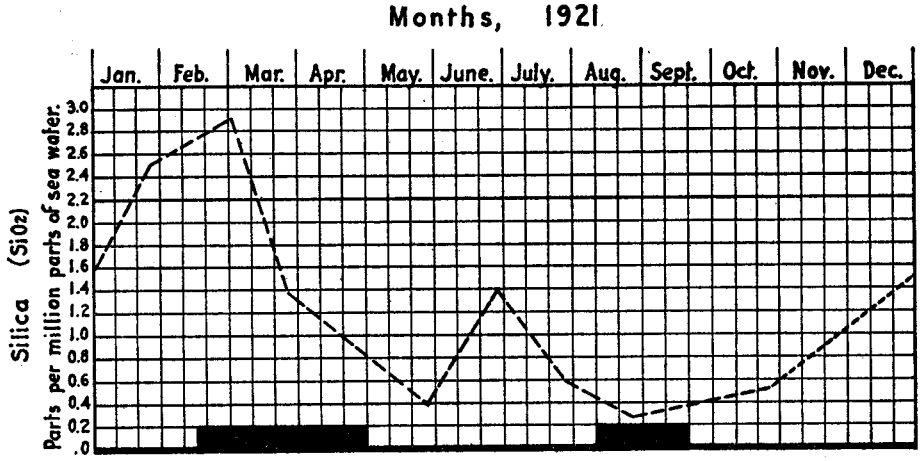

FIG. 134.—The broken curve shows the concentration of dissolved silica (as SiO_2) near Gloucester, monthly, for the year 1921, from determinations by Dr. R. C. Wells (see p. 476). The solid black line indicates the flowering seasons of diatoms for that neighborhood

cially significant, as they extend over two years) show maximum values in winter and minimal in summer, when the water may be almost phosphate free. Atkins's (1925a, p. 718) conclusion that "where illumination is adequate the phytoplankton increases until the phosphate is almost absolutely used up" is supported not only by the parallelism between the increase in phosphoric acid in northern seas in winter, followed by its depletion in late spring, and the vernal flowerings of diatoms, but by experimental evidence, for he had earlier (1923) found that in a culture of the diatom *Nitschia closterium* a great increase in the number of diatoms reduced the phosphoric acid from 2.38 parts per million (milligrams to the liter) to 0.006.[87]

A supply of phosphoric acid being essential for plant growth, it is obvious enough that whenever and wherever this substance is entirely used up the lack of it

[86] In review of these see Mathews (1916) and Atkins (1923a and 1925)

[87] In one of Moore and Webster's (1920) experiments on photosynthesis on a unicellular fresh-water alga a lack of phosphate was demonstrated as the growth-limiting factor.

must, as Atkins points out, limit the abundance of the phytoplankton. He has made interesting calculations of the amounts of diatoms that could be produced, supposing all the phosphate in the water to be consumed. The facts so far garnered, however, do not warrant the assumption that a poverty in phosphorus can safely be invoked as the universal cause for the eclipse of the vernal flowerings of diatoms when this event takes place. As we have seen, a parallelism of the same sort has been established with fair probability between the amount of silica in the water and the abundance of diatoms. There is also good reason to believe that at times and over large areas of sea the supply of available nitrogen falls below the minimum requisite for their active reproduction. The strong probability that different groups of planktonic plants, and even different species within the major groups, differ widely in their nutritive requirement, makes the question complex.

I have no first-hand information to offer on the richness of the Gulf of Maine water in phosphoric acid, but the fact that the vernal swarmings of diatoms are succeeded by peridinians and not by other diatoms over most of the area of the gulf is sufficient evidence that water that is no longer fit to support rich flowerings of the latter, through the exhaustion of some substance essential to their growth, still offers a favorable environment for the former.

Thus it does not seem likely that the spring diatom maxima in Massachusetts Bay and in the southwestern part of the gulf generally as nearly exhaust the phosphates as Atkins found to happen in the English Channel. But if diatoms require a richer supply of phosphates than peridinians do (as they certainly require a more abundant supply of silica) the reduction in the available supply of this nutrient resulting from their consumption of it may terminate the flowerings of diatoms, though still leaving the water rich enough in dissolved phosphates to support an abundance of peridinians. It is true that Brandt (1905, p. 11) and others following him have suggested that peridinians may need more phosphorus than diatoms, not less, but nothing whatever is definitely known as to their requirements.

The desirability of analyses of Gulf of Maine water for phosphoric acid at different times of year is obvious, and further speculation on the dependence of the local phytoplankton on fluctuations in the supply of this nutrient is best postponed until such are undertaken.

In addition to the major foodstuffs which I have mentioned, planktonic plants, like terrestrial plants, require a small but available supply of various other substances—iron, sulphur, sodium, etc. Nothing whatever is definitely known as to their exact requirements in this respect, but recent experiments on the cultivation of diatoms have shown that some species require substances which others can do without. In the case of *Thalassiosira gravida*, E. J. Allen (1914) was unable to obtain good cultures in artificial sea water to which he added the same nutrient solution that had produced abundant growth in natural sea water until a small percentage of the latter was added to the artificial medium, when excellent cultures ensued. Provided this small amount—1 per cent or so—of natural sea water was added, the constituents of the artificial sea water (which formed all but this trifling proportion of the culture medium) could be varied within wide limits, as could its total salinity, without either hindering or apparently helping the growth of the diatoms. Thus this particular genus appar-

ently requires "some specific substance present in minute quantity in the natural sea water" (E. J. Allen, 1914, p. 439), but not in the artificial.

Fritz (1921a), experimenting in the culture of diatoms at St. Andrews, New Brunswick, found that *Melosira hyperborea* not only made considerable growth in artificial sea water but continued to multiply rapidly in cultures in natural sea water long after *Thalassiosira nordenskioldi*, *Chætoceras debile*, and *Skeletonema costatum* became exhausted. Her conclusion that the persistence of Melosira is permitted by its independence of some substances which the other forms required but soon exhausted seems justified.

Suggestive, also, in this connection is Crawshay's (1915) observation that the excretory products of the copepod *Calanus finmarchicus* (apparently not, however, of Pseudocalanus or Acartia) exert a strong fertilizing action on the diatom genus Nitschia; but no such effect followed E. J. Allen's (1914, p. 429) introduction of the crustacean genus Hemimysis, with its fæces, into artificial sea water, which proved as barren for diatom growth with as without them.

Nathansohn (1906) has suggested that the supply of carbonic acid (CO_2) may temporarily fall below the minimum required for active growth of the phytoplankton, a possibility also accepted by Gran (1912, p. 380); and Moore's calculation [88] that 20,000 to 30,000 tons of carbon are annually converted from inorganic to organic form per cubic mile of water in the Irish Sea emphasizes the vast amount which the flowerings of diatoms and peridinians utilize. More recent experimentation on the dynamics of photosynthesis [89] have shown that when the total available CO_2 has been withdrawn from the bicarbonates present in sea water the latter becomes fatally alkaline, and since sea water has never been found in this state or even approximating it, although many determinations of alkalinity have been made, it is safe to conclude that the growth of marine phytoplankton is never prevented by a shortage of carbon dioxide.

The facts outlined above show that the coastal waters of the Gulf of Maine are probably more fertile for diatoms in spring than at any other time of year with respect to dissolved silica; likewise in nitrogen, one of the other nutrients on which this particular group of planktonic plants chiefly depends. The density and state of vertical circulation of the water also influence their abundance, both by governing the availability of the phosphoric acid and compounds of nitrogen that go into solution on the bottom of the sea and by influencing the flotation of the diatoms themselves.

The influence which the state of circulation of the water exerts on the seasonal abundance of diatoms seems first to have been fully appreciated by Whipple (1905, p. 103) for fresh water, for which it is now accepted generally. Briefly it is as follows: During periods of stagnation (that is, when there is no vertical circulation) the bottom waters of lakes are the seat of active decomposition of organic matter, with consequent increase of ammonia and solution of inorganic substances. When vertical circulation recommences this "foul" water is brought to the surface, where,

[88] Quoted from Herdman (1920 and 1923).

[89] Especially Osterhout and Haas (1918); Moore, Prideaux, and Herdman (1915); Moore, Whitley, and Webster (1921).

under further oxidization, compounds favorable to the growth of diatoms result. At the same time the vertical currents bring diatoms up to the surface from the bottom, where they or their spores had previously been resting, prevented from growth by darkness and lack of available food substances. Once near the surface, they multiply rapidly under favorable surroundings, and this multiplication continues either until the available supply of nutrient substances is exhausted or until a cessation of the vertical currents allows them to settle once more below the fertile and illuminated stratum, when they lie over until the next period of vertical circulation.

In the same way the state of stability of the water, joined to the effects of the river freshets, influences the distribution and availability of the food substances on which diatoms depend for their nutrition in coastal seas such as the Gulf of Maine. As Nathansohn (1906) pointed out, wherever there are upwelling currents these may be expected to bring a rich supply of nitrogenous compounds up to the surface from the deeps, where they accumulate from the decomposition of the rain of dead plankton. In the Gulf of Maine local upwellings are a characteristic event along the western and probably along the northern coasts in spring, following offshore winds (Bigelow, 1914a, p. 394). But here and in shoal boreal seas generally the active vertical mixing by tides, by dominant currents, and by winds, which takes place whenever or wherever the water possesses little vertical stability, is no doubt more effective in dispersing accumulations of dissolved nutritive compounds through the upper strata of water than are the more definite upwellings, because more widespread, given an accumulation of organic detritus on the bottom.

The analyses of nitrogen in samples of mud and sand (p. 472) prove this last requisite fulfilled for the area of the Gulf of Maine as a whole; probably most abundantly so around the coastal zone, where submarine vegetation (Zostera and algæ) and animals (bottom dwellers as well as planktonic) die and decay in vast quantity. Atkins (1923 and 1925) has also emphasized the importance of vertical circulation in making available to the phytoplankton of the upper illuminated layers the dissolved phosphates that accumulate in the deeper strata. As Gran (1912, p. 379) has pointed out, it is in areas where the summer and winter temperatures of the surface differ most that vertical circulation is most active during the brief period (or periods) when vertical stability is lost (a period generally coinciding with the lowest surface temperature), and our first winter's work proved that the Gulf of Maine is a typical example of this.

The physical aspect of this subject has been touched upon in earlier papers (Bigelow, 1914a and 1917) and will be discussed in the third part of the present report.[90] It will therefore suffice to note here that the whole coastal zone of the Gulf and the water over its offshore banks, down to a depth of at least 100 meters, is in such an active state of vertical mixing at the end of the winter and during the first days of spring (when the temperature is lowest for the year and just before the river freshets lower the surface salinity appreciably) that it often carries sand in suspension,[91] not to speak of light flocculent material.

[90] Section 2 of Part II, Vol. XL, Bulletin of the Bureau of Fisheries.

[91] In 1920 we had instances of this on Georges Bank in February (station 20047) and on German Bank on Apr. 15 (station 20163).

In the western coastal zone, south of Cape Elizabeth, and in the basin generally, the vernal period of vertical mixing is brief, its activity lessening as soon as the combined effect of solar warming and of the freshening of the surface increases the vertical stability of the water. This becomes very stable indeed by the early summer with very little interchange taking place between the upper and deeper strata from that time until into the autumn. But strong tidal currents keep the water in the northeastern corner of the gulf in a state of more active vertical circulation throughout the year, especially in the Bay of Fundy, along western Nova Scotia, and locally on Georges Bank. In the Grand Manan Channel, an extreme example, the water is kept practically uniform in temperature from surface to bottom, even in midsummer.

Planktonic diatoms, with their silicious frustules and without power of locomotion, tend to sink unless kept afloat mechanically by some movement of the water. Although sinking is more or less hindered by their spines, slime threads, disclike outlines, etc.,[92] they are more liable to sink than other members of the phytoplankton are, as Gran (1915, p. 136) has emphasized.

The mechanical influence of the state of circulation of the water on the flotation of diatoms or on small objects of any sort is obvious. Indeed, particles as heavy as sand may be kept in suspension by active vertical currents, as just remarked; and from what has just been said it is evident that diatoms are more apt to remain in suspension in the coastal waters of the Gulf of Maine from midwinter on through spring, when the water is actively mixing, than in summer. The flotation of diatoms or of any of the unicellular planktonic organisms is likewise made more easy in winter and early spring than in summer by the more viscous condition of the water during the cold season. The importance of viscosity in this respect, first appreciated by Ostwald (1903), is now so generally recognized (Steuer, 1910; Gran, 1912; Murray and Hjort, 1912) that no general discussion of it is called for here.[93] It is in waters such as those of the Gulf of Maine, where a cold winter alternates with a warm summer in the sea as well as in the air, that seasonal differences in this respect are greatest, because the viscosity of the water depends almost wholly on its temperature within the range of salinities there obtaining (say 27 to 34 per mille). The following table is compiled, in a slightly modified form, from Krummel (1907, p. 282), Murray and Hjort (1912, p. 690), and Murray (1913, p. 102).

Viscosity for sea water of 30 to 33 per mille salinity, 100 being that of distilled water at 0° temperature

Temperature in degrees centigrade	Viscosity	Temperature in degrees centigrade	Viscosity
0	104.5–105.2	5	89.1–89
1	100.4–101.1	10	77.2–77.8
2	97.3–98	15	67.5–68.2
3	94.3–95	20	59.9–60.5

[92] For a summary of these arrangements for flotation see Steuer, 1910, p. 193.

[93] As a homely and extreme illustration of the effect of differences in viscosity in fluids familiar to every biologist, consider how much more rapidly a round cover glass, resting on its flat surface (which we may conceive as representing a Coscinodiscus), will sink in water than in ordinary xylol-balsam, fluids hardly differing in specific gravity but of which the latter is much the more viscous.

With the temperature of the upper strata in the coastal waters of the Gulf only about 1 to 0.5° at its annual minimum when the vernal flowerings of diatoms commence, but rising to upwards of 18° off Massachusetts Bay and even to 20° locally in the center of the gulf in August, the viscosity decreases, say, by 40 per cent (from about 100 to about 60) during the spring and early summer. Consequently, other things being equal, a diatom would sink four-fifths faster in midsummer than during the first days of spring. Other things are not equal, however, because the specific gravity of the water as well as its viscosity decreases with the rising temperature and with diminishing salinity of spring. Thus, the surface stratum is not only a thinner fluid but a lighter one absolutely in summer than in winter, which makes for a still greater disparity between the tendency of diatoms to sink in the cold and in the warm seasons.

It would, perhaps, be safe to say that differences in specific gravity of the water and in its viscosity would necessitate twice as active vertical circulation to hold any given object in suspension in summer as in early spring. As we have seen, however, (p. 481), the reverse actually obtains, the active vertical mixing characteristic of spring giving place to a condition of comparative vertical stagnation in midsummer, consequent on the increasing vertical stability of the water, which must increasingly hinder the flotation of diatoms in the gulf, just as happens in the fresh-water lakes described by Whipple (1905). Thus the seasonal cycle of viscosity and of vertical circulation combined tends to put a period to the seasonal multiplication of the species of diatoms which are characteristic of spring by increasing their tendency to sink.

In the preceding pages I have tried to show that on theoretic grounds the gulf, taken as a whole, offers its most favorable environment for planktonic diatoms in spring, because of the following combination of circumstances: The supply of two of the nutrients on which it is probable that diatoms chiefly depend—nitrogen and silica—is then greatest. (European analyses suggest that this also applies to phosphoric acid.) The circulation of the water then tends to bring up a supply of nitrogen compounds and of dissolved phosphates most actively from below, the high viscosity of the water then most favors the flotation of diatoms, and the increasing strength of the sunlight from late winter on increasingly favors the processes of photosynthesis. It is probable that for abundant flowerings of diatoms all these requirements must be satisfied. Conversely, fluctuations in the amount of any one of the essential foodstuffs may govern the amounts of diatoms actually present at any given time or place, and may even terminate the flowerings if it fall below the requisite minimum.

The parallelism that has actually been shown to exist between the fluctuations in the concentration of silica in the sea water of Massachusetts Bay and of the diatoms there (p. 476, fig. 134) makes this our most suggestive illustration. Without the accumulation of this substance (which takes place during the winter when there are few diatoms to make use of it) the tremendously productive flowerings which we have encountered in spring probably could not take place, any more than they could unless there were enough nitrogen in available form to nourish them. But after the flowerings have abounded for a few weeks in this particular location they so reduce the supply of silica (as the analyses show) by converting it into an unavailable

form (that is, their own shells) that the water becomes unable to support their active multiplication.

It is obvious that the water of the coastal zone north of Cape Ann, along the coast of Maine, and in the Bay of Fundy must continue fertile for diatoms until much later in the year, as is proven by the rich flowerings which take place there late in the spring and in early summer (p. 396). On theoretic grounds this regional difference may have any or all of several causes. First, and probably most important, is the discharge from the rivers, richer in nitrogen, phosphorus, and silica than the sea water with which it mixes. The importance of river waters as carriers of dissolved nutrients is so great that the regions immediately off river mouths might be expected to be richest in diatoms. Though this is not strictly the case in the Gulf of Maine, fuller knowledge may show a closer correspondence between the outpourings from the rivers and the vernal diatom flowerings than is now apparent. Certain facts point in this direction, especially the general parallelism between the season of spring freshets and melting snow, on the one hand, and the date of appearance of the diatom flowerings off different parts of the coast, on the other. Thus, generally speaking, it is off the mouths of the most southerly group of large rivers—Merrimac, Piscataquis, and Saco—between Cape Elizabeth and Cape Ann, where the flood waters from the land are felt earliest in the spring, that the diatoms flower earliest in great numbers. There is no important influx of river water into the gulf south of this, and the expansion of the diatom flowerings around Cape Ann into Massachusetts Bay corresponds roughly with the probable expansion of the "spring current" of land water to the southward past the cape.

The large rivers east of Cape Elizabeth—Kennebec, Penobscot, Machias, St. Croix, and St. John's—come into flood later in the season; correspondingly, the augmentation of diatoms commences later in the season along this part of the coast than farther west and south.

As the outflow from the rivers diminishes in late spring and summer, the sea water might be expected to remain richer in silica, phosphorus, and nitrogen near their mouths than elsewhere—i. e., close along the stretch of coast between Cape Elizabeth and Nova Scotia, which includes all the localities where we have actually found notably rich diatom flowerings in summer (p. 392). In line with this is the fact that Fritz (1921a) did not find it necessary to include silica among the nutrients which she added to sea water at the mouth of the St. Croix River in order to obtain abundant growth of several genera of diatoms there.

The viscosity is likewise more favorable for the growth of planktonic diatoms in the northeastern part of the gulf than in the southwestern in summer, in inverse ratio to the local differences in temperature, the Bay of Fundy at 10 to 11°, for example, offering a much more favorable medium for the flotation of diatoms than Massachusetts Bay at 16 to 18° in the proportions given in the viscosity table (p. 481). A similar regional difference exists, with respect to the vertical circulation of the water, during the warm months of the year, this being least active in the southwestern part of the gulf where the tidal currents are weakest, and most active east of Mount Desert, to culminate in complete and constant stirring of the water from surface to

bottom throughout the season in the Grand Manan Channel and locally in the Bay of Fundy.

These several factors unite to make the coastal zone east of Penobscot Bay on the whole a more favorable environment for diatoms in summer than any other part of the gulf except Georges Bank, to be discussed later (p. 485). Since this theoretic generalization corresponds with the quantitative distribution of diatoms as actually observed during the warm months, the factors just mentioned are probably the chief ones which explain the persistence of rich flowerings of diatoms in abundance in the Mount Desert region and in Passamaquoddy Bay throughout the summer, contrasted with their exhaustion in the Massachusetts Bay region by early May. I have not been able to trace the dependence of particular flowerings on physical or chemical conditions in the sea water more closely than this.

Our failure to find diatoms in as great abundance between Mount Desert Island and Grand Manan as the flowerings farther west, on the one hand, or those reported by Fritz (1921) at St. Andrews at the mouth of the St. Croix River, on the other, is puzzling, for this section of the coastal zone not only receives a considerable influx of land water from several streams that may be expected to be rich in dissolved foodstuffs, but there is a dominant outflow along it from the Bay of Fundy.

No part of the gulf becomes uninhabitable for diatoms even when the water becomes warmest and most stable and flotation most difficult. On the contrary, certain species then reach their maximum development, as an example of which the summer flowerings of Asterionella and Skeletonema will serve (pp. 431, 448). The latter, as it occurs in Massachusetts Bay, is especially interesting because the dates when an abundance of Skeletonema has been recorded in 1915 and 1922 (early autumn and late summer, respectively; p. 476) follow so closely the rise in the concentration of silica recorded for late June in 1921 (fig. 134) as to suggest that it is the accumulation of silica taking place during the late spring and early summer (when there are few diatoms in that region) which makes the water there able to support the autumnal flowerings of Skeletonema.

The general scheme of circulation in the gulf (with the water from the rivers tending to swing westward and to hug the coast line during most of the year, as shown by the distribution of salinity) is a sufficient explanation for the fact that the vernal flowerings of diatoms of its inner parts appear first close in to the land and attain a greater abundance and endure longer there than over the deep basin. The contrast in this respect between the coastal zone and the offshore banks, on the one hand, and the central deeps of the gulf on the other, simply reproduces on a small scale that between coastal or neritic waters and more oceanic regions in general. The gradual expansion of the diatom flowerings offshore from the land out over the central part of the gulf, where it does not reach its maximum until early May (p. 388), follows the offshore dispersion of the spring freshets of land water with their load of nitrogen, phosphorous, and silica.

It is in just such areas as the open basin of the Gulf of Maine, where the transition from a state of free vertical circulation in early spring is sudden to one of very pronounced vertical stability in summer, when the supply of nitrogen and of phosphates from the deeps is thereby prevented, and where the silica content of the

water is probably low except for a brief period in spring while the rivers are in flood, that the vernal flowerings of diatoms are briefest and vanish most completely after their culmination.

The case is quite otherwise on Georges Bank, where one diatom community or another flourishes from late winter to midsummer, but where these flowerings are local by contrast to the extensive vernal flowerings in the inner part of the gulf.

The distance of the bank out from the land and the general distribution of salinity in the gulf forbid the possibility that the nutrients on which its diatoms depend are contributed directly by river water, while hydrography in general equally rules out any possible updraught of nutrients from the ocean deeps, this not being an area of upwelling. Neither can we suppose that the general surface outflow from the gulf reaches the bank especially rich in dissolved foodstuffs, for it is only for a brief period in the spring that the basin of the gulf to the north supports an abundant diatom flora.

Probably the rich animal population of the sea floor of the bank makes the bank itself a richer source for nitrogen than its comparative barrenness in fixed plant growth would suggest. The destruction of plankton that takes place along the meeting zone of cool and warm waters just off its southern face also affords a rich potential food supply for pelagic plants as well as animals, though to what extent the products of this decomposition actually reach the shallows of the bank is a question. With the comparatively active vertical circulation that prevails locally on the bank even in midsummer, tending to sweep any organic débris from the bottom up to the upper layers, whether in suspension or in solution, the bottom no doubt contributes a greater store of assimilable nitrogenous compounds to the overlying sea water than in the deeper parts of the gulf to the north. This applies also to phosphates going into solution from the dead bodies of animals decomposing on the sea floor. Furthermore, the activity of vertical circulation on the bank, combined with low surface temperatures of summer dependent thereon, makes its waters a favorable environment physically for the flotation of pelagic plants, and these factors combined may well account for the summer flowerings there. There is also the interesting possibility that small amounts of silica go into solution from the felspathic sands, pebbles, and gravel that floor the bank (p. 475).

The precise causes of the periodic rise and fall of the peridinian flora are even more obscure than those that determine the diatom flowerings which they replace in summer and autumn, partly because, being less spectacular, they have attracted less attention, and partly because the peridinians as a whole are less obviously dependent upon any one nutrient substance than are the diatoms on a sufficiency of silica. And as I have pointed out (p. 478), the suggestion that the abundance of peridinians depends upon the available supply of phosphates is not borne out by the seasonal succession of this group and of diatoms compared with recent analyses for the phosphate content of the water. Nor is it by any means certain that the seasonal fluctuations of the peridinians mirror the fluctuations in the supply of any one food substance in the water as closely as the diatom flowerings are supposed to do. Since the group as a whole is more thermaphile than most of the diatoms characteristic of the Gulf of Maine, with the three most abundant species of Ceratium following

a regular seasonal succession there, temperature is undoubtedly an important factor in their economy.

Recent studies [94] have brought out the possibility that flowerings of pelagic plants may become self-poisoned under certain circumstances when they are most productive by increasing the alkalinity of the water as they draw CO_2 from the dissolved bicarbonates through the process of photosynthesis, thus increasing the proportionate amount of carbonates and making the solution more alkaline. Moore, Whitley, and Webster (1921) have shown that this change probably does exercise a profound biologic effect in inclosed pools, first killing off the animals (which are much more sensitive to high alkalinity than the plants are) and finally the plants themselves. A slight rise in alkalinity has been found to accompany the vernal multiplication of diatoms, etc., in the Irish Sea (Moore, Prideaux, and Herdman, 1915) from Ph 8.1 to 8.16 in December to Ph 8.2 to 8.4 in spring and summer; likewise from Ph 8.14 in the English Channel off Plymouth in December to Ph 8.27 in May (Atkins, 1923). But none of the determinations of alkalinity that have been made anywhere in the open sea have approached the figure fatal to plant cells (Ph about 9) [95]; and it seems certain that this never happens in the Gulf of Maine (which is one of the less alkaline of seas), a considerable number of tests by Mayer (1922) and at our spring, summer, and winter stations for the years 1920 to 1923 giving a maximum alkalinity of Ph 8.1. In short, it is hardly conceivable that the life or multiplication of diatoms or peridinians is ever hindered in the open gulf by a too alkaline state of the water.

It is also possible that the continued existence of exceptionally rich flowerings of diatoms may become self-limited by lack of oxygen, the dissolved supply of this element being used up, so to speak, in the oxidation of the dead plants, just as the decay of organic matter may reduce the supply of oxygen too low to support animal life in water contaminated by sewage. Whether this ever actually takes place in the open sea is yet to be learned, but it is not likely to be other than an exceptional event and one limited to very special inclosed inlets, probably never occurring in waters subject to as free circulation as those of the Gulf of Maine.

[94] See especially Moore, Prideaux, and Herdman (1915); Osterhaut and Haas (1918); and Moore, Whitley, and Webster (1921).

[95] Atkins (1923) states that he was able to maintain a pure culture of the diatom *Nitschia closterium* in water as alkaline as Ph 9.4.