DET KGL. DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE MEDDELELSER, BIND XVIII, NR. 12

PHYTOPLANKTON STUDIES

1. *NITZSCHIA FRIGIDA* GRUN., AN ARCTIC-INNER-BALTIC DIATOM FOUND IN DANISH WATERS

BY

JUL. GRØNTVED

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

Det Kgl. Danske Videnskabernes Selskabs publikationer i 8vo:

Oversigt over selskabets virksomhed,
Historisk-filologiske Meddelelser,
Arkæologisk-kunsthistoriske Meddelelser,
Filosofiske Meddelelser,
Matematisk-fysiske Meddelelser.
Biologiske Meddelelser.

Selskabet udgiver desuden efter behov i 4to »Skrifter« med samme underinddeling som i »Meddelelser«.

Selskabets sekretariat og postadresse: Ny vestergade 23, København V.

Selskabets kommissionær: *Ejnar Munksgaard*, Nørregade 6, København K.

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Printed in Denmark
Bianco Lunos Bogtrykkeri.

1. Introduction.

In 1896 P. T. Cleve (1896b, pp. 3—4) published a report on the discovery in the Baltic of some pelagic species of diatoms, previously known only from Arctic seas: *Coscinodiscus lacustris* var. *hyperboreus*, *Achnanthes taeniata*, *Chaetoceros septentrionalis* (? *C. gracilis Schütt*) and *Navicula septentrionalis* (= *N. Vanhöffenii* Gran).

The intensive plankton investigations of the following decade gave information regarding the occurrence of still other Arctic plankton forms in the Baltic during the winter and spring, but also showed that some of the species in question occurred in the waters which now connect the Arctic seas with the Baltic. Referring here only to the diatoms of the plankton, the following species may be regarded as having a bicentric distribution, being stationary on the one hand in the Arctic seas and on the other in the Baltic: *Achnanthes taeniata* Grun., *Melosira arctica* (Ehrh.) Dickie, *Navicula Vanhöffenii* Gran and *Nitzschia frigida* Grun. Where they have been observed outside these areas, they may be regarded as more or less chance occurrences, even though they may locally occur in great abundance where the ecological conditions have at times been favourable for their reproduction.

According to more recent investigations (Leegaard 1920; Cleve-Euler 1937) this group also includes *Fragilaria cylindrus* Grun., *F. islandica* Grun., *F. oceanica* Cleve, *Thalassiosira hyalina* (Grun.) Gran and possibly a few more.

The Baltic species referred to may be regarded as relicts of the time when there was a direct connection between this sea and the Arctic waters (Cleve 1897, p. 8; Jørgensen 1912, p. 10; Leegaard 1920, p. 39).

The present work received its stimulus from finding *Nitzschia frigida* in Danish waters in Kattinge Bight, one of the innermost branchings of the Isefjord water system. The sample in question, given me by Dr. Aa. Jensen, Dansk Biologisk Station, for investigation, consisted of melting water from the underside of an ice-layer which was about 70 cm. thick, coloured greenish in the lowermost few cm. by the organisms contained in it. I owe thanks to Dr. Jensen for giving me the sample together with Table 2 displaying the hydrographical conditions at the spot where the sample was taken. To Dr. K. J. Purasjoki, Helsingfors, too, who has put me in possession of *Nitzschia frigida* material from Levander's collections in the Gulf of Finland, I would tender my best thanks. During the preparation of this work I have had the opportunity of seeing slides from E. Østrup's great collections of diatoms, now found in the Botanical Museum of Copenhagen University; I wish to thank the Inspector of the Museum, Dr. phil. O. Hagerup, for the loan of these slides.

2. The Morphology of *Nitzschia frigida.*

Nitzschia frigida Grunow 1880, p. 94, Taf. V, Fig. 101. — ? Østrup 1895, p. 447, T. VIII, Fig. 99. — Cleve 1896a, p. 12. — Vanhöffen 1897, p. 264, T. IV, Fig. 1. — Gran 1897a, p. 10, T. I. Fig. 11. — Gran 1905, p. 129, Fig. 173. — Jørgensen 1905, pp. 103—104. — Meunier 1910, p. 335, Pl. XXXIV, Fig. 36. — Lebour 1930, p. 212, Fig. 177. — Ussatschew 1935, p. 75.

Original diagnosis: Bisher nur in ganzen Frusteln beobachtet, welche stets in der Mitte etwas weiter wie an den Enden sind. Kielpunkte klein, 7—9 in 0.01 mm., die mittleren zwei entfernter, mit Andeutungen eines Centralknotens zwischen ihnen, Querstreifen sehr zart, über 35 in 0.01 mm. Länge 0.045—0.075 mm., Breite 0.008—0.0125 mm. Karisches Meer. Eine ähnliche Form mit 9—10 Kielpunkten sah ich von Novaja Semlja.

Description: The form of the cell in valve view is linear, narrowing towards the ends (Fig. 1 (right)); in girdle view the cell form is approximately linear-lanceolate (cp. Pl. I, Fig. 2f). Length[1]: 33—81 μ; breadth (in valve view): 5.6—12.5 μ; 2 chrom-

[1] As in the diagnose the cell length and breadth here mean the length of the apical and transapical axis respectively.

atophores separated by the cell nucleus lying centrally; the valve is linear with truncated ends (Fig. 1 (left)). Breadth[1]: 4.5—5.5 μ; keel eccentric with 7—10 keel-points in 10 μ; there is a weakly developed central nodule between the 2 midmost keel-points (Fig. 1); the striae of the valves are very faint[2]; the cells form irregular colonies which at some places are branched like a tree, in other parts the cells are connected linearly or in zig-zag formation (Pl. I, Fig. 1).

In a diatom material from an East Greenland coastal area (73°14′ — 75°37′ N. Lat.) ØSTRUP found a species which he refers—with some doubt—to *Nitzschia frigida* (ØSTRUP 1895, p. 447, T. VIII, Fig. 99a—e); ØSTRUP's figures are reproduced here in Fig. 2a—e. 2a is undoubtedly *N. frigida*, but 2d showing a valve view and 2b—c showing an oblique position are not this species; it has a rhomboid form with central keel, whilst *N. frigida* has a linear valve with eccentric keel. ØSTRUP states that the species in question usually took up the position in the slides shown in Fig. 2a, but it was also sometimes observed in an oblique position, as shown in 2e; it was only in special preparations that he succeeded in seeing it in valve view (Fig. 2d). If ØSTRUP's Figs. 2a and 2d represented the same species, practically all solitary cells (and ØSTRUP no more than the original diagnosis mentions formation of colonies) would take up the position shown in Fig. 2d, as they will settle on the broadest side; however, the opposite was the case, and it may be concluded from this alone, that Figs. 2a and 2d do not belong to the same species. ØSTRUP does not seem to have seen cells like Fig. 2d in girdle view and he has not seen isolated *N. frigida* valves.

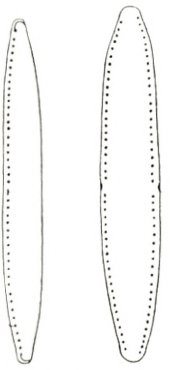

Fig. 1. *Nitzschia frigida;* valve (left) and frustula (in valve view). Kattinge Bight $^5/_3$, 1947. (×1000).

A transverse section of the *N. frigida* cell shows a rhomboid figure with diagonally placed keels at the pointed angles of the rhomboid; in glow preparations isolated cells almost always are placed on one of the valves and the keels are lateral; in

[1] Neither Grunow nor any of the other authors dealing with the morphology of the species has seen isolated valves; the breadth given here for the valve comes from measurements on the Kattinge Bight population, which consisted of rather small cells; thus it cannot be taken to cover the whole range of variation.

[2] Apart from the original diagnosis there is nowhere any information about the number of striae, and the present author has not been able to determine it either.

colonies, on the other hand, where the single cells are held in position by their connection with the neighbouring cells, the keels are not rarely seen centrally in the cell, which in this position has an almost linear-lanceolate circumference (cp. Pl. I, Fig. 2f). MEUNIER (1910) in a drawing of an *N. frigida* colony (Pl. XXXIV, Fig. 36) shows some cells in this position and regards it as a valve view; it is an oblique girdle view.

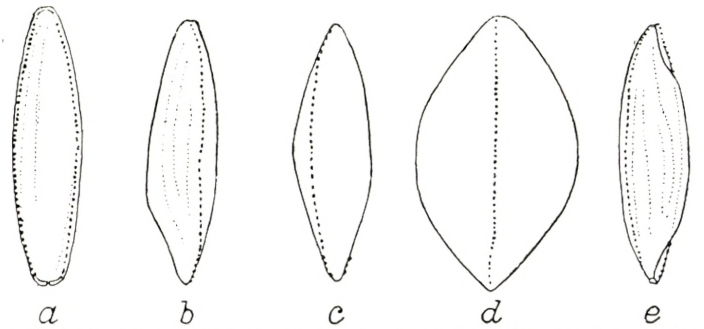

Fig. 2. *Nitzschia frigida*? (from Østrup 1895, T. VIII, Fig. 99). (×600).

3. The Geographical Distribution of *Nitzschia frigida*.

The geographical distribution of *N. frigida* is shown in Figs. 3 and 4, where a filled-in circle marks a finding place with this position; in Fig. 3 also shaded places indicate areas within which the species is said to be found, but without precise information about the localities; not marked in this Fig. we have the following summary data of finds of *N. frigida:* CLEVE and GRUNOW 1880, p. 94 (Novaja Semlja, Karisches Meer); CLEVE 1898, p. 26 (Barents Meer). When CLEVE (1883, p. 481) gives the species from Discovery Bay this seems to be a mistake and the locality in question therefore is not marked on the map.

The sources in the literature forming the basis of the distribution maps are the following; for the Arctic region (Fig. 3):

ØSTRUP 1895, p. 447; CLEVE 1896, p. 12; VANHÖFFEN 1897, p. 264; GRAN 1897a, pp. 2, 10; GRAN 1897b, p. 133; CLEVE 1900a, p. 6; CLEVE 1900b, p. 334; GRAN 1900, pp. 62—63; GRAN 1902, p. 181; Bulletin des Résultats, etc. Année 1902—1903, p. 163; GRAN 1904, pp. 515, 544; JØRGENSEN 1905, pp. 76, 80, 84, 103, 104; BROCH 1909, Table I; OSTENFELD 1910, p. 281; MEUNIER 1910,

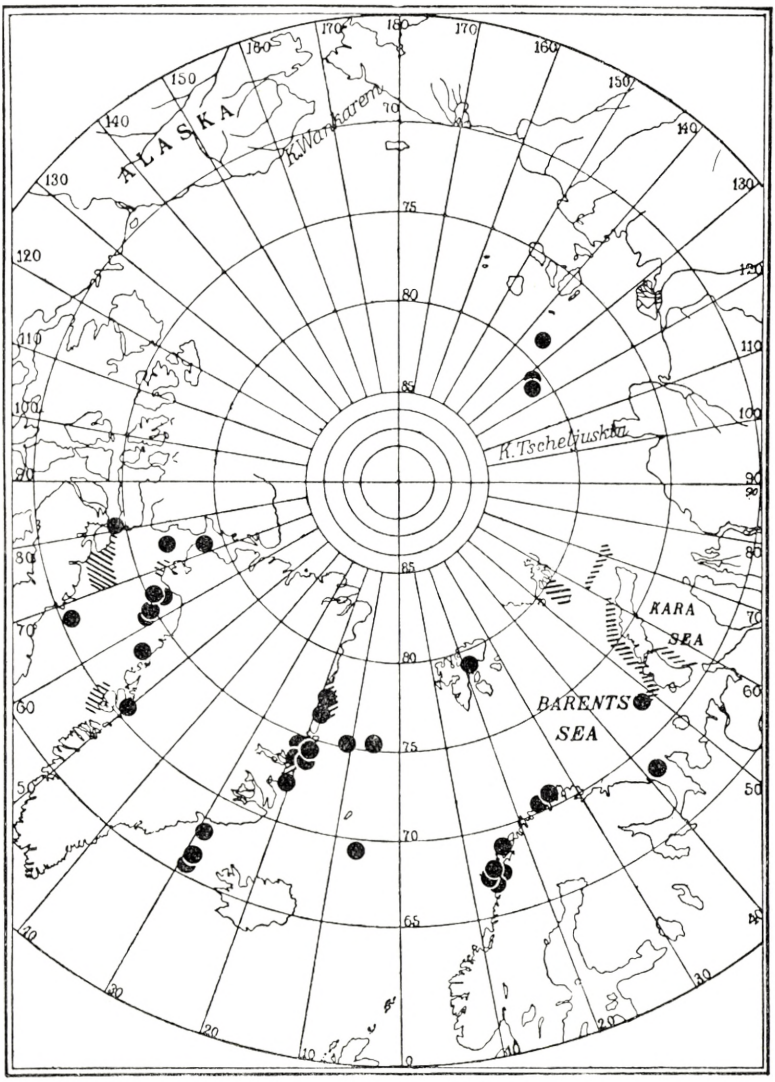

Fig. 3. Distribution of *Nitzschia frigida* in Arctic seas.

p. 336; Ussatschew 1935, pp. 14, 30, 75; Braarud 1935, pp. 97, 138, 160, 164; Grøntved and Seidenfaden 1938, pp. 52 seq., 137 seq., 350, 363, 366.

And for the Baltic distribution (Fig. 4):

Bulletin des Résultats, etc. Année 1902—1903, p. 148; Année 1903—1904, pp. 148, 150, 152; Année 1904—1905, p. 138. Bulletin

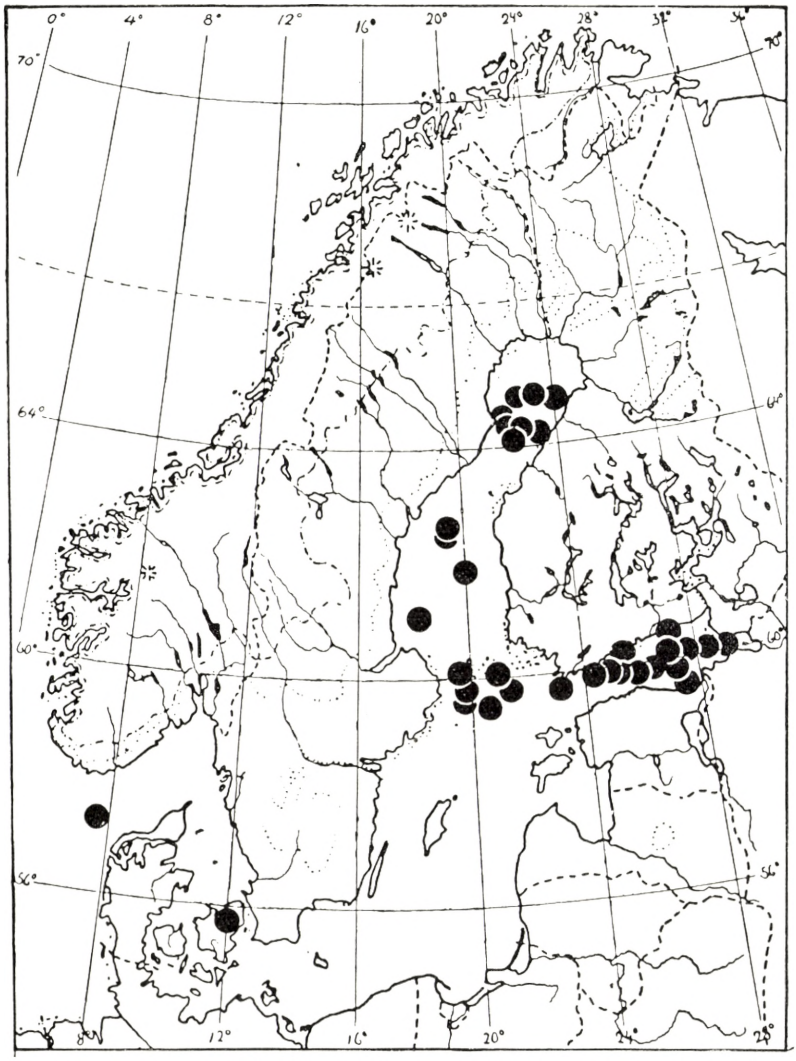

Fig. 4. Distribution of *Nitzschia frigida* in the Baltic; on the chart also the Danish finds in Kattinge Bight and one in the North Sea.

Trimestriel, etc. Année 1905—1906, pp. 96, 98. Bulletin Planktoniques, etc. Années 1908—1911, pp. 23, 24—25. VÄLIKANGAS 1926, p. 279, LEVANDER 1947, pp. 5, 7, 13, 19, 21, 31, 32, 35, 39.

Fig. 4 likewise shows the Danish finds in Kattinge Bight; furthermore one made in the North Sea (57°32′ N.; 7°36′ E.) in November 1906, which is mentioned in the Bulletin Trime-

striel, etc. Année 1906—07, p. 53; this may have been an occasional occurrence, probably carried out by the current from the Baltic.

The two distribution maps (Figs. 3 and 4) show that *N. frigida* has a bicentric distribution; apart from the larger area in the Arctic it occurs also in the smaller inner-Baltic; in the latter it seems reasonable to regard it as a relict (see Introduction).

Nitzschia frigida is a neritic species, but like a number of other Arctic-neritic diatoms it is "in irgend einer Weise vom Eise abhängig" (Gran 1904, p. 545); when it has been found far from the coast it has always been with or near the ice.

4. *Nitzschia frigida* in Kattinge Bight.

Kattinge Bight is a small sheltered bight in the innermost part of Roskilde Fjord (Fig. 5), which again branches off from the Isefjord; the latter has its outlet on the north coast of Sealand and thus stands in direct communication with the Kattegat. In a small central part the depth in the bight is ca. 12 m., but for the rest the bottom is fairly level outside the 4-m. curve, which runs at a short distance from the shore; there is a freshwater inlet in the south-western corner, to the east it has a narrow connection with Roskilde Fjord, ca. 3 km. from the place where the fjord receives the sewage of the town of Roskilde.

On $^5/_3$, 1947, when Roskilde Fjord and Kattinge Bight were covered with ice about 70 cm. thick, Dr. Aa. Jensen carried out hydrographical investigations under the ice at Stations 1—4 (see Fig. 5 and Table 2); at St. 3 and St. 4 the underside of the ice was strongly green-coloured in a layer of some cm.s thickness; a sample of the melting water from this coloured ice from St. 3 was preserved and given to the present author for examination; the sample proved to contain *Nitzschia frigida* cells to the number of ca. 1.1×10^6 per cm^3, in addition a green flagellate also in strong concentration; otherwise no plankton organisms were present.

In the rich *N. frigida* material there was a good opportunity of making a morphological study of the species; reference to this has been made in a previous section; here it is only necessary to

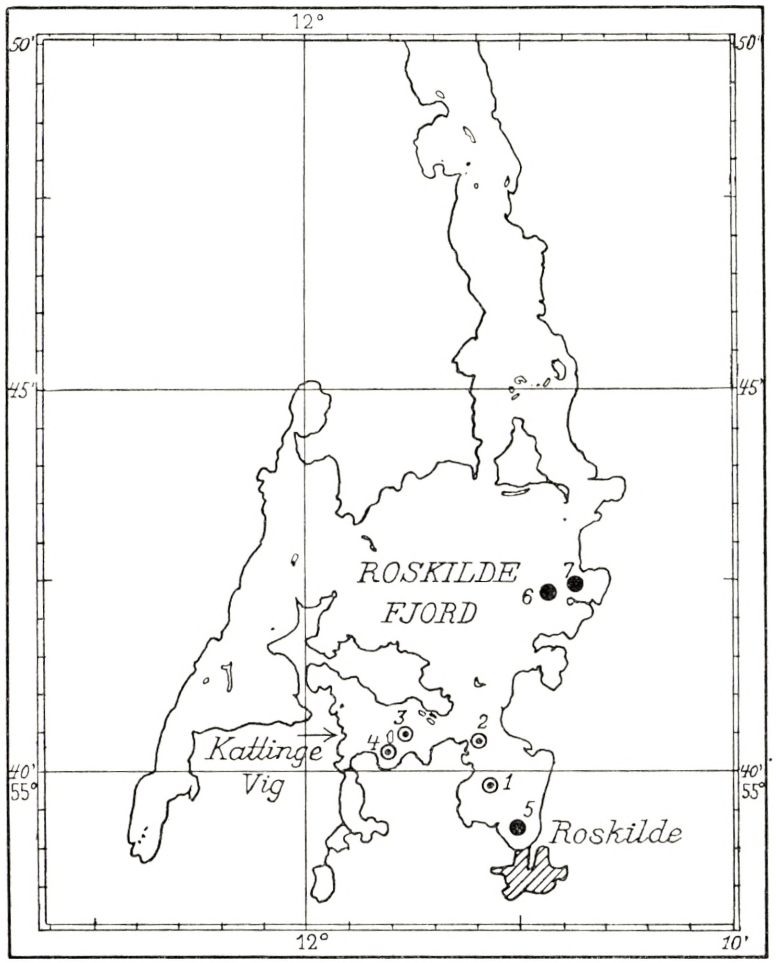

Fig. 5. Chart of the inner part of Roskilde Fjord with Kattinge Bight, showing the stations (1—7) where collections were made—$^{5}/_{3}$ and $^{18}/_{3}$, 1947.

give the results of measurements of the cell length in this population and—for comparison—the corresponding values from a plankton sample from the inner-Baltic area of the species.

Only one specimen was measured in each colony; in the somewhat sparse Porkala material 200 measurements were made as against 1000 in the sample from Kattinge Bight.

The length of the Kattinge Bight cells varies from 38 to 50 μ, whilst the variation in the Porkala material covers a range from 33 to 70 μ; such a difference between a uniform and a more mixed

Table 1. The cell length of *Nitzschia frigida* from Kattinge Bight ($^{5}/_{3}$—47) and from Porkala in the Gulf of Finland ($^{20}/_{4}$—04).

Units of measurement 2.5 μ	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total number
Kattinge Bight.....			2	53	357	417	155	16									1000
Porkala	1	5	22	22	34	32	20	23	15	10	7	5		2	1	1	200

population might be expected; Kattinge Bight is a fairly isolated area and *N. frigida* is not known in its neighbourhood, whereas the plankton station in Porkala stands in open connection with the rest of the Finnish coastal waters where the species has often been observed. It should be noted, however, that the measurements from the two localities are not directly comparable, since the Porkala material was taken by means of a plankton net, which filters a relatively large mass of water, whereas the sample from Kattinge Bight came from melting water from the underside of the ice and the measurements in this sample thus are only average values for the 100 cm^3 mass of water contained in the sample bottle. The result of the measurements cannot, therefore, be taken as decisive evidence that the stock in Kattinge Bight, in agreement with the small variation in size of individuals, comes from a single or some few mother cells, and that the Porkala material has a more diverse origin. The measurements only apply to the two available samples, but these are not to the same degree representative of the populations in question as a whole.

There can be no doubt that the development of the stock of *N. frigida* found in the Kattinge Bight actually occurs on the spot and that the density of the organisms has been greatest in the uppermost layer, where the light is relatively strong, though reduced by the passage through the ice. With regard to the need for light, to judge from the occurrence in Kattinge Bight and elsewhere (e. g. Vanhöffen 1897, p. 264; Gran 1897 a, p. 2), *N. frigida* may be considered a "shadow-species", which carries on assimilation by very faint light. Directly under the ice cell division has continued in rapid succession, a considerable number of individuals being in process of dividing up, and the development of the numerically strong population must have taken place in a fairly short time, as is also evident from the fact that organisms in

macroscopically appreciable quantities were only found in the lowermost few cm. of the ice.

In addition to the light the content of dissolved nutrient salts is a factor with a direct influence on the plankton production and the development of a plankton like the one in question must have required a great consumption of nutrient materials. In culture experiments ATKINS (1923, pp. 22—23) found that 1.12 mlgr. P_2O_5 is necessary for the production of 1×10^9 *Nitzschia closterium* individuals; *N. frigida* can hardly be supposed to have smaller requirements and in the uppermost parts of the productive layer the amount of P_2O_5 must have been more than 1 mlgr. per litre for such a stock of *N. frigida* to have developed as that found in the sample examined, provided that no phosphates had been added during the period in which the stock was under development. Eutrophication of the water in Kattinge Bight takes place in several ways; in the first place through the current in Roskilde Fjord which carries waste water from the town of Roskilde; *N. frigida* is certainly not an organism which keeps to unclean water, but we are here so far from the source of contamination that it obviously can make use of the food brought to it without being damaged by the other stuffs found in the waste water; further nutrient materials are brought to Kattinge Bight from the freshwater inlet in the inner part and it is possible that dissolved nutrient salts rise to the upper layers from the bottom, where in the deeper middle part a certain amount of self-contamination takes place. In spite of the great eutrophication a nutrient content of the dimensions noted for the phosphates seems improbable and additional nutriment must therefore have come during the development of the population; since—in spite of the currents—it has been able to keep its place, this may be connected with the biological condition that the species is inclined to attach itself to the underside of the ice; when the colonies are anchored here they are fixed in place; their further growth downward then takes place at a rate corresponding somewhat to the increasing thickness of the ice.

N. frigida is fairly indifferent to the salinity of the water; it thrives in the brackish waters of the Finnish coasts and in the Arctic it occurs both at places where the salinity is $34\,^0/_{00}$ and in ponds on the ice not communicating with the sea (GRAN 1900,

p. 62), thus in water of a very low salinity; on the other hand it seems to be stenothermal, as we do not know any dense concentration where the temperature is over 3°.

The mass occurrence of *N. frigida* in Kattinge Bight, under conditions where no other diatoms occur, shows that it is a species with an ecological constitution different from the plankton diatoms which generally live here and in similar localities on our coasts.

Along with Dr. Aa. Jensen the present author on $^{18}/_{3}$, 1947, made an excursion to Roskilde Fjord and collected plankton and hydrographical samples under the ice at Sts. 5, 6 and 7 (Fig. 5); at St. 5 there was a great undersaturation of oxygen, especially at the bottom; in the plankton there were several specimens of *Euglena* sp. and a strong concentration of bacteria; a considerably higher degree of oxygenation was found at St. 6, without reaching saturation; no plankton organisms were found in the samples from here; at St. 7, which has a fairly sheltered position, the oxygen content was slightly higher than at St. 6, but saturation had not been reached; the underside of the ice was fairly strongly coloured and in samples from this melting ice there were green flagellates in considerable concentration; further a few colonies of *N. frigida*; in the water samples from this station some flagellates were found, but otherwise no plankton; here, therefore, a short time before the excursion was made, there has been a considerable production of plankton; that the stock had suddenly disappeared may probably have been due to the fact that the ice had become covered with a good layer of snow, which of course reduced the amount of light under the ice.

The mass occurrence of *N. frigida* in the inner part of Roskilde Fjord in March 1947 seems, according to these investigations, to have been restricted to Kattinge Bight, where it was observed on $^{5}/_{3}$.

With the object of making further investigations on *N. frigida* a collection of plankton samples was made in Kattinge Bight $^{18}/_{3}$, 1948. The temperature at the surface varied between 3°,94 and 4°,02. *Sceletonema costatum* dominated the plankton and *Melosira moniliformis* was fairly abundant, but *N. frigida* was not found; it was also absent in some small samples taken of the bottom-material.

N. frigida was again sought for in Kattinge Bight on $^{23}/_{11}$, 1948, special attention being paid this time to the collection of bottom

samples. A special procedure was used, as shown in the sketch Fig. 6; a heavy piece of iron with irregular edges was used to stir up the bottom material and a fraction of the suspended material was collected by a plankton net with silk-gauze no. 25. The length

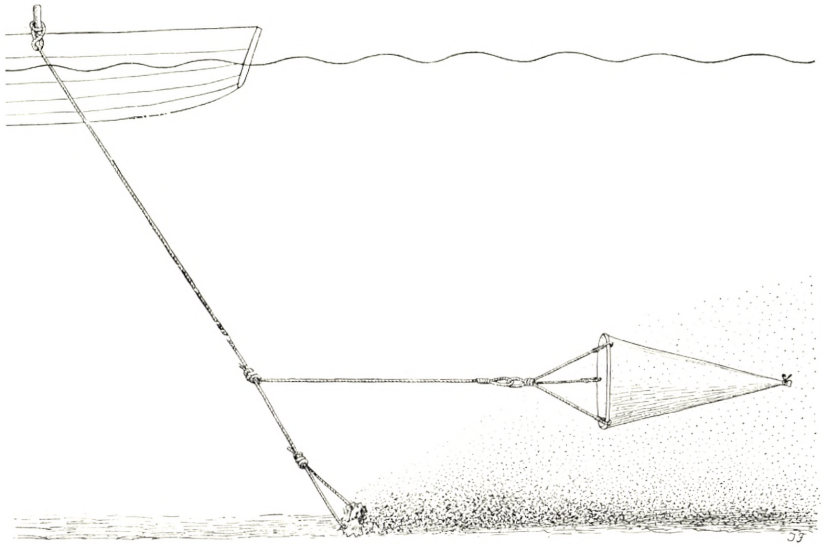

Fig. 6. Sketch to illustrate the procedure used in making collections of bottom diatoms (see text).

and fixing point of the line connecting the plankton net with the line of the iron-piece can be adapted for the object of the collecting; the finer the fraction of the bottom-material required, the longer the plankton net line must be; further attention has to be paid to the speed of the boat, depth of the water and nature of the bottom. When it is not a question of quantitative collecting of bottom diatoms, this method is quite applicable and it has the advantage over the usual bottom sampler, that the material is sorted out and the possibility is increased of obtaining rare species, a relatively great area of the bottom being searched over. In the bottom samples collected in this way a few solitary *N. frigida* cells were found, varying somewhat more in size (45—60 μ) than was the case in the population found in the ice in this locality $^{5}/_{3}$, 1947; otherwise the cells had the same appearance.

In the plankton from this excursion no specimen of *N. frigida* was found; the most abundant species were *Melosira moniliformis*

and *Synedra crystallina*. The temperature at the surface varied between 4°,35 and 4°,75.

On $^{22}/_{3}$, 1949, *N. frigida* was again sought for in Kattinge Bight; the temperature at the surface was 2°,80, at the bottom 2°,60; in the plankton, which was not specially rich, *Diatoma elongatum*, *Melosira moniliformis*, *Synedra* sp. and *Dinobryon* sp. were fairly frequent; *N. frigida* was not seen here, but a few solitary cells of this species were found in the bottom mud, of which samples were taken in the same way as on the previous excursion; no resting spores were found and there is every probability that *N. frigida* outside its flowering periods lives at the bottom as solitary cells, morphologically not different from those which form colonies in the plankton during the flowering period.

A biological importance of a flowering of the winter plankton, as that observed in Kattinge Bight in March 1947, is shown in Table 2, a survey of the temperature of the water, salinity, and oxygen content. Considering here the oxygen content: at Sts. 1 and 2 both lying in the current carrying the waste water of Roskilde northwards, the water of all depths is undersaturated with oxygen,

Table 2. Hydrographical investigations at St. 1—4; $^{5}/_{3}$, 1947.

Station No.	Depth m	Temperature °C	Salinity ‰	Oxygen cm³/litre
1	1	÷ 0.65	13.33	3.93
«	2	1.61	14.36	3.64
«	3	2.18	15.37	1.28
2	0.75	÷ 0.69	13.48	6.26
«	2	0.90	14.24	6.36
«	3	0.62	15.50	7.44
«	4	0.90	15.99	4.63
3	0.75	0.25	13.39	13.89
«	2	1.61	14.22	6.97
«	2.25	1.42	14.25	7.02
«	2.50	1.05	..	7.02
«	3.50	0.78	14.96	7.16
«	4.50	0.62	15.93	6.32
4	0.75	÷ 0.56	13.33	15.40
«	1.25	1.00	13.53	13.41
«	2	1.89	14.15	5.30

most at St. 1, which lies nearest the sewage outlet. At St. 3, at a depth of 0.75 m., that is just under the ice, there is a considerable oversaturation, but from 2 m. to the bottom there is a less degree of undersaturation. The melting water with the rich content of *N. frigida* came from this station; at the shallow-water St. 4 there is a supersaturation with oxygen directly under the ice and at 1.25 m.; at 2 m., as at St. 3, there is undersaturation; no samples for plankton investigations were taken at St. 4, but according to information from Dr. Aa. Jensen the underside of the ice and the uppermost layer of water had the same green colour as at St. 3; both stations have undoubtedly been populated with the same plankton organisms, which in a layer of almost 1 m. in depth have been able to utilize the weak light for photosynthesis, whereby the water has become enriched with oxygen, so that fishes and other animals could live there during an otherwise critical period; that such a dense stock of phytoplankton may play a considerable part as nutrient source for plankton animals emphasizes further the importance of a plankton flowering in the winter.

The occurrence of *N. frigida* in the Kattinge Bight seems to be due to an immigration from the inner-Baltic area, from where the species probably has been carried by the currents to the Kattegat and from there into the Isefjord; the pelagic mode of life offers great opportunity for spreading in the case of marine organisms; it cannot be considered improbable, that the species occurs in other Danish fjords and bays in the Kattegat and the Baltic, but when—as in the present case—its flowering period does not come before the ice has reached a considerable thickness, it is conceivable that it has not been observed in previous investigations in our inner waters. It may be mentioned in this connection, that the present author, immediately after the finding in Kattinge Bight in March 1947, sought for the species in Præstø Fjord, an area which has considerable exchange of water with the Baltic and plankton with a partly Baltic character (Grøntved 1950)—but with negative results.

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Indleveret til selskabet den 2. juni 1950.
Færdig fra trykkeriet den 18. november 1950.

Explanation of Plate I.

Microphotographs of *Nitzschia frigida* GRUN. Except Fig. 2 *a*, which is from a plankton sample from Porkala in the Gulf of Finland (LEVANDER $^{20}/_{4}$, 1904), all the figures are from material from Kattinge Bight (AA. JENSEN $^{5}/_{3}$, 1947).

Fig. 1. Colony formation. The cells are connected irregularly so that the colony is at some places branched like a tree; in other parts the cells are placed linearly or in zig-zag formation. Glow preparation. (×160).

Fig. 2 *a*—*b*. Frustules, seen in valve view. Glow preparations. (2 *a* × ca. 1300; 2 *b* × ca. 1350.

Fig. 2 *c*. The two valves are separated at the ends of the frustule. Glow preparation. (× ca. 1350).

Fig. 2 *d*. On preparation the two valves have become more separated. Material treated with nitric acid. (× ca. 1300).

Fig. 2 *e*. An isolated valve. Material treated with nitric acid. (× ca. 1300).

Fig. 2 *f*. Frustule; through connections with neighbouring cells it is held in a position which represents an oblique girdle view; the transapical concavity to the left is due to preparation. Glow preparation (× ca. 1300).

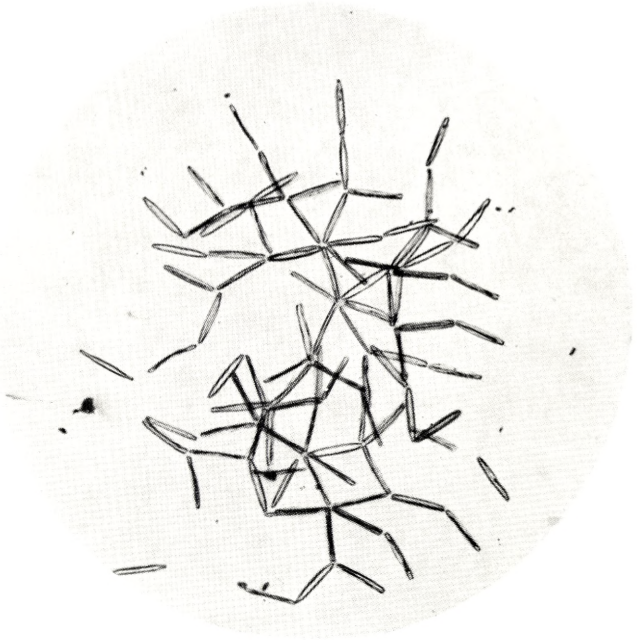
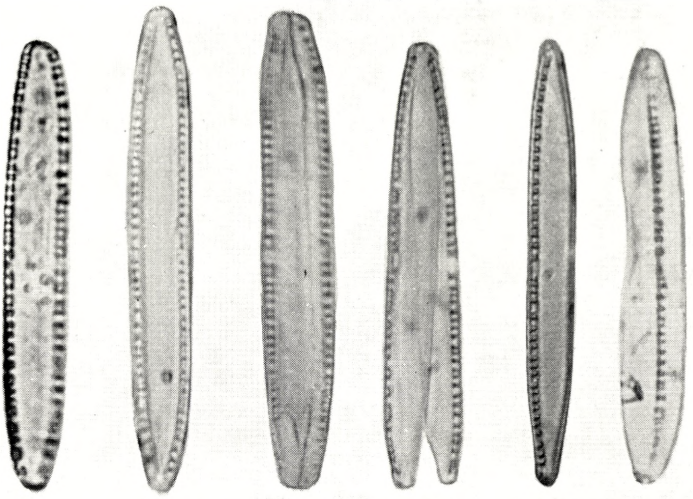


Fig. 1.



a *b* *c* *d* *e* *f*

Fig. 2.

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