

The Size of Diatoms.

I. The diameter variation of *Rhizosolenia styliformis* Brightw. and *R. alata* Brightw. in particular and of pelagic marine diatoms in general.

By

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With one Plate and 12 Figures in the Text.

THE investigations of which this paper is a first contribution owe their inception partly to the need of establishing the identity of great patches of the diatom *Rhizosolenia styliformis*, which from time to time interfere with the East Anglian Herring Fishery, and partly to a desire to find out whether there occurs among diatoms the tendency, which appears to be broadly true in the zooplankton, for individual organisms to be larger in colder areas and at colder seasons.

For this purpose the present paper takes the form of a study of diameters. By this means it has been possible to trace the origin of the *Rhizosolenia styliformis* patch arising in the south-west swirl area of the Dogger Bank in 1934 and to establish its independence of another patch system off the Firth of Forth. The consideration of diatom cell diameters in relation to the temperature of the habitat has revealed, so far as it has been pursued, a result that was surprising and quite unexpected. Cell diameters in diatoms, instead of increasing with a lower temperature in the way that zooplankton size tends to do, appear to decrease.

I am indebted to Dr. W. R. G. Atkins and Mr. G. M. Spooner of the Marine Laboratory, Plymouth and to Dr. John Hart of the "Discovery" Expedition for reading the MS. of this paper and for the helpful criticisms and suggestions they made as a result of this.

RHIZOLENIA STYLIFORMIS.

In 1932 and 1933 the diatom *Rhizosolenia styliformis* was particularly abundant in the North Sea and during that time, and also in 1934, the origin and movements of the dense patches in which this species is wont to occur have been subject to extensive investigations which are published elsewhere (Savage and Hardy [16] and Savage and Wimpenny [17]). Here it is sufficient to say that *Rhizosolenia* appears to be a regular inhabitant of the S.W. Dogger Bank Swirl. It is also present in the Firth

of Forth Swirl and there is no doubt that these areas may be seeded from the north by the Atlantic water of which it is an inhabitant. There is no evidence of the species having been observed to enter the North Sea through the straits of Dover.

The observational data in this paper consists of diameter measurements

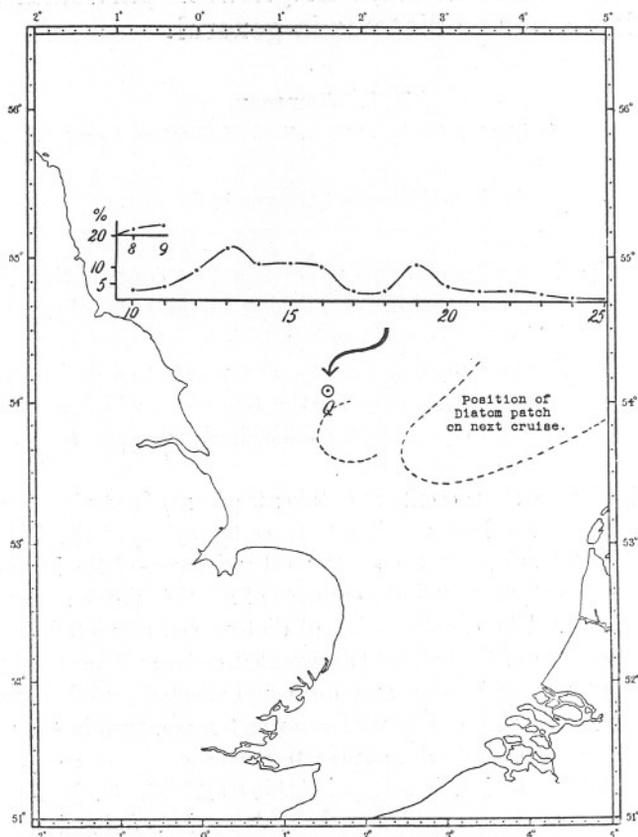


FIG. 1.—The percentage of *Rhizosolenia styliformis* cells at different diameters from station Q, cruise H, October, 1932. The units of the abscissa are approximately equal to 4μ . The position of a dense patch of this diatom is shown by dotted contours.

for samples usually of 100 individuals taken, mainly by the Hensen net, from positions in important patches during the course of the investigation just mentioned. These positions are given in Table I. The measurements (Table II) were made with the aid of a micrometer in a No. 10 eye-piece and using a 4 mm. objective. The arbitrary units thus obtained are approximately equal to 4μ . Care was taken to make the sampling free from bias by spreading a mixed sub-sample on the surface of a ruled slide. Usually

all whole cells cutting a ruled line were measured in succession until the desired number was obtained. In sparse samples both whole and broken cells were measured in this way, and occasionally every available cell, whole or broken, in one or more sub-samples had to be dealt with. The results of these measurements showed multimodal populations recalling

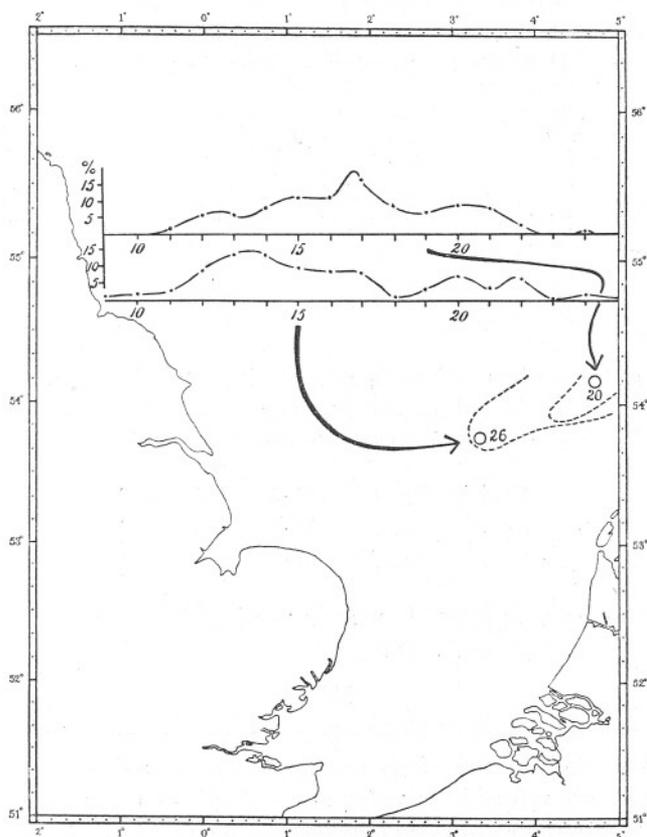


FIG. 2.—The percentage of *Rhizosolenia styliiformis* cells at different diameters from stations 20 and 26 of cruise J, October 1932. The position of a dense patch of this diatom is shown by dotted contours.

those revealed in Wesenberg-Lund's classical work on the fresh-water diatoms of Denmark (19). The observations may now be dealt with year by year.

1932.

In October of this year successive cruises revealed a patch moving round the southern edge of the Dogger Bank. The positions from which measured samples were taken on the two voyages are shown in Text-Figures

1 and 2. The measurements for each length unit are plotted on the charts near the appropriate station and the dotted outlines of the patch on each cruise show the supposed direction of drift. The position shown in Text-Figure 1 is nearer the colder northern water and those in Text-Figure 2, successively further away from this origin. The temperatures at different depths for the three stations considered show the degree to which this was the case. But it is the origin of the water masses rather than the temperature differences which are important.

m.	Cr. H. Stn. Q (Fig. 1)		m.	Cr. J. Stn. 26 (Fig. 2)		m.	Cr. J. Stn. 20 (Fig. 2)	
	°C.	Salinity		°C.	Salinity		°C.	Salinity
0	12.23		0	12.21	34.67	0	12.42	34.78
10	12.23	34.43	20	12.34	34.71	20	12.44	34.64
30	12.23					40	12.43	34.92
50	12.23							
70	12.19							

Bearing these observations in mind it is interesting to note that the cell diameters of the subsequent and warmer samples show an increase in the following progression of their means :

Cr. H.	Stn. Q.	15.3	(14-10-32)
Cr. J.	Stn. 26	16.0	(29-10-32)
Cr. J.	Stn. 20	16.8	(28-10-32)

The increase is also apparent from an inspection of the diameter frequencies plotted in Text-Figures 1 and 2.

1933.

In this year samples of *Rhizosolenia* from populous or relatively populous catches were measured for July and September as well as October. All the samples are referable to patch areas of this diatom whose drift and growth are elsewhere discussed (Savage and Wimpenny [17]). The results are shown in Table II. The July and September samples came from a position near the South-West Patch of the Dogger Bank. Both of these samples seem bimodal at about 12 and 20 units, but while in September the values were rather evenly distributed, in July the majority were grouped around the mode with the lower value. The July *Rhizosolenia* were therefore narrower, the mean being 13.6 units compared with 16.7 in September. The corresponding surface temperatures had meanwhile increased from 13.58 in July to 15.78° C. in September.

The four samples from each of the October cruises all showed the same tendency to be bimodal that has already been referred to. With the exception of Station 28, Cruise K, and Station 35, Cruise L, the mode

at the higher of the two values (*circa* 20 units) was the dominant one and the mean diameters were greater than in the September sample. Stations 28, Cruise K, and 35, Cruise L, consisted mainly of diatoms with narrower diameters and though the water at Station 35, Cruise L, was actually warmer (14.08° C. at surface) than that at another station on the same cruise where the diatoms were wider (Station 30, 12.64° at surface),

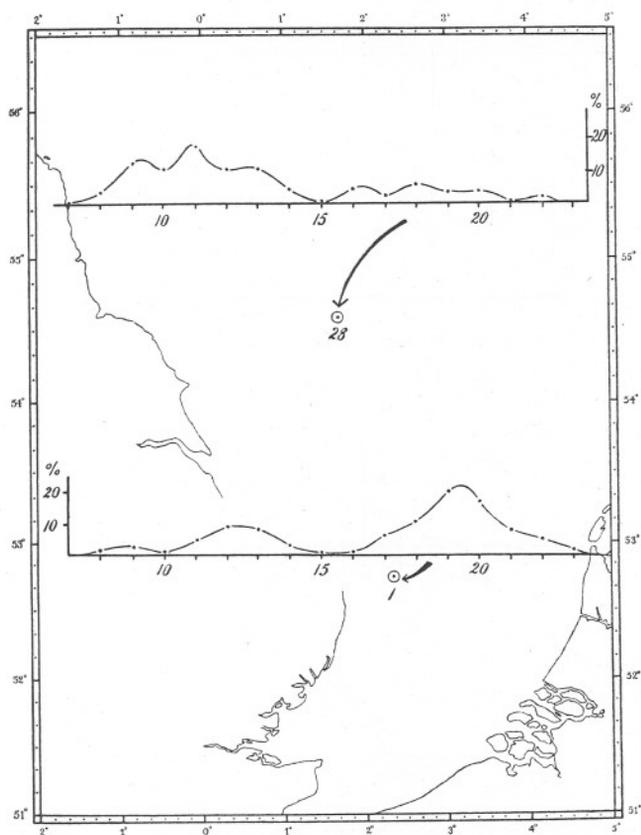


FIG. 3.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 1 and 28 of cruise K, October 1933.

both stations lay in the track of water entering the S.W. North Sea from the thermocline area in the north.

The diameters of the *Rhizosolenia* typical of the north and south parts of the area discussed are shown graphically for the two October cruises in Text-Figures 3 and 4, where the positions of the stations are also given. If we compare the measurements for October, 1933 with those of the previous year (Figs. 1 and 2 with 3 and 4 and Table II) we see that

in 1933 there were more wide diatoms. It may also be added that the species spread further south.

1934.

Though only nine samples were measured in this year, they were more widely spread in time. The first sample was taken from a light patch found off the N.E. coast in May, which was believed to be moving in the

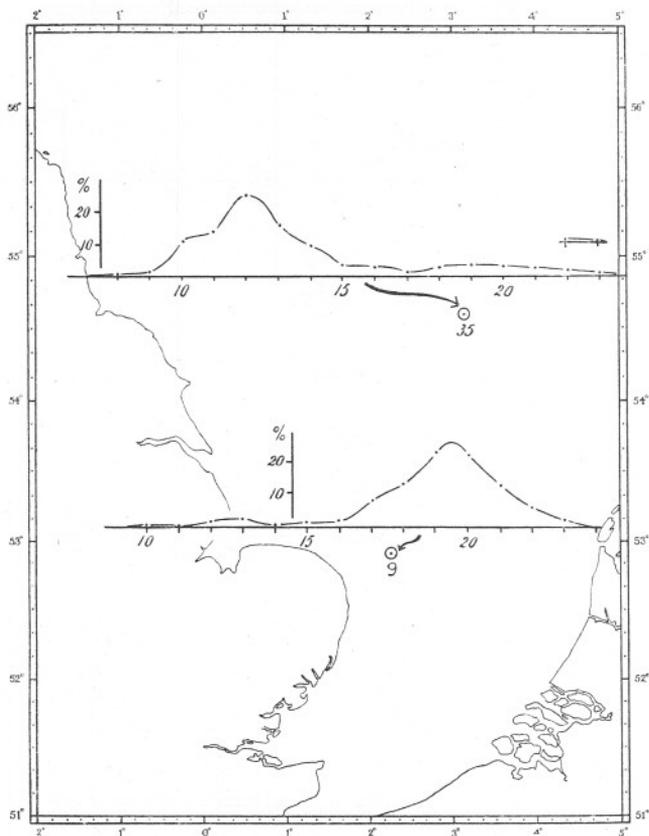


FIG. 4.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 9 and 35 of cruise L, October 1933.

Firth of Forth Swirl (cf., Tait [15], Savage and Wimpenny [17]). The outline of the patch, the position of the station from which the sample was obtained and a diagram showing the frequencies at the different diameter units are shown in Text-Figure 5. It is clear that there is a peak in the measurement scale in the neighbourhood of 10-11. Another series of measurements was taken in June from what was thought to be the same patch system, together with a sample from a different population in the

neighbourhood of the S.W. Patch of the Dogger Bank and probably near or under the influence of the S.W. Dogger Swirl. The surface water in the northern patch was 11.33°C . compared with 7.60°C . the month before and the main group of measurements had a mode between 11 and 12. There were also indications of another group of diatoms at a diameter of 18 units. The increase in size of the principal group is slight and may be

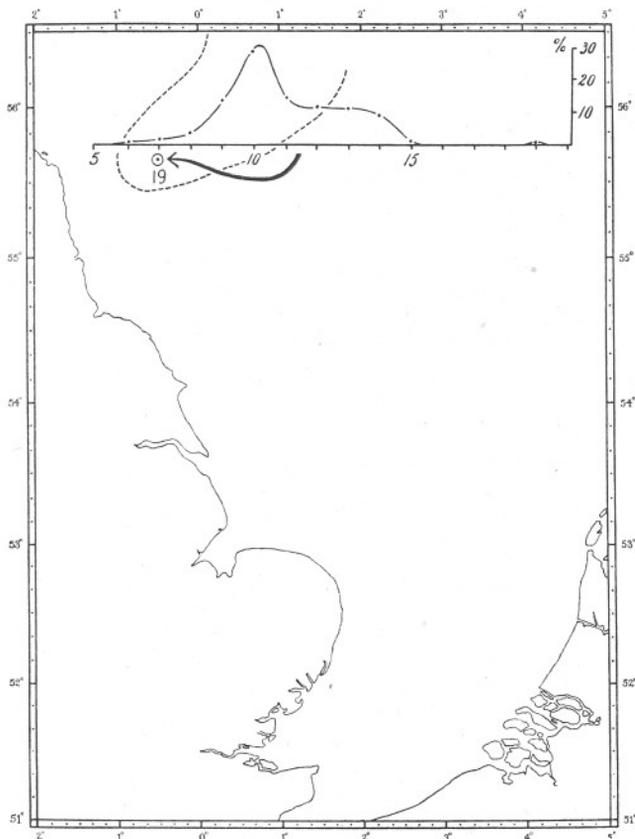


FIG. 5.—The percentage of *Rhizosolenia styliiformis* cells at different diameters from station 19 of cruise C, May 1934. The area of a patch of this diatom is shown by a dotted line.

unreal, but in view of the other occasions in which increase in size parallels increase in temperature, I feel bound to draw attention to it here. The principal mode found in the Firth of Forth area was absent from the sample taken on the S.W. Dogger Bank and, as will be seen from an inspection of Text-Figure 6, the diameter values were rather evenly grouped around 17–18. The mean size of this sample was 17.02 compared with 11.89 from the one further north. The temperatures and salinities

throughout the water column for these two stations show that the southern one was actually hotter and less salt than a comparison of surface values would make it appear.

	Northern Station (E 5)		Southern Station (E 17)	
	T.°C.	Salinity	T.°C.	Salinity
0	11.33	34.97	11.46	34.79
10	11.32	35.02	11.36	.79
20	9.39	.00	10.66	.79
30	8.01	.01	10.58	.78
40	7.59	.01		
60	7.57	.00		

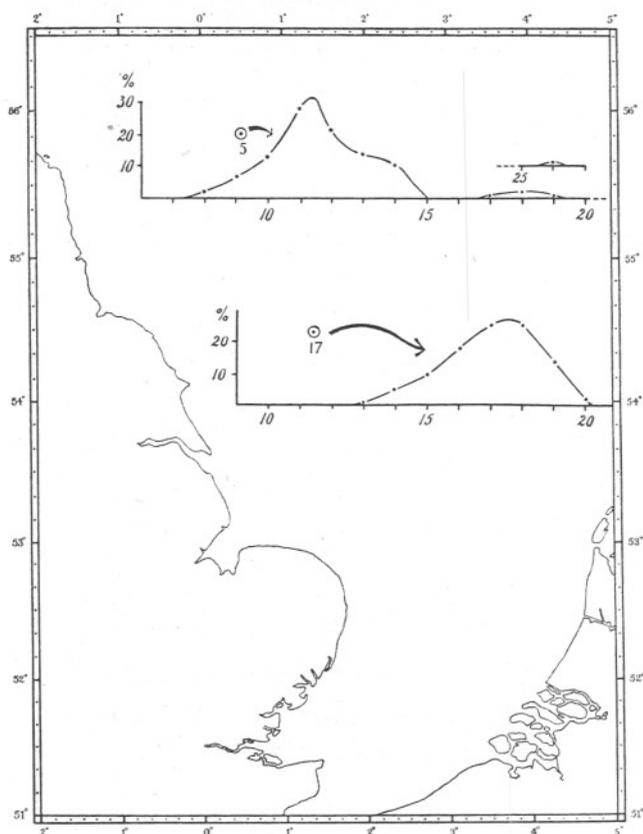


FIG. 6.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 5 and 17 of cruise E, June 1934.

Samples from the S.W. Dogger Bank area are available for July (G5), September (L17), October (M14), and December (Onaway 35 station 6). In July and September the wide diatoms only were present (Table II).

The mode decreased slightly from June onwards though the mean rose to 17.39 and thence fell to 16.15, 15.86 and 15.75, the corresponding surface temperature being 11.46, 15.39, 16.33, 13.04 and 10.93°C. At the end of the year and in October the wide cells are not so homogeneously distributed around a mode and the greater number of cells in these months lies between 15 and 17 units of diameter. The diameters for three stations in October are shown in Figure 7. Station 14 near the S.W. Patch of the Dogger Bank has already been referred to and Station 21, N.E. of the Frisian Islands, is seen to be generally similar, though the surface temperature is much higher (13.04 and 15.13) and the salinity 0.2‰ lower. The remaining position, Station 3, is near that shown in Figure 5 and described as likely to be in the Firth of Forth Swirl. The diatoms from this station fall into two groups, one centred around measurement units 15-17 and the other having a mode at 7-8. The smaller group is similar to that found in May except that the mode has moved back 3 units. The large group is generally similar to those further south. In spite of the small group the mean diameter of the diatoms present at this northern station in October was 12.50 compared with 10.94 in May. In the meanwhile the surface temperature had risen from 7.60°C. to 11.42°C. and the salinity had declined 0.1‰. Conditions throughout the water column were uniform at the May station but in October this was not so as the following list of temperatures and salinities will show.

Depth (m.)	Cr. C. Stn. 19 (May)		Cr. M. Stn. 3 (October)	
	T.°C.	Salinity	T.°C.	Salinity
0	7.60	35.03	11.42	34.89
10			11.38	34.90
20	7.58	35.05	11.32	34.90
30			11.16	34.93
40	7.56	35.05	10.31	34.97
50			9.98	35.09
60	7.43	35.01	9.67	34.94
100			9.11	35.11

Conditions below 40 m. in October approach those of May and it may be that there is some selective distribution of the different sizes of cell throughout the water column. Samples taken at different depths in the Southern Bight do not show any marked differences in size but in these cases the water was nearly uniform in temperature and salinity from top to bottom.

RELATION OF SIZE TO TEMPERATURE.

Of the years 1932-34, 1933 was the year in which the highest temperatures and salinities and the greatest production of *Rhizosolenia*

styliformis were found in the area we are discussing (Savage and Wimpenny [17]). In this year the largest diameters were met with. Also, within each year there was a seasonal difference in size which we have seen may be broadly related to temperature. Below I give a list showing the mean measurements of my series of samples and corresponding temperatures and salinities at 20m.

Cruise	Station*	Date	Mean Size	T.°C. at 20m.	Salinity at 20m.
1932					
H	Q.	14-10	15.30	12.23	34.43
J	20	28-10	16.78	12.44	34.64
J	26	29-10	16.01	12.24	34.71
1933					
F	5	13-7	13.60	13.64	34.74
J	5	19-9	16.70	15.60	34.71
K	1	7-10	17.10	16.34	34.56
K	12	9-10	19.00	15.28	34.70
K	13	9-10	17.60	15.51	34.72
K	28	13-10	12.80	14.59	34.81
L	9	18-10	18.92	14.96	34.56
L	15	19-10	17.40	14.89	34.88
L	30	21-10	18.04	12.64	34.76
L	35	22-10	13.35	14.08	34.85
1934					
C	19	21-5	10.94	7.58	35.05
E	5	15-6	11.89	9.39	35.00
E	17	17-6	17.02	10.66	34.79
G	5	18-7	17.39	14.08	34.79
L	17	22-9	16.15	16.33	34.87
M	3	7-10	12.50	11.32	34.90
M	14	9-10	15.86	13.04	34.71
M	21	10-10	15.75	15.15	34.66
Onaway 35	6	20-11	15.75	10.93	-

The correlation coefficient with temperature is +0.59 and with salinity -0.59. It seems likely that these relations have some significance, for the correlation values just quoted would only arise in a chance manner less than once in a hundred times.

Change in diameter is well known to take place in diatoms (cf. Fritsch [3]). At each division the cell becomes slightly smaller. In the course of time the cell becomes much smaller and an auxospore is formed producing very much wider daughter cells which in turn commence to divide and

* The station numbers of the different cruises do not necessarily correspond.

diminish in size. The diminution in size appears to be slow but the increase is of course sudden. Schütt [13] who has described the auxospore formation of *Rhizosolenia alata* in the Baltic, found the change in mean diameter between November–December, 1884, and March, 1885, as 5.49μ to 5.41μ . In August 1885 the mean diameter was 3.34 ; the auxospores producing a generation at 9.35 which had diminished to 8.32 by September.

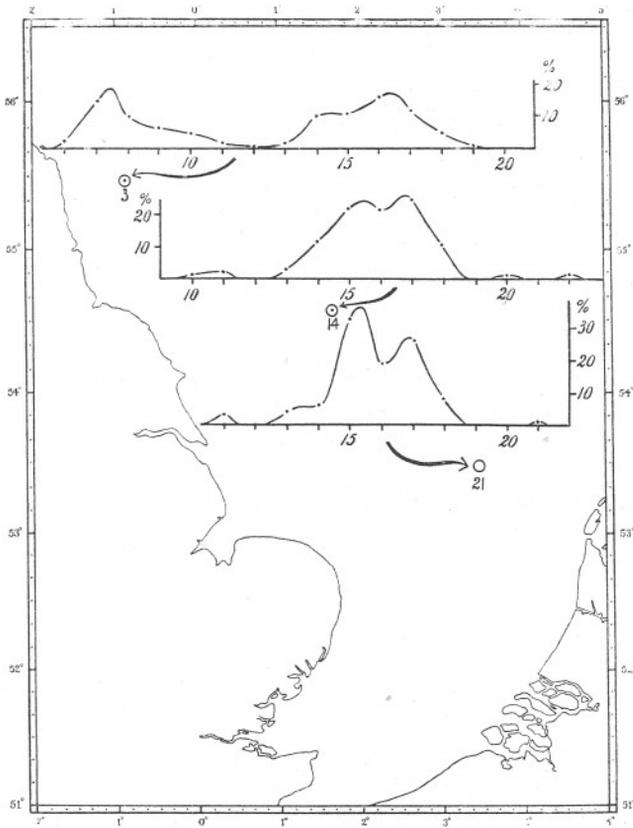


FIG. 7.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 3, 14 and 15 of cruise M, October 1934.

Schütt considers that auxospore formation in this species takes place in August–September each year. The auxospores of *Rhizosolenia styliformis* have been described by Gran (4), who found them in August–September, 1900, between north Norway and Bear Island and also between $41\frac{1}{2}^{\circ}$ and $31\frac{1}{2}^{\circ}$ W Longitude at about $70\frac{1}{2}^{\circ}$ N Latitude. In this case the mother cells measured 22–25 and the auxospore 100—figures similar to the smallest and largest dimensions mentioned in this paper. Auxospore formation in

these two cases, it will be noted, fell at the warmest time of the year. No auxospores were seen during examination of the material discussed here, but the largest sized diatoms dominant in 1933 must have had this origin. Whether the warmer sea temperatures of the Southern Bight had anything to do with auxospore formation one cannot say definitely, but the fact that auxospore formation in the genus occurs at the warmest season makes one think that a warmer year might be especially favourable to it.

Of a progressive diminution of size due to cell division the data affords several examples. A comparison of Text-Figure 1 with Text-Figure 3 suggests that a small group in 1932 had become smaller in 1933. Similarly the large group of October, 1933, seems to be identical with a smaller group in 1934 (compare Text-Figs. 3 and 4 with 7). Finally in 1934 there is a decrease in size of what appears to be the same small group found off the N.E. coast between May and October and a decrease in modal size throughout the year for the larger group found in the neighbourhood of the S.W. Patch of the Dogger Bank.

Apart from auxospore formation and the continuous reduction of size due to cell division there is a survival of larger individuals, even in populations whose modes are growing smaller, which seems likely to be related to increase of temperature. This apparent selection of the wider cells as the patch drifted into areas of higher temperature is shown by comparing the diameter distributions for October, 1932, given in Text-Figure 1, with those in Text-Figure 2 which show conditions a fortnight later. On the later October cruise itself, the sample taken in the warmer part of the patch shows a continuation of this effect when compared with a sample from a cooler part. Again, in 1934, the large group found in the S.W. Dogger Bank neighbourhood increased in average size between June and July parallel to the rise of temperature, although the mode showed a decrease (Table II). In both these cases temperature and salinity rose together.

On the whole, therefore, I am inclined to think that it is increase in temperature rather than decrease in salinity which may operate in a selective way by favouring the larger individuals of a normal strain of cells in a manner discussed later, and possibly by stimulating auxospore formation at a larger size. The general correlation with decreasing salinity is due, perhaps, to the special conditions of the area where the main river outflow and shallower water is found in the warmer south. If this is so the correspondence between small diatoms and high salinity would be fortuitous.

THE RELATION OF LENGTH TO DIAMETER IN *R. styliformis*.

In Text-Figure 8 I have plotted the diameter of 100 cells from Station 35 Cruise L, 1933, against their length measured from the base of each cell

“beak” and not from the tip of the “beak” itself. It will be seen that the cells increase little in length with increasing diameter, nevertheless they do not diminish and so the cells with bigger diameters are in fact bigger cells. The whole question, however, needs a wider investigation.

RHIZOLENIA ALATA.

During a cruise made between October 5–15, this species was met with over a considerable area of the S.W. North Sea and at several stations

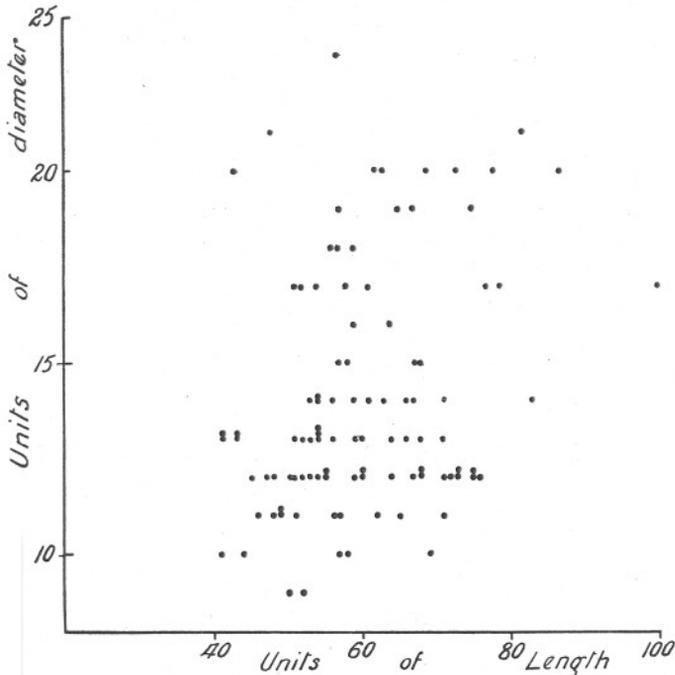


FIG. 8.—The diameter plotted against the corresponding length for 100 cells of *Rhizolenia styliiformis* taken at station 35, cruise L, 1933.

it was noticed to be in the process of forming auxospores. The distribution is shown in Text-Figure 9 where its presence is denoted by a cross and its absence by a dash. Those stations at which auxospores were seen are indicated by a circle round the cross. The southern limit of the area in which the surface water was still cut off from the bottom water by a sharp temperature difference is shown by a strong dashed line. It will be seen that auxospore formation did not take place within the thermocline area but on its edge, where the layering had broken down and where vertical mixing was taking place.

The diatom only occurred densely at Station 8, a position about

30 miles N.E. of Scarborough. Here it appeared to be multiplying briskly and of 50 cells measured for diameter no less than 9 were forming auxospores.

The auxospore of *R. alata* has been well described by Schütt (13) and

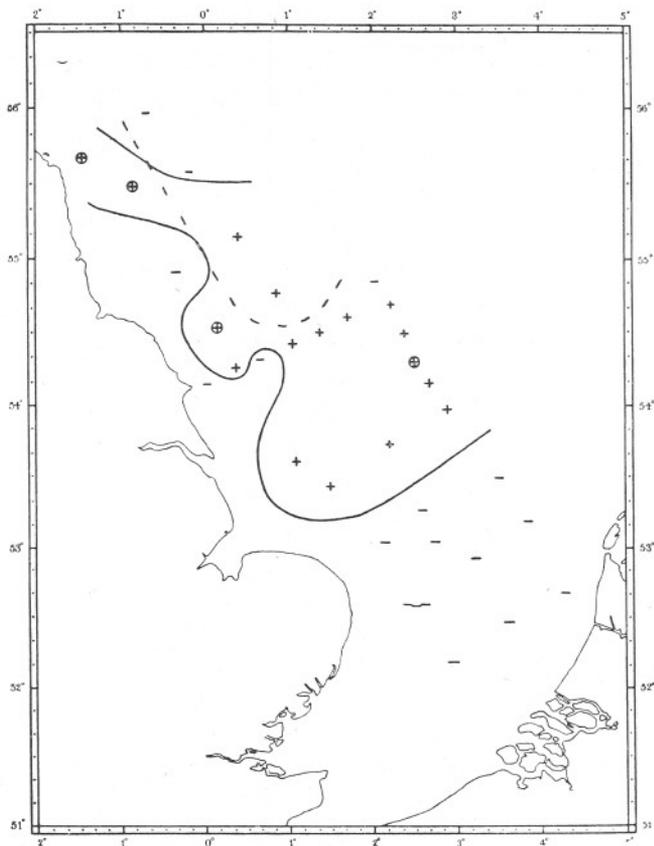


FIG. 9.—The stations of cruise M, October 5–15, 1934. The presence of *Rhizosolenia alata* is denoted by a cross, its absence by a dash. Where auxospore were present the cross is surrounded by a circle. The dotted line indicates the southward and westward limit of the thermocline area and the whole area of distribution is bounded by a continuous line.

the abundant material from my Station 8 is in agreement with his descriptions. Commonly-met stages are reproduced in the photomicrograph of Plate I, as well as in the drawings of Text-Figure 10. There is a difference in the relation of the size of the original cell to the auxospore between my material and that which Schütt collected in the Baltic in August, 1885, which is worthy of note. This is that whilst in my material the auxospore

diameters represented a fourfold increase from approximately 4 to 16 μ , Schütt's comparable increase was threefold—from 3 to 9.

The fifty individuals constituted a random sample of Station 8. Their diameters in μ are given in Table III and are expressed graphically in Text-Figure 11. In this figure the free cell diameters are plotted above the

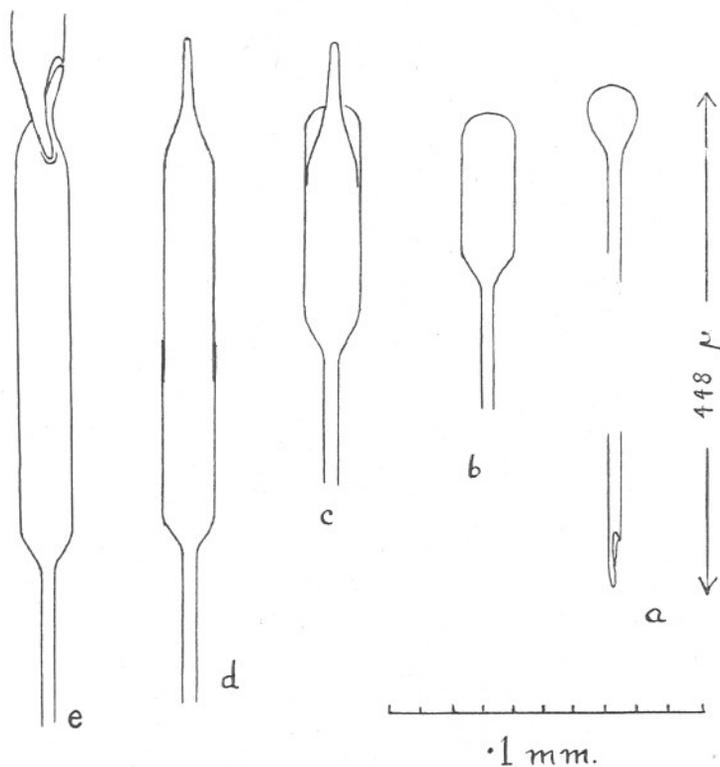


FIG. 10.—Different stages in the development of the auxospore of *Rhizosolenia alata*.

- (a) Auxospore, a spherical capitulum, newly formed at broken end of mother-cell.
- (b) Auxospore capitulum extending as cylinder of increased diameter.
- (c) New calyptra formed within cylindrical auxospore and rupturing distal wall.
- (d) Cell having extended in length and resulting in primary increasing cell of wide diameter.
- (e) Primary increasing cell having divided to produce secondary increasing cell and new wide cell of the daughter generation.

abscissa, whilst below these are expressed the two diameters of each auxospore-forming individual. The wide auxospore diameters are on the right of the diagram and have been distinguished by blackening the area of their distribution curve. The diameters of the original cell to which they belong have been indicated by figures in brackets. The ordinates above and below the line express the results as a percentage which, of

course, does not take into account the black areas. Below I give the individual measurements in μ of the nine auxospore-forming cells of this sample.

Diameter of original cell	Diameter of auxospore
3	12
4	15
4	16
4	16
4	16
4	16
4	16
4	18
5	15

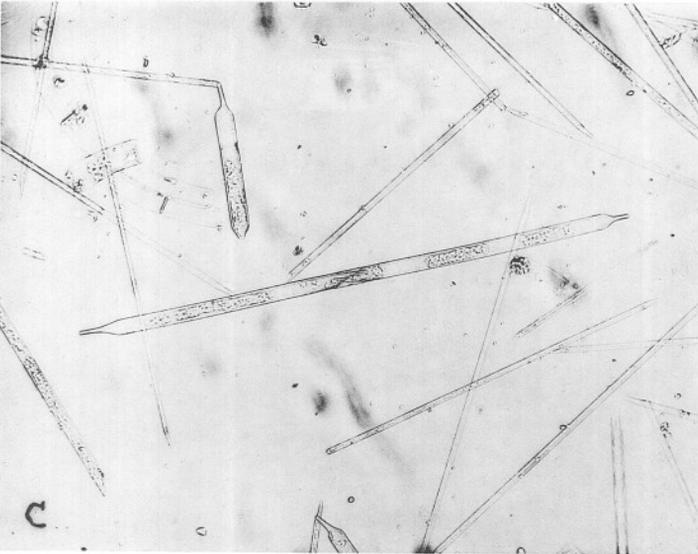
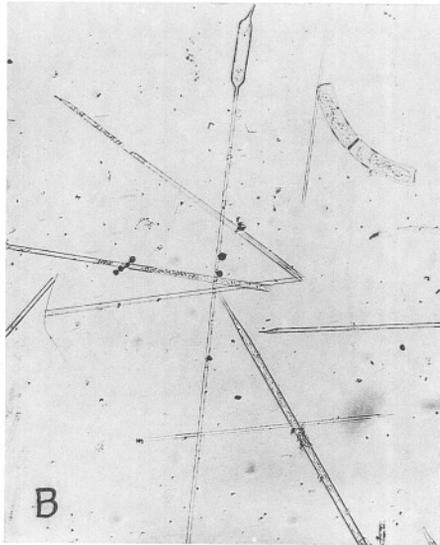
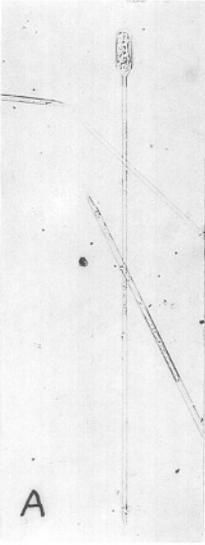
It will be seen that at Station 8, Cruise M, the sample consisted mainly of very narrow cells a considerable proportion of which were forming auxospores. Samples of a hundred cells of the same diatom from each of two stations further to the south and from the same cruise have been similarly measured. The results are shown in the table and figure already mentioned. In these cases there were neither auxospores nor any of the very thin cells, the majority being in the neighbourhood of 12μ in diameter and likely, therefore, to be related to the auxospore generation whose formation was taking place further north.

The general water movements in the area covered by Cruise M, 1934, have been discussed elsewhere by Savage and Wimpenny (17). According to these deductions the water from Station 8 would be moving to Station 17 and turning thence to Station 15. In this case it would be easy to understand that the auxospore generation formed at Station 8 with a diameter of about 16μ would drift southwards, continuing its division and so reducing its size to the mode at about 12μ . If this account of the water movements is correct, it would however be expected that the diameters at Station 15 would be rather smaller than those at Station 17. An inspection of Figure 11 shows that in fact this is not the case and that the cells at Station 15 were on the whole wider than those at Station 17. In these circumstances it is worth while to inquire into factors which

PLATE I.

Photomicrographs of *Rhizosolenia alata* during and after auxospore formation. Magnification $\times 100$.

- A. Auxospore newly formed from mother-cell. B. First cell of increased size arising from the auxospore. C. Newly formed thick daughter cells in process of division.



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might cause a size selection. Temperatures and salinities at different depths at each of the three stations are available and I give them below :

Depth m.	Station 8		Station 17		Station 15	
	T.°C.	S.‰	T.°C.	S.‰	T.°C.	S.‰
0	11.04	34.74	13.98	34.64	15.15	34.95
10	11.00	34.79	13.99	34.72	15.18	34.76
20	10.96	34.74	14.01	34.71	15.16	34.75
30	10.63	34.79			15.17	34.76
40	9.66	34.81			15.17	34.78
50	9.63	34.74			15.17	34.73
60	9.63	34.78				

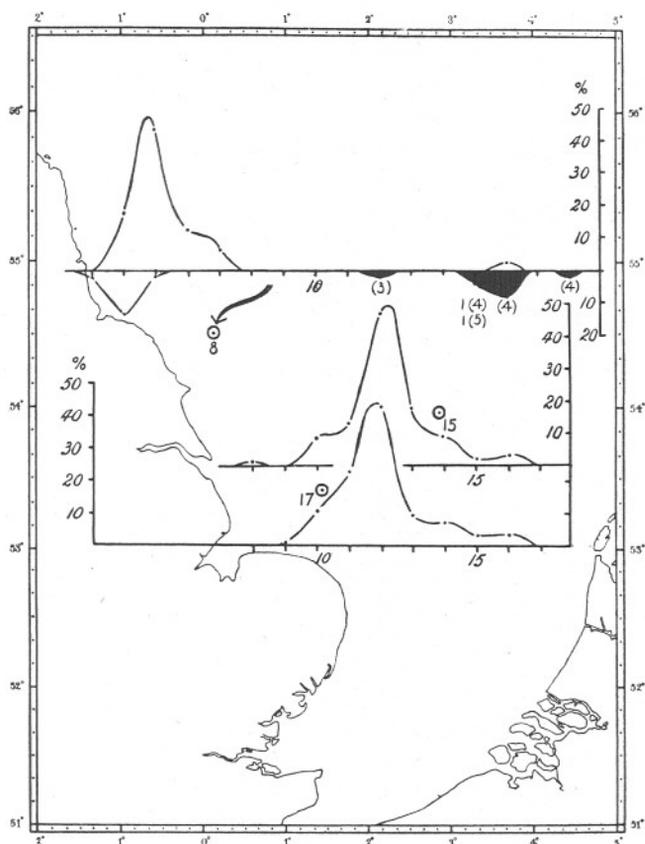


FIG. 11.—The measured diameters in μ for 100 individuals of *Rhizosolenia alata* from stations 15 and 17 and for 50 individuals from station 8 of cruise M, October 5-15, 1934. For station 8, the diameters of the cells of the old generation are plotted above the abscissa, whilst below the two diameters of each auxospore-forming individual. (See also text.)

The thin sample occurred at the station of lowest temperature and for the two stations from which the new generation came it will be seen that the temperature was higher at the station where the cells were of slightly greater diameter.

The salinity does not show any relation to the question of size, for though it decreases from Station 8 to Station 17 whilst there is an increase of diameter, from Station 17 to 15 there is an increase of both diameter and salinity.

THE DIAMETERS OF PELAGIC MARINE DIATOMS IN GENERAL.

The emergence of a relation between temperature and cell diameter in *Rhizosolenia*, whether causal or not, was surprising and unexpected, particularly so in view of the fact that copepods and other zooplankton forms so often diminish in size at higher temperatures.

It therefore seemed useful to examine the size of other pelagic diatoms according to their geographical distribution as a whole and the distribution of species and varieties of the same genera.

Of all diatoms *Ethmodiscus gazellæ* appears to be the largest, the diameter being given by Castracane (1) as 1600μ . This species comes from the warm Atlantic waters near the Cape Verde Islands. Arctic and Antarctic seas do not appear to possess very large diatoms which would appear to be restricted to warmer seas. Small diatoms on the other hand appear to be found in both warm and cold seas, though I hope to show later that more small species are found in the colder seas. It is difficult to say which is the smallest diatom, but it is probable that the Arctic *Chaetoceros filiformis* with a diameter of 3μ is a strong candidate for this record. Using the diameter as the measurement in common use is convenient but it is misleading on occasions. For instance, in the genus *Thalassiothrix*, the cold-loving species is long and hairlike, this length representing the diameter. Actually the cell is so extremely thin owing to its diminutive true length that it is possibly less bulky than its southern congeners. For reasons of which the case just quoted is an extreme example, it is not possible to say with the data available which is the smallest marine diatom.

A consideration of the diameters of species and varieties of the same genus allows us to draw a more definite deduction on the relation of small size to distribution in colder seas. In Table IV I have taken an arbitrary list of species and varieties of which there are more than one in a given genus, and set down their diameters according to their geographical distribution. The list is taken from Dr. Lebour's *The Planktonic Diatoms of Northern Seas* (8), and the species appear in the order set down in that

book. Most of the diameters appear in the work just quoted but in some cases where they do not appear in the book I have been able to obtain them from other authorities, particularly Gran (5). The two species of the genus *Skeletonema* have been omitted as they both appear to be cosmopolitan. The geographical distribution follows the division made by Ostenfeld (10) except that I have divided the group "Temperate neritic" into "North temperate neritic," "Temperate neritic" and "South temperate neritic." In the interests of brevity I have also regarded the small number of littoral and tychopelagic species as neritic. This analysis has been condensed into four groups of genera, which are given below :

Genera showing species of smallest diameters in cold areas.	Genera showing species of smallest diameters in warm areas.	Genera showing species of largest and smallest diameters in cold areas.	Genera showing* species of largest diameters in cold areas.
Melosira	Lauderia	Schröderella	Biddulphia
Coscinodiscus	Leptocylindrus		Thalassiothrix
Chætoceros	Bacteriastrum		
Rhizosolenia			
Thalassiosira			
Stephanopyxis			
Fragilaria			
Asterionella			
Achnanthes			
Navicula			
Nitzschia			
Actinoptychus			
Asteromphalus			

Out of the nineteen genera whose distribution could be dealt with it will be seen that in thirteen of them the species with the smallest diameters come from the colder part of their assumed area of distribution, and in only three genera do the smallest species come from the warmer part of the generic range. For the latter group it is possible that narrower cells of the warm water *Lauderia* and *Bacteriastrum* actually represent bulkier cells, as their length is much greater than in the wider species. One genus has its largest and smallest diameter in cold areas and in the last group there are two genera having their widest species in cold areas. One of the genera of this group, *Thalassiothrix*, has already been discussed, and in the case of *Biddulphia* the reference of the genus to this group and not to the majority group

* Owing to the number of possible combinations this column does not coincide with column 2 as might be expected.

depends upon the inclusion of *Biddulphia arctica* which is a littoral and not truly planktonic species. This series of species known to workers in the North Temperate zone may, therefore, be taken to show a correspondence between small diameters and cold areas.

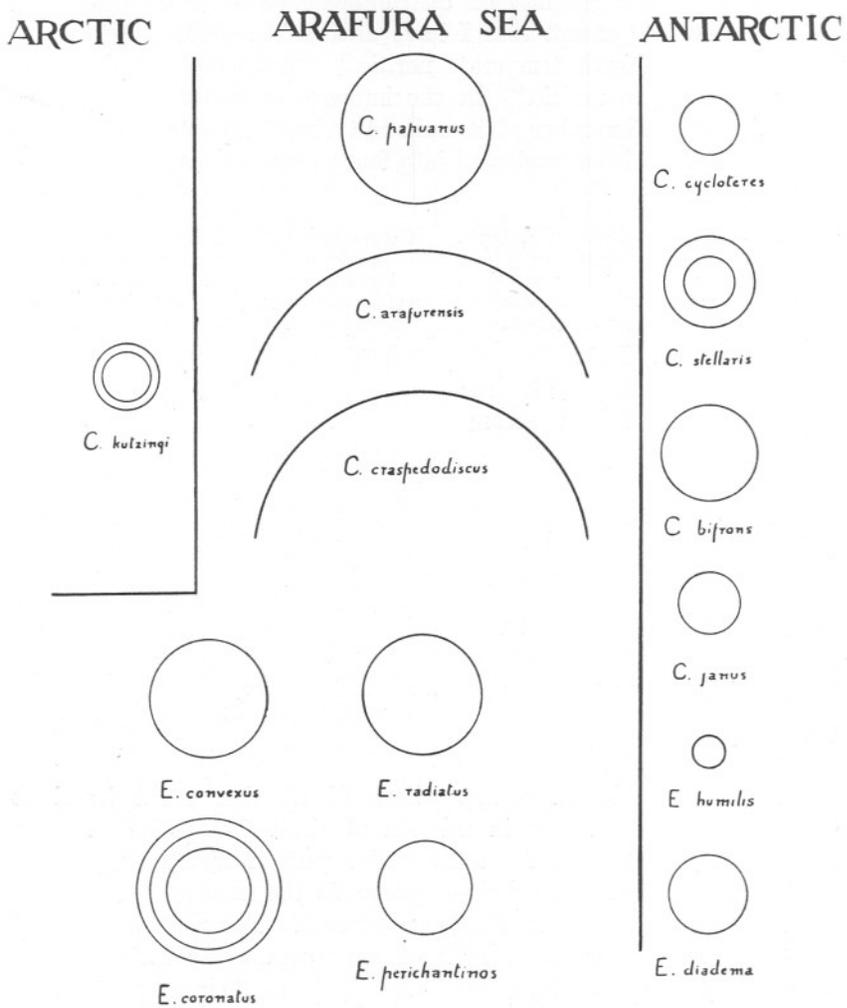


FIG. 12.—Valvar aspect of all species of *Coscinodiscus* and *Ethmodiscus* figured in the Challenger Report on diatoms, as coming from the Arctic, the Arafura Sea, and the Antarctic. Where several diameters are given for one species these diameters represent different varieties. Castracane's nomenclature has been retained.

I have attempted to work out another "random" sample to test the supposed relation between diameter and low temperature, by drawing all the members of the genera *Ethmodiscus* and *Coscinodiscus* that

Castracane has figured in the Challenger Reports (1) as having come from three areas—the Arctic, the Antarctic and the Arafura Sea in the East Indies. These diameters appear in Text-Figure 12 and it will be seen that the smallest of them come from the colder areas in the case of each species.

The following measurements in μ of the extreme diameter values for six genera common to three areas investigated by the "Valdivia" Expedition afford similar evidence:—

	Arctic Ocean	Atlantic Ocean	Indian Ocean
Coscinodiscus	14-280	30-1074	32-544
Asteromphilus	22-136	88	90-180
Actinocyclus	32-124	112-232	26
Dactyliosolen	6-88	22-45	10-28
Rhizosolenia	5-278	10-400	12-272
Fragillaria	6-12	42	50

DISCUSSION.

In the earlier part of this paper it has been shown that there are changes in the diameters of *Rhizosolenia styliformis* cells found in the North Sea, and that these changes are related to spatial and seasonal distribution in such a way as to suggest that temperature is an important influence. The result of experiences in the North Sea would lead one to expect large *Rhizosolenia* cells at high temperatures, and low salinities. Later the general question of cell diameter in marine diatoms was considered, and evidence was brought forward to show that within the limits of certain available information there is a tendency for the species or variety that has the smallest diameter to be found in the coolest part of the generic range. The tendency for diatom size to increase with temperature is thus a deduction common to both sections of the work. The connection with salinity would, however, seem less consistent. Whereas the relation between *Rhizosolenia* size and salinity in the North Sea would suggest a similar inverse one for diatoms generally, it is in fact found that as salinity tends to be higher in the warmer seas, the general relation between diatom size and salinity appears to be a direct one. On account of this inconsistency and on account of the consistency of the temperature relation, I am inclined to think that temperature stands in the more significant relation to diatom diameter.

Let us, therefore, consider the effects that an increase or decrease of temperature might be expected to have on a diatom cell postulated to be floating in equilibrium with its medium, or of diatom cells of the same species suddenly transported to warmer or cooler seas.

1. There would be a tendency for increase in the salinity due to increase

of temperature, which by causing a rise in the specific gravity of the sea water, would cause the cell to rise or would allow a larger cell with relatively less surface to float whereas formerly it would have sunk.

2. The viscosity of sea water decreases with rise of temperature. According to Ostwald (11) this importantly affects the suspension of plankton organisms. Hence a rise in temperature would cause our diatom to fall and would only support a diatom having a greater surface compared with its volume, that is to say a smaller diatom of its own shape.

3. An increase or decrease in temperature increases or decreases the rate of respiration, but it does not follow that this rise will accelerate or diminish assimilation at an equal rate. Indeed, there is some experimental proof that respiration increases more rapidly than photosynthesis with a rise of temperature for *Fucus* (Kniep [7]). In this case a temperature rise might cause respiration to overtake assimilation and cause the death of the diatom. On the other hand a larger diatom with a surface relatively less compared with its volume and a lower metabolic rate to start with, might be able to sustain its vital metabolism. As the division rate of the larger species of diatom is lower than that of the smaller a lower metabolic rate in larger diatoms seems likely.

4. Calcium in the form of its carbonate and bicarbonate is more soluble in cold water. A rise of temperature would therefore mean a little less available calcium. In the open sea Wattenburg (18) has proved that there is less dissolved calcium in the warmer parts. According to Pearsall's views (12) the presence of calcium tends to cause the earlier wall-hardening in *Ceratium hirundinella* and so reduces the size of the cell. The differences in calcium content found by Wattenburg were, however, so small that it is not thought likely that the cell walls of marine diatoms would be noticeably affected.

5. Consider our postulated diatom in its newly-formed auxospore stage. At this time the auxospore is a protoplast surrounded by a thin pellicle and it seems likely that with a rise of temperature the surface tension would be less and the auxospore would therefore assume a larger size.

Changes in specific gravity corresponding to salinity changes are likely to be inconsiderable and might in any case be offset by osmotic effects. For this reason I am not inclined to think the effect important. It should be noted, however, that it would encourage the larger diatoms in the hotter seas if it operated appreciably.

The second consequence works in a direction contrary to all others, in that it would favour smaller diatoms in warmer water. According to Ostwald the viscosity of sea water falls about 2% for each degree rise in temperature and, other things being equal, a passively floating organism would have to increase its surface compared with its volume to keep floating as the temperature rises. This may be done by the development

of specially formed organs or by a diminution in size for organisms of the same shape. The work of Steuer (14), Marshall (9) and Bogorov (2) suggests that diminution of size with rise in temperature is broadly true for the copepods of the zooplankton. For diatoms the balance of the evidence in the present paper indicates increasing size with rise of temperature, and for this reason it is a matter of some importance to note that the opinions expressed by Professor Gran cannot be urged in support of such a generality. Gran (6) says that a number of species show winter and summer or hot water and cold water varieties, in which the summer and hot water forms have a more slender structure and thinner walls, though at the same time their surface is comparatively larger. The more slender types of *Chaetoceros decipiens* found in summer and in the warmer parts of its range, other species of *Chaetoceros*, and *Biddulphia aurita* are cited as examples. A viscosity effect cannot, therefore, be dismissed and may explain some cases but cannot, I think, do so for the majority of diatoms.

The remaining possibilities are largely speculative but it is possible that they all fit the facts and are all involved. The effect of temperature on respiration seems to me the most likely way in which temperature might affect diameter by a selection of the larger cells as it rises. Surely, as temperature rises respiration must be increased, but assimilation may not be able to increase as the needs for it are at times lacking. Now, if the general metabolism, including respiration and assimilation, proceeds in proportion to the relation of surface to volume, those cells with the greatest relative surface—the smallest—will be the first to be adversely affected by a rise in temperature. This selection should take place rather more rapidly than the last two effects, and it is interesting to see, on pages 37, 40 and 46 above, the evidence of a gradual selection in size of *Rhizosolenia* between months and running parallel to the temperature. This apparent selection is particularly interesting between June and July, 1934, where, though the mode shows that the stock is proceeding to get smaller, as a characteristic diatom stock undergoing division must do, the actual mean size is increased as a result of the greater numbers of wider diatoms. The respiration-size effect would be difficult to try out by an *in vitro* experiment, but it seems possible that Pearsall's wall-hardening theory may be dealt with in this way, using very small differences in calcium content, such as are found in the sea. The possibility of there being variations in the size of auxospore on first formation should be cleared up as a result of continued observations at sea, but up to the present there are no indications of wide differences in size, my observations in the southern North Sea in 1932-3 agreeing fairly well with those of Gran made in the Norwegian sea in the summer of 1900.

SUMMARY.

1. The diameters of samples of *Rhizosolenia styliformis* taken in the S.W. North Sea between 1932 and 1934 revealed the presence of large and small populations. The largest diatoms were found in 1933, in which year, or late in 1932, it was thought that auxospore formation might have taken place.

2. The large and small groups mentioned in (1) gave indications of a continuous diminution of size judging by an inspection of their modes. Notwithstanding this there appears to have been some selection of the larger cells, as the whole samples tended to increase in size with a rise of temperature.

3. The correlation coefficient between the temperature at 20m. and the mean diameters was 0.59. That for salinity in the same circumstances was -0.59. The inverse correlation with salinity is thought to be due to the topography of the area.

4. Auxospore formation in *Rhizosolenia alata* was observed on a cruise in October 1934, and was seen to be the cause of a large and small generation in the plankton.

5. Evidence is produced showing that in general the widest diatoms with the largest diameters come from warmer areas and the smallest from cold ones. In this case the relation with salinity would be direct and not inverse as was the case with *Rhizosolenia styliformis*.

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TABLE I.
 DATES AND POSITIONS OF STATIONS FROM WHICH RHIZOSOLENIA
 MEASUREMENTS WERE MADE.

Cruise.	Station.	Date.	Latitude.	Longitude.	No. measured.
H	Q	14/10/32	54° 05'	1° 34' E.	100
J	26	29/10/32	53° 45'	3° 20' E.	100
J	20	28/10/32	54° 10'	4° 45' E.	100
F	5	13/7/33	54° 30'	1° 20' E.	100
J	5	19/9/33	54° 27'	1° 21' E.	100
K	1	7/10/33	52° 44'	2° 19' E.	100
K	12	9/10/33	53° 33'	1° 21' E.	203*
K	13	9/10/33	53° 50'	2° 02' E.	100
K	28	13/10/33	54° 35'	1° 40' E.	100
L	9	18/10/33	52° 55'	2° 15' E.	300
L	15	19/10/33	53° 19'	3° 07' E.	299
L	30	21/10/33	54° 17'	1° 42' E.	300
L	35	22/10/33	54° 36'	3° 08' E.	295
Onaway 25	8	10/11/33	15' N.N.W.	"Tea Kettle Hole"	102
„ 25	9	10/11/33		"Tea Kettle Hole"	300
„ 29	"Tea Kettle Hole"	1/12/33		"Tea Kettle Hole"	100
C	19	21/5/34	55° 40'	0° 29' W.	100
E	5	15/6/34	55° 51'	0° 31' E.	100
E	17	17/6/34	54° 29'	1° 22' E.	100
G	5	18/7/34	54° 14'	0° 21' E.	100
L	17	22/9/34	54° 29'	2° 23' E.	100
M	3	7/10/34	55° 28'	0° 53' W.	100
M	14	9/10/34	54° 35'	1° 41' E.	100
M	21	10/10/34	53° 28'	3° 27' E.	100
Onaway 35	6	20/11/34	54° 28'	1° 41' E.	100

* 100 Hensen, 103 in tow-net at 10m.

TABLE II.

MEASUREMENTS OF *Rhizosolenia styliformis* (DIAMETERS).

Figures denote % frequencies. Top row measurement units.

1932: Cruise H Hensen haul and Cruise J surface tow-nets.

Cruise.	Station.	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
H	Q	2	3	3	4	9	16	11	11	10	3	3	11	4	3	3	2	1	1
J	26		1	2	3	9	14	14	10	9	2	4	8	4	7	1	2	1	
J	20				2	6	6	8	12	12	17	9	7	9	8	3	-	1	-

1933: Hensen hauls.

Cruise.	Station.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
F	5	1	4	7	6	9	20	18	5	6	5	2	1	3	4	5	3	-	1
J	5			2	8	9	10	5	4	3	1	5	4	14	8	13	5	9	
K	1		1	3	1	5	9	8	3	1	1	6	10	20	17	8	5	2	
K	12						1	1	3	3	3	10	11	20	24	21	2	1	
K	13			1	-	2	7	6	6	5	3	9	13	11	21	11	5		
K	28	1	4	13	11	18	11	11	5	1	5	3	6	4	4	1	2		

1933 continued: Tow-net hauls, means of surface, mid-water and bottom.

Cruise.	Station.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
K	12							1	1	3	-	4	11	15	25	15	14	9	1	1		
L	9				.7	.3	2	3	.3	1.3	2	8.7	13.7	23.7	22.7	13.3	6.3	2				
L	15			2.3	2.7	5.4	7.4	6.4	3.3	2	5	2.7	11.7	13.4	14.4	12	9	2		.3		
L	30				.7	3.3	7.3	6	4.7	2	2	5.3	13.4	15	17	12	6	3	1.3	-	.7	.3
L	35	.3	.7	1.4	10.8	13.6	25.1	15.9	9.8	4.1	3.1	1.4	2.7	3.1	3.0	2.4	1.7	.3	.3	.3		
Onaway																						
25	8						2	-	-	1	1	5	7	8	19	15	14	11	7	6	3	1
"	9				.3	.3	.3	.7	.7	1.3	2	4.3	17.7	25.4	21.4	13.3	6	5.7	.3	.3		
"	"Tea Kettle Hole"				1	-	1	-	2	6	6	6	17	27	19	13	7	1				

TABLE IV.

(For explanation see text, p. 46)

	Northern neritic.				Temperate neritic.			Northern Oceanic.			Temperate and sub-tropical.
	Arctic Baltic.	Arctic.	Arctic Boreal.	Boreal.	N. Tem-perate.	Tem-perate.	S. Tem-perate.	Arctic.	Arctic Boreal.	Boreal.	
<i>Melosira</i>											
<i>borreri</i>	.	.	-	-	-	25-60	-	-	-	-	-
<i>hyperborea</i>	.	.	14-30	-	-	-	-	-	-	-	-
<i>Coscinodiscus</i>											
<i>cxentricus*</i> (50-90).	-	-	-	-	-	-	-	-	-	-	-
<i>lineatus</i>	.	.	-	50-60	-	-	-	-	-	-	-
<i>leptopus</i>	.	.	-	-	-	?	-	-	-	-	-
<i>nodulifer*</i>	.	.	-	-	-	-	-	-	-	-	-
<i>radiatus*</i> (30-120)	.	.	-	-	-	-	-	-	-	-	-
<i>centralis</i>	.	.	-	-	-	-	-	-	-	120-300	-
<i>sub-bulliens</i>	.	.	-	-	-	-	-	-	65-150	-	-
<i>commutatus†</i>	.	.	-	-	-	-	-	-	-	-	-
<i>concinuus</i>	.	.	-	-	150-450	-	-	-	-	-	-
<i>granii</i>	.	.	-	-	50-150	-	-	-	-	-	-
<i>pavillardii</i>	.	.	-	-	-	-	-	-	-	150-300	-
<i>curvatulus</i>	.	.	-	45-100	-	-	-	-	-	-	-
<i>subtilis</i>	.	.	-	40-120	-	-	-	-	-	-	-
<i>kutzingi</i>	.	.	50-63	-	-	-	-	-	-	-	-
<i>foergensenii</i>	.	.	50-80	-	-	-	-	-	-	-	-
<i>stellaris</i>	.	.	-	-	-	-	-	-	-	75-175	-
<i>Actinopterychus</i>											
<i>undulatus</i>	.	.	-	-	-	40-140	-	-	-	-	-
<i>splendens</i>	.	.	-	-	-	-	70-180	-	-	-	-
<i>Asteromphalus</i>											
<i>heptactis</i>	.	.	-	-	-	-	-	-	-	50-100	-
<i>hookeri</i>	.	.	-	-	-	-	-	-	-	25-50	-
										(N. Temperate)	
<i>Actinocyclus</i>											
<i>ehrenbergi</i>	.	.	-	-	-	55-156	-	-	-	-	-
						(Cosmopolitan)					
<i>ralfsii</i>	.	.	-	-	-	50-200	-	-	-	-	-
						(More southerly than <i>ehrenbergi</i>)					
<i>Thalassiosira</i>											
<i>nordenskiöldii</i>	.	.	-	12-43	-	-	-	-	-	-	-
<i>decipiens</i>	.	.	-	-	12-40	-	-	-	-	-	-
<i>gravida</i>	.	.	-	-	17-62	-	-	-	-	-	-
<i>rotula</i>	.	.	-	-	-	35	-	-	-	-	-
<i>fallax</i>	.	.	15	-	-	-	-	-	-	-	-
<i>hyalina</i>	.	.	-	16-50	-	-	-	-	-	-	-
<i>baltica†</i>	.	.	-	-	-	-	-	-	-	-	12-15
<i>bioculata</i>	.	.	-	-	30-60	-	-	-	-	-	-
<i>condensata</i>	.	.	-	-	-	17-30	-	-	-	-	-
<i>subtilis</i>	.	.	-	-	-	-	-	-	-	15-32	-
<i>Coscinoseira</i>											
<i>polychorda*</i> (n 24-76)	-	-	-	-	-	-	-	-	-	-	-
<i>ostrupi*</i> (o 10-24)	-	-	-	-	-	-	-	-	-	-	-
<i>Lauderia</i>											
<i>borealis</i>	.	.	-	-	-	34-38	-	-	-	-	-
<i>glacialis</i>	.	.	-	-	36-64	-	-	-	-	-	-
<i>Schröderella</i>											
<i>delicatula</i>	.	.	-	-	-	-	22-28	-	-	-	-
<i>schröderi</i>	.	.	-	-	13-40	-	-	-	-	-	-
<i>Stephanopyxis</i>											
<i>turris</i>	.	.	-	-	-	-	35-65	-	-	-	-
<i>palmeriana</i>	.	.	-	-	-	-	-	-	-	-	80
<i>Dactyliosolen</i>											
<i>antarcticus</i>	.	.	-	-	-	-	-	-	-	38-88	-
<i>mediterraneus</i>	.	.	-	-	-	10-30	-	-	-	-	-
<i>Leptocylindrus</i>											
<i>danicus</i>	.	.	-	-	6-11	-	-	-	-	-	-
<i>minimus</i>	.	.	-	-	-	5	-	-	-	-	-

* Cosmopolitan species.

† Brackish water forms.

TABLE IV. (cont.).

	Northern neritic.				Temperate neritic.			Northern Oceanic.			Tem- perate oceanic.	Tropical and sub- tropical.
	Arctic Baltic.	Arctic. Arctic.	Boreal. Boreal.	Boreal.	N. Tem- perate.	Tem- perate.	S. Tem- perate.	Arctic.	Arctic Boreal.	Boreal.		
<i>Bacteriastrium</i>												
<i>delicatulum</i>	12-40	-
<i>hyalinum</i>	20-55	-
<i>elongatum</i>	7-10
<i>solitarium</i>	38-48	-
<i>Rhizosolenia</i>												
<i>alata f. genuina</i>	7-15	-
<i>alata f. gracillima</i>	5-7	-
<i>alata f. indica</i>	40-70
<i>obtusa</i>	4-8	.	.	-
<i>delicatula</i>	14-20	-
<i>feröense</i>	25-70	-
<i>fragillima</i>	20	-
<i>stolterfothii* (15-40)</i>	-
<i>cylindrus</i>	26
<i>robusta</i>	160-170
<i>shrubsolei* (10-40)</i>	-
<i>setigera</i>	6-25	-
<i>styliformis* (22-102)</i>	-
<i>calcar-avis</i>	30-65
<i>hebetata</i>	4.5-12.5	.	.	-
<i>acuminata</i>	35-50
<i>bergonii</i>	100
<i>castracanei</i>	150
<i>arafurensis</i>	120
<i>Chaetoceros</i>												
<i>atlanticus</i>	15-40	.	.	-
<i>neapolitanus</i>	13	-
<i>janischianus</i>	20-45	-
<i>polygonus</i>	12-15
<i>densus</i>	10-40	-
<i>eibonii</i>	30-45	-
<i>borealis</i>	14-46	.	.	.	-
<i>glandazi</i>	15-20	-
<i>coarctatus</i>	20
<i>convolutus</i>	11-30	.	.	.	-
<i>convexicornis</i>	17-30
<i>concavicornis</i>	12-34	.	.	.	-
<i>danicus</i>	8-20	-
<i>tetrastichon</i>	10
<i>decipiens</i>	12-78	.	.	.	-
<i>mitra</i>	.	.	20	-
<i>lorenzianus</i>	20-50
<i>teres</i>	.	.	.	18-48	-
<i>lauderi</i>	19	-
<i>compressus</i>	.	.	.	22	-
<i>didymus</i>	11-36	-
<i>constrictus</i>	.	.	.	14-35	-
<i>affinis</i>	9-22	-
<i>laciniosus</i>	.	.	.	7-42	-
<i>brevis</i>	20-21	-
<i>diadema</i>	.	.	11-46	-
<i>coronatus</i>	14-19	-
<i>holsaticus</i>	6-24	-
<i>seiracanthus</i>	12-24	-
<i>difficilis</i>	8-10	-
<i>furca</i>	12-14
<i>diversus</i>	10	-
<i>similis</i>	.	.	.	7-17	-
<i>subtilis</i>	5-15	-
<i>wighami</i>	7-15	-
<i>perpusillus</i>	.	.	.	4-5	-
<i>filiformis</i>	.	3	-
<i>exospermus</i>	+	-
						(Brackish water)						
<i>karianus</i>	15	-
<i>fragilis</i>	8	-
<i>crinitus</i>	15-25	-
<i>pseudocrinitus</i>	8-29	-
<i>ingolfianus</i>	9-18	-
<i>curvisetus</i>	10-29	-
<i>debilis</i>	12-29	-
<i>pseudocurvisetus</i>	26	-
<i>adhaerens</i>	28	-
<i>imbricatus</i>	12-20	-

* Cosmopolitan species.

TABLE IV. (cont.).

	Northern neritic.				Temperate neritic.			Northern Oceanic.			Temperate and sub-tropical.
	Arctic Baltic.	Arctic Arctic.	Boreal.	Boreal.	N. Tem- perate.	Tem- perate.	S. Tem- perate.	Arctic.	Arctic Boreal.	Boreal.	
<i>Chaetoceros</i> .— <i>contd.</i>											
<i>externus</i>	-	-	-	-	-	-	10-20	-	-	-	-
<i>scolopendra</i>	-	-	-	-	9-25	-	-	-	-	-	-
<i>cinctus</i>	-	-	-	-	-	-	5-15	-	-	-	-
<i>furcellatus</i>	-	8-20	-	-	-	-	-	-	-	-	-
<i>tortissimus</i>	-	-	-	-	-	11-16	-	-	-	-	-
<i>socialis</i>	-	-	4-5-15	-	-	-	-	-	-	-	-
<i>radians</i>	-	-	-	-	-	-	5-10	-	-	-	-
<i>gracilis</i>	-	-	-	6-10	-	-	-	-	-	-	-
<i>septentrionalis</i>	-	4-8	-	-	-	-	-	-	-	-	-
<i>simplex</i>	-	-	-	-	-	-	6-30	-	-	-	-
<i>ceratosporus</i>	-	-	-	-	-	10	-	-	-	-	-
<i>Biddulphia</i>											
<i>biddulphiana</i> †	-	-	-	-	-	-	60-90	-	-	-	-
<i>aurita</i>	-	-	-	-	30-80	-	-	-	-	-	-
<i>mobiliensis</i>	-	-	-	-	-	50-60	-	-	-	-	-
<i>regia</i>	-	-	-	-	-	-	60-180	-	-	-	-
<i>sinensis</i>	-	-	-	-	-	-	-	-	-	-	90
<i>granulata</i>	-	-	-	-	-	50-80	-	-	-	-	-
<i>rhombus</i>	-	-	-	-	-	50-180	-	-	-	-	-
<i>obtusa</i>	-	-	-	-	-	35	-	-	-	-	-
<i>arctica</i> †	-	-	-	100-300	-	-	-	-	-	-	-
<i>favus</i>	-	-	-	-	-	-	125	-	-	-	-
<i>alternans</i>	-	-	-	-	-	35-50	-	-	-	-	-
<i>vesiculosa</i>	-	-	-	-	-	50-140	-	-	-	-	-
<i>Eucampia</i>											
<i>zoodiacus</i>	-	-	-	-	-	-	25-73	-	-	-	-
<i>greenlandica</i>	-	? 13-20	-	-	-	-	-	-	-	-	-
<i>Climacodium</i>											
<i>frauenfeldianum</i>	-	-	-	-	-	-	-	-	-	-	100
<i>biconcavum</i>	-	-	-	-	-	-	-	-	-	-	35-65
<i>Fragilaria</i>											
<i>islandica</i>	-	13-49	-	-	-	-	-	-	-	-	-
<i>oceanica</i>	-	-	8-40	-	-	-	-	-	-	-	-
<i>cylindrus</i>	-	6-32	-	-	-	-	-	-	-	-	-
<i>striatula</i>	-	-	-	-	-	55	-	-	-	-	-
<i>Asterionella</i>											
<i>japonica</i>	-	-	-	-	-	-	50-85	-	-	-	-
<i>kariana</i>	-	-	-	37-68	-	-	-	-	-	-	-
<i>notata</i>	-	-	-	-	-	-	-	-	-	-	50-100
<i>bleakeyleyi</i>	-	-	-	-	-	-	55	-	-	-	-
<i>Thalassiothrix</i>											
<i>longissima</i> †	-	-	-	-	-	-	-	3000-4000	-	-	-
<i>nitzschoides</i>	-	-	-	-	10-80	-	-	-	-	-	-
<i>frauenfeldii</i>	-	-	-	-	-	-	-	-	-	100	-
<i>Grammatophora</i>											
<i>serpentina</i>	-	-	-	-	-	-	18-127	-	-	-	-
<i>marina</i>	-	-	-	-	-	-	10-104	-	-	-	-
<i>Achnanthes</i>											
<i>teniata</i>	-	11-40	-	-	-	-	-	-	-	-	-
<i>longipes</i>	-	-	-	-	-	75	-	-	-	-	-
<i>Navicula</i>											
<i>membranacea</i>	-	-	-	-	-	-	50-90	-	-	-	-
<i>septentrionalis</i>	-	20-30	-	-	-	-	-	-	-	-	-
<i>granii</i>	-	50-57	-	-	-	-	-	-	-	-	-
<i>pelagica</i>	-	15	-	-	-	-	-	-	-	-	-
<i>vanhöfeni</i>	-	29-45	-	-	-	-	-	-	-	-	-
<i>Nitzschia</i>											
<i>closterium</i> * (20-90)	-	-	-	-	-	-	-	-	-	-	-
<i>frigida</i>	-	45-75	-	-	-	-	-	-	-	-	-
<i>seriata</i>	-	-	-	100	-	-	-	-	-	-	-
<i>delicatissima</i>	-	-	-	?	-	-	-	-	-	-	-

* Cosmopolitan species. † Bottom form or littoral not truly planktonic. ‡ Thread-like.