



HAL
open science

THE DIATOM FRAGILARIOPSIS CYLINDRUS AND ITS POTENTIAL AS AN INDICATOR SPECIES FOR COLD WATER RATHER THAN FOR SEA ICE

Cecilie H von Quillfeldt

► **To cite this version:**

Cecilie H von Quillfeldt. THE DIATOM FRAGILARIOPSIS CYLINDRUS AND ITS POTENTIAL AS AN INDICATOR SPECIES FOR COLD WATER RATHER THAN FOR SEA ICE. *Vie et Milieu / Life & Environment*, 2004, pp.137-143. hal-03218115

HAL Id: hal-03218115

<https://hal.sorbonne-universite.fr/hal-03218115>

Submitted on 5 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THE DIATOM *FRAGILARIOPSIS CYLINDRUS* AND ITS POTENTIAL AS AN INDICATOR SPECIES FOR COLD WATER RATHER THAN FOR SEA ICE

CECILIE H. von QUILLFELDT

Norwegian Polar Institute, The Polar Environmental Centre, 9296 Tromsø, Norway
cecilie.quillfeldt@npolar.no

FRAGILARIOPSIS CYLINDRUS
DIATOM
INDICATOR
PHYTOPLANKTON
SEA ICE
COLD WATER
ARCTIC
ANTARCTICA

ABSTRACT. – The importance of the diatom *Fragilariopsis cylindrus* (Grunow) Krieger in Helmcke & Krieger in the Arctic and Antarctic is well known. It is used as an indicator of sea ice when the paleoenvironment is being described. It is often among the dominant taxa in different sea ice communities, sometimes making an important contribution to a subsequent phytoplankton growth when released by ice melt. However, it may also dominate phytoplankton blooms in areas never experiencing sea ice. The use of *F. cylindrus* as an indicator for reconstruction of palaeoceanographic conditions is assessed from literature records. Its potential as an indicator species for sea ice appears to vary from region to region, but it is a good indicator of cold water.

FRAGILARIOPSIS CYLINDRUS
DIATOMÉE
ESPÈCE INDICATRICE
PHYTOPLANKTON
GLACE DE MER
EAUX FROIDES
ARCTIQUE
ANTARCTIQUE

RÉSUMÉ. – L'importance de la diatomée *Fragilariopsis cylindrus* (Grunow) Krieger in Helmcke & Krieger est reconnue en Arctique et Antarctique. Ce taxon est utilisé comme indicateur de la présence de glace de mer quand le paléoenvironnement est décrit. Elle est souvent citée parmi les taxons dominants de différentes communautés des glaces de mer, parfois participant de manière importante au développement phytoplanctonique après sa dispersion à la débâcle, lors de la fonte des glaces. Cependant, elle peut aussi être dominante lors de floraisons phytoplanctoniques dans des régions toujours libres de glace. L'utilisation de *F. cylindrus* comme indicateur pour la reconstruction des conditions paléocéanographiques est inventoriée au travers des documents bibliographiques. Ces potentialités en tant qu'espèce indicatrice de glace de mer varie d'une région à l'autre, mais ce taxon est un bon indicateur d'eaux froides

INTRODUCTION

Fragilariopsis cylindrus is one of several species being used, both in the Arctic and the Antarctic, to track sea ice distribution over time when reconstructing the palaeoceanographic history. It is the only currently living species of *Fragilariopsis* with a bipolar distribution, occurring between 80 – 50°N and 76 – 55°S (Hasle 1976), but there could be considerable population differences between the hemispheres due to ecological processes driven by complex physical, chemical and biological interactions (Lizotte 2001). One other is a cosmopolite, one has a warm water distribution, the rest occur either in the Arctic or the Antarctic (Hasle & Medlin 1990, Hasle & Syvertsen 1996). Several of these are possible to misidentify as *F. cylindrus*, especially in water mounts, although they differ in

essential features possible to resolve in empty cells. Information on their distribution may also be used knowing that some of them are typical plankton species, while others prefer ice. However, *F. cylindrus* and a few others may thrive in more than one type of habitat (Hasle & Medlin 1990, von Quillfeldt 2001). Living *Fragilariopsis* species appear in ribbon-shaped colonies (Hasle 1993).

F. cylindrus has been reported from sediment in areas with seasonal sea ice (Stockwell *et al.* 1991, Taylor *et al.* 1997, von Quillfeldt *et al.* 2003) and it is an important species when downcore data are being analysed in order to study climatic events in the past (Koç Karpuz & Schrader 1990, Koç *et al.* 1993, Leventer *et al.* 1993, Douglas *et al.* 1996, FulfordSmith & Sikes 1996, Gersonde & Zielinski 2000, Sedwick *et al.* 2001, Yoon *et al.* 2002, Armand & Leventer 2003, Cremer *et al.* 2003). However, the question arises to what extend is *F.*

cylindrus a good indicator of sea ice since occurrences today show that it may be among the dominant phytoplankton species in areas that never experience sea ice (Paasche 1960, Halldal 1953, Ramsfjell 1954, Hegseth *et al.* 1995, von Quillfeldt 1996)? In order to consider this, the distribution and habitat preferences of *F. cylindrus* and related species in the Arctic and the Antarctic are outlined.

Reports of *Fragilariopsis cylindrus* and resembling species

The Antarctic

In the Antarctic, *F. cylindrus* has a wide preference with respect to habitat. It has been reported as being among the dominant in phytoplankton in ice-covered areas (Garrison *et al.* 1983, Garrison & Buck 1985, Garrison *et al.* 1987, Rawlence *et al.* 1987, Fryxell & Kendrick 1988, Nöthig *et al.* 1991, Garrison *et al.* 1993, Gleitz & Thomas 1993, Kang & Fryxell 1993, Moisan & Fryxell 1993, Scharek *et al.* 1994, Hegseth & von Quillfeldt 2002 pers obs) and from open water (Kopczynska & Ligowski 1982, Perrin *et al.* 1987, Nöthig *et al.* 1991, Kang & Fryxell 1992, 1993, Brandini 1993, Moisan & Fryxell 1993, Hegseth & von Quillfeldt 2002). In open water, it is often found following ice break-out in fjords (McMinn & Hodgson 1993) or occurs in areas affected by sea ice melt (Kang & Fryxell 1991, Stockwell *et al.* 1991, Lizotte 2001), but may also be among the dominant diatoms in an advanced bloom phase (Socal *et al.* 1997). The species thrives very well in ice, being among the dominant taxa in a wide range of ice communities (pools, sub-ice, infiltration and different interior communities), both in fast ice (Krebs *et al.* 1987, Bartsch 1989, McMinn 1996, Gunther & Dieckmann 2001, Hegseth & von Quillfeldt 2002) and pack ice (Garrison *et al.* 1983, 1987, Bartsch 1989, Garrison & Buck 1989, Ligowski *et al.* 1992, Lizotte 2001, Hegseth & von Quillfeldt 2002 pers obs), in young (Garrison & Buck 1985, Gersonde 1984, Ligowski 1987) as well as multi-year ice (Fritsen & Sullivan 1997).

Several Antarctic-restricted *Fragilariopsis* species resemble *F. cylindrus* in water mounts, i.e. *F. linearis* (Castracane) Frenguelli, *F. sublinearis* (Heurck) Heiden or *F. curta* (Van Heurck) Hustedt. The former two are typical for ice, while the latter may also be common in plankton (Hasle & Medlin 1990). In water mounts the species most often occur in colonies seen in girdle view, as opposed to in permanent slides where they occur as solitary cells seen in valve view. In the latter case they are easy to distinguish, while it may be more problematic for inexperienced observers when in water mounts. Paleooceanographic studies usually involve preparation of cleaned samples, but this is not always the case for living material. Thus, records of the distri-

bution of *Fragilariopsis* species should be treated with caution if only water mounts have been studied. Gersonde & Zielinski (2000) suggested that it was possible to use the relative distribution pattern of *F. curta*, *F. cylindrus* and *F. obliquecostata* (Van Heurck) Heiden in late Pleistocene sediment cores as a proxy for past winter and summer sea ice variations.

The Arctic

In the Arctic, *Fragilariopsis cylindrus* is usually reported as most abundant early in the spring bloom (Gran 1897, Østrup 1897, Cleve 1900, Gran 1904, Grøntved & Seidenfaden 1938, Horner 1969, Motoda & Minoda 1974, Booth 1984, Hegseth *et al.* 1995, von Quillfeldt 2000, 2001), but not always (Paasche 1960). It may occur most of the year in some areas (Halldal 1953, Motoda & Minoda 1974, Bursa 1961a, von Quillfeldt 1996) and ice cover is not required for it to be found (Halldal 1953, Ramsfjell 1954, Hegseth *et al.* 1995, von Quillfeldt 1996). It is also widespread in the Baltic Sea, characterized as a marine arctic species with freshwater affinity (Snøeijls & Vilbaste 1994). It may be one of the main biomass producers in the plankton (Halldal 1953, Ramsfjell 1954, Bursa 1961b, Paasche 1960). It is also regularly recorded from sea ice (Grunow 1884, Gran 1897, Østrup 1895, Usachev 1949, Horner & Schrader 1982, Hsiao 1980, 1983, Booth 1984, Okolodkov 1992). It occurs in melt ponds (von Quillfeldt 1997) and throughout the ice (pers obs), but when among the most common species it is usually as a member of bottom communities, either the interstitial or the sub-ice community, usually from first-year ice, but sometimes from multi-year ice (Grunow 1884, Syvertsen 1991, von Quillfeldt 1997, Melnikov *et al.* 2002).

In water mounts, *Fragilariopsis cylindrus* may be confused in the Arctic with *F. cylindroformis* (Hasle) Hasle and *F. oceanica* (Cleve) Hasle, the latter often being more abundant than *F. cylindrus* in the water column at high northerly latitudes (Grøntved & Seidenfaden 1938, Braarud 1935, Ramsfjell 1954, Paasche 1960, von Quillfeldt 1997, Lovejoy *et al.* 2002). *F. cylindrus* can, on the other hand, be very abundant also at lower latitudes (Ramsfjell 1954, Halldal 1953, von Quillfeldt 1996). Both *Fragilariopsis oceanica* and *F. cylindrus* are reported from sea ice in the Arctic, but *F. oceanica* not as often as *F. cylindrus* (von Quillfeldt 2001). However on some occasions, *F. oceanica* and not *F. cylindrus* has been reported from sea ice (Druzhkov *et al.* 2001, Wiktor & Szymelfenig 2002). *Fragilariopsis cylindroformis* is regarded as a planktonic species (Hasle & Medlin 1990), reported from the eastern subarctic Pacific (Hasle & Booth 1984). It is, however, possible that it also occurs in the Antarctic (Cremer *et al.* 2003).

Origin of the sea ice

The diatom composition in sea ice reflects the origin of the ice and proximity to the coast and water depths are important factors. The potential number and composition of neritic species incorporated will also depend on the seasonal dynamics of the diatom community which has been observed to be most diverse in the winter and summer in some coastal areas (Ryabushko & Ryabushko 1991). Moreover, the biological regimes in sea ice from coastal areas will also differ from those further off the coast (Gradinger 1999), and therefore influence species composition. Also, the presence of freshwater species will indicate a coastal formation of ice (Abelmann 1992, von Quillfeldt *et al.* 2003).

The majority of species found in the sediment will occur in the ice and vice versa, especially in shallow areas. Incorporation of sediment, and its associated microalgae, is episodic and likely to correspond with storm or high-wind events (Tucker *et al.* 1999). In shallow water there may also be rapid resuspension or transport processes and a short residence time in the water column for species being released from the sea ice (Tuschling *et al.* 2000). In the Chukchi Sea most species recorded in the sediment, also occurred in the sea ice, *F. cylindrus* being one of them, though not dominant (von Quillfeldt *et al.* 2003). Instead, resting spores of typical phytoplankton spring bloom species dominated. There may also be a large interannual variation in the amount of species incorporated into ice from the benthos. Demers *et al.* (1984) found that benthic diatoms constituted as much as 50% of the ice community one year, while the following year the ice microflora was entirely dominated by pelagic species. Furthermore, the pelagic component will be more prominent further off the coast than the benthic component (von Quillfeldt *et al.* 2003). Regional differences are also likely, in spite of circumpolar ocean currents and ice drift patterns distributing species over large areas.

Thus, in elucidating sea ice extents, it is important to use an approach which takes into account species abundances and their individual relationships to sea ice cover.

Fragilariopsis cylindrus in open and ice-covered waters

F. cylindrus can dominate in both environments as described earlier. When part of the phytoplankton, the colonies often have 60–70 cells, but the colonies can be up to several hundred cells long (pers obs). In the ice they usually appear as shorter colonies (less than 10 cells), often composed of smaller cells, sometimes even as solitary cells or only a few cells together. I have, however,

on a few occasions in Antarctic sea ice recorded chains up to 30 cells long or more, but then the cells were never longer than 2.5 – 4 μm , had thin valves and the colonies occurred in bottom communities. Actually, it is possible that the smallest form of *F. cylindrus* may be a different species or a variety of *F. cylindrus*. However, the presence of ice is certainly not a requirement for the existence of the species. In the Norwegian Sea it has been found to be the most common species, typical for Atlantic water (Halldal 1953, Ramsfjell 1954) and among the dominant spring species in fjords of northern Norway (Hegseth *et al.* 1995, von Quillfeldt 1996). Neither of these areas have seasonal ice cover. However, when it dominates spring blooms in northern Norway it is at relatively low temperatures, around 3–5°C, even though it may occur at somewhat higher temperatures later in the season (Hegseth *et al.* 1995, von Quillfeldt 1996). Though near the marginal ice-edge zone and therefore likely to be influenced by melt-water, *F. cylindrus* had highest number of cells in open waters compared to ice-covered waters in the Antarctic (Kang & Fryxell 1992). Based on similar observations, Cremer *et al.* (2003) suggested that the widely observed predominance of *F. cylindrus* (and *F. curta*) in the water column and in the sediments might reflect warmer climatic conditions and the presence of meltwater-stratified surface waters during summer as a result of strong ice melting. In the Baltic Sea it is actually characterized as a species with freshwater affinity (Snøeijis & Vilbaste 1994). Even though it is usually characterized as a spring species, it may occur year round in some areas. Paasche (1960) concluded that it was more typical in the summer plankton, than in the spring plankton. Furthermore, in the Siberian Laptev Sea it occurred in the surface water, but was not incorporated into the ice during autumnal freeze-up (Tuschling *et al.* 2000).

Possible indicators of sea ice

Two factors are especially important when using affinity of diatoms to ice in order to track historical changes of its distribution. First of all, the species must preserve well in the sediment, secondly they should be quite abundant and a regular component of ice communities. Additionally, it is an advantage if they are easy to identify, even when only parts of the valve is intact. However, instead of relying on just a few diatoms associated with sea ice, combined abundance data of as many diatoms as possible is preferable, even though this means more extensive analyses, especially since there are likely to be regional differences. Bloom size, species composition and sedimentation is a function of upper water column structure, differences in the amount of sea ice melting, type of sea ice, water

depth etc. Besides, the contribution from fast-ice communities to the phytoplankton is often low, but this doesn't necessarily apply for pack ice communities (McMinn 1996). Furthermore, there may be problems associated with the dissolution and winnowing in diatom preservation relative to modern and past conditions (Armand & Leventer 2003). Therefore, knowledge about today's ice algae doesn't necessarily apply when interpreting historical data.

There are not that many species of diatoms associated only with sea ice, but some are more typical of ice than others. In the Arctic, *Nitzschia frigida* Grunow, *N. promare* Medlin and *Melosira arctica* Dickie are regarded as typical ice algal species, often dominating in ice communities (Medlin & Hasle 1990, Syvertsen 1991). Another, *Fossula arctica* Hasle, Syvertsen, von Quillfeldt may be predominant both in ice and early spring blooms in ice-covered waters (Hasle *et al.* 1996, von Quillfeldt 2000). Both *M. arctica* and *F. arctica* form resting spores which is advantageous for preservation in the sediment. Additional information about the ice can be gained, knowing that *M. arctica* is most common in multi-year ice and older first-year ice, *N. frigida* and *N. promare* in older first-year ice and *F. arctica* in both young and older first-year ice. Moreover, *Fossula arctica* was not described until 1996 (Hasle *et al.* 1996), but is now reported from ice, water and sediment all over the Arctic (Hasle *et al.* 1996, von Quillfeldt 2000, Lovejoy 2002, von Quillfeldt *et al.* 2003). Before that it must have been reported as a similar species, i.e. *Fragilariopsis cylindrus*, *F. oceanica* or *Fragilaria islandica* Grunow, even though it is easy to recognize in water as well as permanent mounts (von Quillfeldt 2001). Likewise, *N. promare* was described in 1990 (Medlin & Hasle 1990). In addition, epiphytic species (*Attheya septentrionalis* (Østrup) Crawford, *Pseudogomphonema arcticum* (Grunow) Medlin and *Synedropsis hyperborea* (Grunow) Hasle, Medlin et Syvertsen) are often regular, or among the most common members of ice communities, sometimes despite low numbers of their most common supporting algae, when they are attached directly to the ice.

In the Antarctic, *Berkeleya adeliensis* Medlin, *Navicula glaciei* Van Heurck, *Nitzschia stellata* Manguin, *Synedropsis laevis* (Heiden) Hasle, Syvertsen et Medlin and *S. recta* Hasle, Syvertsen et Medlin are common components of bottom sea ice communities (Hasle *et al.* 1994, Cremer *et al.* 2003). *Berkeleya adeliensis* was described in 1990 (Medlin 1990) and *Synedropsis recta* in 1994 (Hasle *et al.* 1994). As discussed earlier, there are also other members of the genus *Fragilariopsis* (e.g. *F. linearis* and *F. sublinearis*) that are more restricted to sea ice than *F. cylindrus*. Furthermore, also members of other genera, e.g. *Entomoneis*,

sometimes dominate sub-ice communities both in the Arctic and Antarctic.

In summary, due to quite recent descriptions of some common ice algal species, the combination of diatom abundance data being used should be reviewed. As opposed to *F. cylindrus*, the species mentioned above, are more restricted to the ice itself or at least to ice covered waters. In addition, there are many other species, both colonial, but especially solitary pennate ones, being more or less regular members of different ice communities. The relative abundances of these species are often related to origin of the ice (shallow/deep areas, neritic/oceanic environment) as discussed earlier.

CONCLUSION

Combined abundance data of *Fragilariopsis cylindrus* and other diatoms characterized as sea ice indicators is being used in order to define past sea ice conditions. While some of these species have a preference for ice, *F. cylindrus* may equally well occur in open water, even in areas never covered by sea ice. If this is the case today, it is reasonable to believe that it also might have been the case in the past. It is unquestionable however, that *F. cylindrus* has a cold water distribution, and is perhaps better suited as an indicator of that rather than of ice itself. In spite of *F. cylindrus* seldom being the only species representing sea ice conditions, an effort should be made to find suitable species which could substitute for *F. cylindrus* when past sea ice extent is determined. This being said, different species combinations reflecting past ice conditions should probably be applied for different regions.

ACKNOWLEDGEMENTS. – Comments on the manuscript by the referees are gratefully acknowledged.

REFERENCES

- Abelmann A 1992. Diatom assemblages in Arctic sea ice-indicator for ice drift pathways. *Deep-Sea Res* 39: 525-538.
- Armand LK, Leventer A 2003. Palaeo sea ice distribution – reconstruction and palaeoclimatic significance. In Thomas DN & Dieckmann GS eds, *Sea ice. An introduction to its physics, chemistry, biology and geology*. Blackwell, Oxford: 333-372.
- Bartsch A 1989. Sea ice algae of the Weddell Sea (Antarctica): species composition, biomass and ecology of selected species. *Ber Polarforsch* 63: 1-110.
- Booth JA 1984. The epontic algal community of the ice edge zone and its significance to the Davis Strait ecosystem. *Arctic* 37: 234-243.

- Braarud T 1935. The "Øst" expedition to the Denmark Strait. II. The phytoplankton and its conditions of growth (including some qualitative data from the Arctic in 1939). *Hvalråd Skr* 10: 173 p.
- Brandini FP 1993. Phytoplankton biomass in an Antarctic coastal environment during stable water conditions – implications for the iron limitation theory. *Mar Ecol Prog Ser* 93: 267-275.
- Bursa AS 1961a. Phytoplankton of the Calanus expedition in Hudson Bay, 1953 and 1954. *J Fish Res Bd Can* 18: 51-83.
- Bursa AS 1961b. The annual oceanographic cycle at Igloodik in the Canadian Arctic II. The phytoplankton. *J Fish Res Bd Can* 18: 563-615.
- Cleve PT 1900. Microscopical examination of dust from drift-ice north of Jan Mayen. *Översikt af K Vet Aka Förhandl* 4: 393-397.
- Cremer H, Roberts D, McMinn A, Gore D, Melles M 2003. The Holocene diatom flora of marine bays in the Windmill Islands, east Antarctica. *Bot Mar* 46(1): 82-106.
- Demers S, Therriault J-C, Descolas-Gros C 1984. Biomasse et composition spécifique de la microflore des glaces saisonnières: influences de la lumière et de la vitesse de congélation. *Mar Biol* 78: 185-191.
- Douglas MSV, Ludlam S, Feeney S 1996. Changes in diatom assemblages in lake C2 (Ellesmere Island, Arctic Canada): Response to basin isolation from the sea and to other environmental changes. *J Paleolimnol* 16 (2): 217-226.
- Druzhkov NV, Druzhkova EI, Kuznetsov LL 2001. The sea-ice algal community of seasonal pack ice in the southwestern Kara Sea in late winter. *Polar Biol* 24: 70-72.
- Fritsen CH, Sullivan CW 1997. Distribution and dynamics of microbial communities in the pack ice of the western Weddell Sea, Antarctica. In Battaglia B, Valencia J & Walton DWH eds, *Antarctic communities*. Cambridge University Press, Cambridge: 101-106.
- Fryxell GA, Kendrick GA 1988. Austral spring microalgae across the Weddell Sea ice edge: spatial relationships found along a northward transect during AMERIEZ 83. *Deep-Sea Res* 35(1): 1-20.
- FulfordSmith SP, Sikes EL 1996. The evolution of Ace Lake, Antarctica, determined from sedimentary diatom assemblages. *Palaeogeogr Palaeocl* 124 (1-2): 73-86.
- Garrison DL, Buck KR 1985. Sea ice algal communities in the Weddell Sea: Species composition in ice and plankton assemblages. In Grey JS & Christiansen ME eds, *Marine Biology of polar regions and effects of stress on marine organisms*. John Wiley & Sons, New York: 103-122.
- Garrison DL, Buck KR 1989. The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula Regions. *Polar Biol* 10: 211-219.
- Garrison DL, Ackley SF, Buck KR 1983. A physical mechanism for establishing algal populations in frazil ice. *Nature* 306(5941): 363-365.
- Garrison DL, Buck KR, Gowing MM 1993. Winter plankton assemblages in the ice edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distribution. *Deep-Sea Res* 40(2): 311-338.
- Garrison DL, Buck KR, Fryxell GA 1987. Algal assemblages in Antarctic pack ice and ice-edge plankton. *J Phycol* 23: 564-572.
- Gersonde R 1984. Siliceous microorganisms in sea ice and their record in sediment in the southern Weddell Sea. *8th Diatom Symp (1984)*: 549-566.
- Gersonde R, Zielinski U 2000. The reconstruction of late Quaternary Antarctic sea-ice distribution – the use of diatoms as a proxy for sea ice. *Palaeogeogr Palaeocl* 162(3-4): 263-286.
- Gleitz M, Thomas DN 1993. Variation in phytoplankton standing stock, chemical composition and physiology during sea-ice formation in the southeastern Weddell Sea, Antarctica. *J Exp Mar Biol Ecol* 173: 211-230.
- Gradinger R 1999. Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. *Mar Biol* 133: 745-754.
- Gran HH 1897. Bacillariaceae vom kleinen Karajakfjord. *Bibl Bot* 8 (42): 13-24.
- Gran HH 1904. Diatomaceae from ice floes and plankton of the Arctic Ocean. In Nansen F ed, *Sci Res Norw N Polar Exped* 4(11): 3-74.
- Grunow A 1884. Diatomeen von Franz Josef-Land. *Denk Akad Wien* 48: 1-394.
- Grøntved J, Seidenfaden G 1938. The Godthaab expedition 1928. *Medd Grønland* 82(5): 1-136.
- Gunther S, Dieckmann GS 2001. Vertical zonation and community transition of sea-ice diatoms in fast ice and platelet layer, Weddell Sea, Antarctica. *Ann Glaciol* 33: 287-296.
- Halldal P 1953. Phytoplankton investigations from weather ship M in the Norwegian Sea, 1948-49 (including observations during the "Armauer Hansen" cruise, July 1949). *Hvalrådedets Skr* 38: 1-91.
- Hasle GR 1976. The biogeography of some marine planktonic diatoms. *Deep-Sea Res* 23: 319-338.
- Hasle GR 1993. Nomenclatural notes on marine Planktonic diatoms. The family Bacillariaceae. *Nova Hedwigia Beih* 106: 315-321.
- Hasle GR, Booth BC 1984. *Nitzschia cylindroformis* sp. nov., a common and abundant nanoplankton diatom of the eastern subarctic Pacific. *J Plankton Res* 6(3): 493-503.
- Hasle GR, Medlin LK 1990. Family Bacillariaceae: Genus *Nitzschia*, section *Fragilariopsis*. In Medlin LK & Priddle J eds, *Polar marine diatoms*. British Antarctic Survey, Cambridge: 181-196.
- Hasle GR, Medlin LK, Syvertsen EE 1994. *Synedropsis* gen. nov., a genus of araphid diatoms associated with sea ice. *Phycologia* 33(4): 248-270.
- Hasle GR, Syvertsen EE 1996. Marine diatoms. In Tomas CR ed, *Identifying marine diatoms and dinoflagellates*. Academic Press, San Diego: 5-385.
- Hasle GR, Syvertsen EE, Quillfeldt CH von 1996. *Fosula arctica* gen. nov., spec. nov., a marine Arctic araphid diatom. *Diatom Res* 11: 261-272.
- Hegseth EN, Quillfeldt CH von 2002. Low phytoplankton biomass and ice algal blooms in the Weddell Sea during the ice-filled summer of 1997. *Antarct Sci* 14(3): 231-243.
- Hegseth EN, Svendsen H, Quillfeldt CH von 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In Skjoldal HR, Hopkins C, Eriks-

- tad KE & Leinaas HP eds, Ecology of fjords and coastal waters. Elsevier Science BV: 45-72.
- Horner R 1969. Phytoplankton studies in coastal waters near Barrow, Alaska. Dr thesis, Univ Washington, 216 p.
- Horner R, Schrader GC 1982. Relative contributions of ice algae, phytoplankton and benthic microalgae to primary production in nearshore regions of Beaufort Sea. *Arctic* 35: 485-503.
- Hsiao SIC 1980. Community structure and standing stock of sea ice microalgae in the Canadian Arctic. *Arctic* 33: 768-793.
- Hsiao SIC 1983. A checklist of marine phytoplankton and sea ice microalgae recorded from Arctic Canada. *Nova Hedwigia* 37 (2+3): 225-313.
- Kang S-H, Fryxell GA 1991. Most abundant diatom species in water column assemblages from five leg 119 drill sites in Prydz Bay, Antarctica: distributional patterns. *Proc ODP, Sci Results* 119: 645-666.
- Kang S-H, Fryxell GA 1992. *Fragilariopsis cylindrus* (Grunow) Krieger – The most abundant diatom in water column assemblages of Antarctic marginal ice-edge zones. *Polar Biol* 12(6-7): 609-627.
- Kang S-H, Fryxell GA 1993. Phytoplankton in the Weddell Sea, Antarctica: composition, abundance and distribution in water-column assemblages of the marginal ice-edge zone during austral autumn. *Mar Biol* 116: 335-348.
- Koç Karpuz N, Schrader H 1990. Surface sediment diatom distribution and Holocene paleotemperature variations in the Greenland, Iceland and Norwegian Sea. *Paleoceanography* 5(4): 557-580.
- Koç N, Jansen E, Hafliðason H 1993. Paleooceanographic reconstructions of surface ocean conditions in the Greenland, Iceland and Norwegian Seas through the last 14 ka based on diatoms. *Quat Sci Rev* 12: 115-140.
- Kopczynska EE, Ligowski R 1982. Phytoplankton abundance and distribution in the southern Drake Passage and the Bransfield Strait in February-March 1981 (BIOMASS-FIBEX). *Pol Polar Res* 3(3-4): 193-202.
- Krebs WN, Lipps JH, Burckle LH 1987. Ice diatom floras, Arthur Harbor, Antarctica. *Polar Biol* 7: 163-171.
- Leventer A, Dunbar RB, Demaster DJ 1993. Diatom evidence for late Holocene climatic events in Granite Harbor, Antarctica. *Paleoceanography* 8(3): 373-386.
- Ligowski R 1987. Sea ice microalgae community of the floating ice in the Admiralty Bay (South Shetland Islands). *Polar Res* 8(4): 367-380.
- Ligowski R, Godlewski M, Lukowski A 1992. Sea ice diatoms and ice edge planktonic diatoms at the northern limit of the Weddell Sea pack ice. *Proc NIPR Symp Polar Biol* 5: 9-20.
- Lizotte MP 2001. The contribution of sea ice algae to Antarctic marine primary production. *Am Zool* 41(1): 57-31.
- Lovejoy C, Legendre L, Martineau M-J, Bâcle J, Quillfeldt CH von 2002. Distribution of phytoplankton and other protists in the North Water Polynya (Arctic) *Deep-Sea Res II* 49: 5027-5047.
- McMinn A 1996. Preliminary investigations of the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. *Polar Biol* 16(4): 301-307.
- McMinn A, Hodgson D 1993. Summer phytoplankton succession in Ellis Fjord, eastern Antarctica. *J Plankton Res* 15: 925-938.
- Medlin LK 1990. *Berkeleya* spp. from Antarctic waters, including *Berkeleya adeliensis* sp. nov., a new tube dwelling diatom from the undersurface of sea-ice. *Nova Hedwigia Beih* 100: 77-89.
- Medlin LK, Hasle GR 1990. Some *Nitzschia* and related diatom species from fast ice samples in the Arctic and Antarctic. *Polar Biol* 10: 451-479.
- Melnikov IA, Kolosova EG, Welch HE, Zhitina LS 2002. Sea ice biological communities and nutrient dynamics in the Canadian Basin of the Arctic Ocean. *Deep-Sea Res I* 49: 1623-1649.
- Moisan TA, Fryxell GA 1993. The distribution of Antarctic diatoms in the Weddell Sea during austral winter. *Bot Mar* 36: 489-497.
- Motoda S, Minoda T 1974. Plankton of the Bering Sea. In Hood DW & Kelley EJ eds, Oceanography of the Bering Sea. Institute of Marine science, University of Alaska, Fairbanks: 207-241.
- Nöthig E-M, Bodungen B von, Sui Q 1991. Phyto- and protozooplankton biomass during austral summer in surface waters of the Weddell Sea and vicinity. *Polar Biol* 11: 293-304.
- Okolodkov YB 1992. Cryopelagic flora of the Chukchi, East Siberian and Laptev Seas. *Proc Nat Inst Polar Res Symp. Polar Biol Tokyo* 5: 28-43.
- Paasche E 1960. Phytoplankton distribution in the Norwegian Sea in June, 1954, related to hydrography and compared with primary production data. *Fisker Skr Havund* 12 (11): 1-77.
- Perrin RA, Lu P, Marchant, HJ 1987. Seasonal variation in marine phytoplankton and ice algae at a shallow antarctic coastal site. *Hydrobiologia* 146: 33-46.
- Quillfeldt CH von 1996. Ice algae and phytoplankton in north Norwegian and Arctic waters: species composition, succession and distribution. Dr thesis, Univ Tromsø, Norway: 250 p.
- Quillfeldt CH von 1997. Distribution of diatoms in the Northeast Water Polynya, Greenland. *J Mar Syst* 10: 211-240.
- Quillfeldt CH von 2000. Common diatom species in Arctic spring blooms: their distribution and abundance. *Bot Mar* 43: 499-516.
- Quillfeldt CH von 2001. Identification of some easily confused common diatom species in arctic spring blooms. *Bot Mar* 44: 375-389.
- Quillfeldt CH von, Ambrose WG, Clough LM 2004. High number of diatom species in first year ice from the Chukchi Sea. *Polar Biol* (in press).
- Ramsfjell E 1954. Fytoplanktonet i den nordlige delen av Norskehavet i begynnelsen av juni 1952 og 1953. Master Sc Thesis, Univ Oslo: 158 p.
- Rawlence DJ, Ensor PH, Knox GA 1987. Summer tide-crack phytoplankton at White Island, McMurdo Sound, Antarctica. *N Ze J Mar Freshw Res* 21: 91-97.
- Ryabushko LI, Ryabushko VI 1991. The structure of a community of diatom algae of hard substrata in the upper intertidal zone of Vostok Bay, the Sea of Japan. *Biologiya Morya-Mar Biol* 3: 14-21.
- Scharek R, Smetacek V, Fahrbach E, Gordon LI, Rohardt G, Moore S 1994. The transition from winter to early spring in the eastern Weddell Sea, Antarctica: Plankton biomass and composition in relation to hy-

- drography and nutrients. *Deep-Sea Res* 41(8): 1231-1250.
- Sedwick PN, Harris PT, Robertson LG, McMurtry GM, Cremer MD, Robinson P 2001. Holocene sediment records from the continental shelf of Mac. Robertson Land, East Antarctica. *Paleoceanography* 16 (2): 212-225.
- Snøeijls P, Vilbaste S 1994. Intercalibration and distribution of diatom species in the Baltic Sea, Vol 2 Opulus Press Uppsala (The Baltic Marine Biologists Publ 16 b) 126 p.
- Socal G, Nöthig EM, Bianchi F, Boldrin A, Mathot S, Rabitti S 1997. Phytoplankton and particulate matter at the Weddel/scotia Confluence (47 degrees W) in summer 1989, as a final step of a temporal succession (EPOS project). *Polar Biol* 18 (1): 1-9.
- Stockwell DA, Kang S-H, Fryxell GA 1991. Comparison of diatom biocoenoses with holocene sediment assemblages in Prydz Bay, Antarctica. *Proc ODP Sci Results* 119: 667-673.
- Syvrtsen EE 1991. Ice algae in the Barents Sea: types of assemblages, origin fate and role in the ice-edge phytoplankton bloom. *Polar Res* 10(1): 277-288.
- Taylor F, McMinn A, Franklin D 1997. Distribution of diatoms in surface sediments of Prydz Bay, Antarctica. *Mar Micropaleontol* 32: 209-229.
- Tucker III WB, Gow AJ, Meese DA, Bosworth HW 1999. Physical characteristics of summer sea ice across the Arctic ice. *J Geophys Res* 104: 1489-1504.
- Tuschling K, Juterzenka KV, Okolodkov YB, Anoshkin A 2000. Composition and distribution of the pelagic and sympagic algal assemblages in the Laptev Sea during autumnal freeze-up. *J Plankton Res* 22: 843-864.
- Usachev PI 1949. The Microflora of Polar Ice. Trudy Instituta Okeanologii, Moscow 3: 216-259.
- Wiktor J, Szymelfenig M 2002. Patchiness of sympagic algae and meiofauna from fast ice of North Open Water (NOW) Polynya. *Pol Polar Res* 23: 175-184.
- Yoon HI, Park BK, Kim Y, Kang CY 2002. Glaciomarine sedimentation and its paleoclimatic implications on the Antarctic Peninsula shelf over the last 15 000 years. *Palaeogeogr Palaeocl* 186(3-4): 235-254.
- Østrup E 1895. Marine diatomeer fra Østgrønland. *Medd Grønland* 18: 397-476.
- Østrup E 1897. Kyst-Diatomeer fra Grønland. *Medd Grønland* 15: 305-362.

Reçu le 3 novembre 2003; received November 3, 2003
Accepté le 15 janvier 2004; accepted January 15, 2004

