# Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom

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Ice algal accumulations were recognised by their vertical distribution in the ice, as surface, interior and bottom assemblages. The latter were quantitatively the most important in the Barents Sea and in particular the sub-ice assemblage floating towards, or attached to, the under-surface of the sea ice. Colonisation of the ice takes place by a "sieving" of the water between closely spaced platelets on the ice under-surface. Once associated with the ice, the assemblage undergoes a succession terminated by the dominance of ice specialists. In a horizontal S-N section through the ice, three distinct zones may be recognised: at the ice edge the recently colonised ice has a layer of algae up to a few millimeters in thickness consisting primarily of planktonic species. Further into older first year ice the algal layer becomes thicker and is typically dominated by the pennate diatom Nitzschia frigida Grunow. Below multi-year ice in the central polar basin decimetre-thick mats of algae are found, consisting almost exclusively of the centric diatom Melosira arctica (Ehrenberg) Dickie and a few associated, mostly epiphytic, species. The predominantly planktonic sub-ice assemblages at the ice edge can grow under stable conditions as soon as the light becomes adequate in the spring, and they are able to multiply actively for one to two months before planktonic growth is possible. The sub-ice plankton assemblage thus forms an inoculum released to the stabilising water when the ice starts melting. This may explain how a phytoplankton bloom can develop explosively at the ice edge as soon as the ice melting commences, at a time when the number of algal cells in the water column is still very low.

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### Introduction

The first reports of diatoms from Arctic sea ice were published more than a hundred years ago (Ehrenberg 1841, 1853; Cleve & Grunow 1880; Cleve 1883; Grunow 1884). These early works were primarily taxonomic and biogeographic in nature. As pointed out by Apollonio (1985), Sutherland (1852) and Dickie (1852) were the first to relate characteristic ice algal assemblages to specific types of ice. Their observations were made mainly in decaying ice during spring and summer at the west coast of Greenland. Nansen (1897, 1906) and Gran (1904), however, gave extensive descriptions of algal assemblages in Arctic sea ice from year-round studies.

More recent studies have been concerned with the vertical distribution of algae in the ice and have concluded that most of the biomass is found between ice crystals and in cavities and brine channels in the lower part of the ice (Apollonio 1961, 1965; Meguro et al. 1967; Alexander et al. 1974; Grainger 1977; Dunbar & Acreman 1980; Hsiao 1980; Horner & Schrader 1982; Poulin et al. 1983). This distribution has been explained as the result primarily of light and salinity (e.g. Apollonio 1961; Meguro et al. 1967).

Bursa (1961) reported films of diatoms on the under-surface of ice turned over by ice breakers near Baffin Island. He considered the ice undersurface to serve as a "second sea floor" where benthic diatoms could attach. Apollonio (1961) studied similar assemblages in the Canadian Arctic. In some cases more loosely attached mats and strands of algae on the ice under-surface, reaching considerable thicknesses, have been reported from the Arctic (e.g. Usachev 1949; Cross 1982; Melnikov & Bonderchuk 1987; Melnikov 1989).

A few authors have been concerned with the origin and fate of the algae in and on the ice. Meguro et al. (1966, 1967) suggested that diatoms were frozen into the ice in the autumn whereafter they formed "resting cysts" to survive the winter. Many microalgae do not form distinct cysts or resting spores, however, and there have been speculations as to whether they could survive the winter in any other way. Allen (1970, 1971) suggested that diatoms could sustain the long dark period by heterotrophy, but this was considered to be of little importance by Horner & Alexander (1972). From the Antarctic, mechanisms of colonisation such as physical incorporation of algal cells during flooding (Meguro 1962) and frazil ice formation (Garrison et al. 1983) have been suggested. It is poorly understood, however, how incorporation in and colonisation of the ice take place in the Arctic.

Many terms have been used to describe ice algal assemblages. One and the same term has often been employed for different kinds of assemblages and habitats. In other cases a number of different terms have been applied for similar assemblages. This has partly been due to a lack of knowledge about the characteristic assemblages found in discrete parts of the ice, partly the result of a search for more descriptive terms. The better solution so far seems to be the proposal of Ackley et al. (1979) who related characteristic assemblages to the particular location within, or on, the ice where they are found. A further subdivision and standardisation of these terms was suggested by Horner et al. (1988).

Most of the literature has been concerned with the vertical distribution of algae in the ice. Much less importance seems to have been attached to the horizontal distribution of ice algae and possible species successions.

This paper considers the various algal assemblages found in the Barents Sea and briefly discusses their possible origin, development and fate. Most attention will be paid to the sub-ice algae which have constituted the most abundant assemblages in the present investigations. Ice freezing, colonisation of the ice under-surface by algae and their subsequent succession is a dynamic process, in large repeated in a similar way from one year to the next.

The Barents Sea is relatively shallow, on the

average about 300 m deep, all of it overlying the continental shelf. The present investigations have mainly taken place in areas away from the coasts and there is reason to believe that assemblages and successions in nearshore Arctic waters will be substantially different, as the ice in these areas is likely to be influenced by the benthic flora of the sea bottom, neritic plankton and algae of brackish and fresh water origin.

## Material and methods

P10 Mare cruises were carried out with R/VLANCE, (Aug, 1984, May 1986), M/S POLARBJØRN, (April/May 1985), K/V NORDKAPP (Feb./March and June 1987), K/V SENJA (Oct. 1987) and K/V ANDENES (May and Sept. 1988). Some of the material used during this investigation, however, has been obtained on earlier cruises in the same area.

Interior assemblages were sampled by coring and subsequent thawing of subsamples in seawater at low temperature.

All under-ice sampling was carried out by scuba diving, either directly from a floe or an ice edge, by means of a smaller boat or rubber boat, or in stabilised leads. Qualitative sub-ice algal samples were collected by the use of an electric suction pump (Lønne 1988), where the material was collected in a cylindrical plankton net with 10 or 20 µm mesh width, to avoid passage through the pump. However, an ordinary plankton net was occasionally attached to the outlet of the pump, and this also seemed to function without damaging the cells. Quantitative samples from the ice under-surface were collected by using cylindrical acrylic incubation chambers which could be pressed or hammered into the ice and thereafter capped off.

Samples for identification and estimation of cell numbers were preserved either with neutralised formaldehyde (100 g hexamethylentetramine per liter of 20% aqueous solution) or formaldehyde with acetic acid added (equal amounts of 40% formaldehyde and concentrated acetic acid). Both fixatives were used so as to get a 0.4% final solution in the samples. In extremely dense samples the amount of preserving agent was doubled.

Terminology for ice biota follows Horner et al. (1988). In addition one new term has been introduced: *pressure ridge assemblage*, a peculiar

assemblage found on top of more or less horizontal ice surfaces in pressure ridges and rafted ice, below water level.

### Observations

During the first Pro Mare cruises and on earlier expeditions to the Barents Sea attempts were made to obtain ice algal material by coring through the ice. The cores were melted and the algal content collected from 10 cm sections of the core. In most cases there were algae in the ice, but except for the very bottom part, these algae seemed to have been accidentally frozen into the ice (i.e. they had neither colonised the ice interior nor been actively growing there). There were no obviously viable and growing assemblages to be found, even if it was occasionally possible to establish cultures from algae melted out of the ice. The only living and multiplying algal assemblages were found in the very few bottom centimetres of ice, in the water within the matrix of ice crystals and ice platelets protruding down from the ice under surface. No sub-ice algal mats or films were obtained by coring. When scuba diving was employed, however, ice algae were found in quantity, on the under surface of all undisturbed sea ice in the spring and summer (February-September) before the melt-down commenced. In fact, this method also made it easier to detect band assemblages in the ice by observing the vertical sides of newly broken ice floes.

Fig. 1 gives a schematised representation of a vertical section through the ice and the various

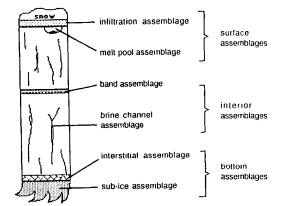


Fig. 1. Schematised representation of a vertical section through undisturbed sea ice, showing the various main types of algal assemblages presently known from undisturbed sea ice (redrawn from Horner et al. 1988).

main types of algal assemblages which are presently known from undisturbed sea ice. In addition to these assemblages, evenly dispersed cells accidentally frozen into the ice may in some cases be sufficiently numerous to be recognised as separate internal assemblages.

Fig. 2 represents a schematical section through the ice in the Barents Sea in spring and summer and indicates the various kinds of ice algal assemblages that have been observed during this investigation.

No *infiltration assemblage* has hitherto been observed in the Arctic. Occasionally algae may be found in the pore water of submerged snow in

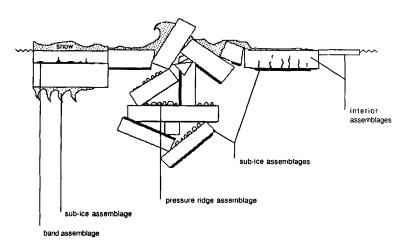


Fig. 2. Schematised section through the sea ice in the Barents Sea, showing the various types of ice algal assemblages observed. pressure ridges and rafted ice, but this is not a regular phenomenon and has been observed only once.

Pool assemblages have been astonishingly few, even if pools created by melting and wave action on floes and ice edges have been common on decaying ice during summer. On one occasion only, in August 1984, two pools were found having a thin film of pennate diatoms on the bottom and a few flagellates in the water. These pools were relatively saline (ca. 25) and were probably in contact with the underlying seawater through channels and cracks in the melting ice. In the same area (82°20'N, 21°25'E), consisting of a mixture of multi-year and annual ice, the rim of the floes of about 10 m width was covered with cylindrical holes, 10-15 cm apart, 2-5 cm in diameter and 5-20 cm deep. On the bottom of each hole there was a firm, bleached ball of algae, consisting mainly of Melosira arctica (Ehrenberg) Dickie. The phenomenon came into existence during periods of rough weather with heavy wind and wave action, when new leads opened and the algal assemblages on the under side of the ice floated up to the surface. The ice algae were subsequently washed up onto the ice in the form of relatively regularly sized tufts. When the weather improved, solar heating caused the cells to melt down into the ice. At the same time the shade-adapted cells appeared to be photooxidised by the strong light, leaving them as bleached, dead lumps on the bottom of the melt holes. Low salinity in the meltwater may have been an additional factor in causing the cells to die.

Band assemblages of algae have never been documented with certainty from Arctic ice. During this investigation such assemblages were found only once in any quantity (Oct. 1987, ca. 77°51'N, 30°19'E). On this occasion brown bands of algae were fairly common in two-year-old ice on the boundary between the first and second year ice. The species composition was characterised by a number of brackish water species, the most easily recognisable being Thalassiosira hyperborea var. hyperborea (Grunow) Hasle. This indicates that the algae had been growing as a subice assemblage during ice melting the preceding summer. During winter they became entrapped by the accretion of new ice on the ice undersurface, probably in the form of rising frazil ice. When seen in a section through the ice (as they appeared in newly opened leads), the assemblages were characteristically evident as narrow, irregular bands of a few millimetres or centimetres in thickness, straight on the lower side and with larger or smaller rounded or pointed extensions upwards. The latter is caused by sub-ice algae aggregating or becoming trapped in hollows and brine channel openings, a phenomenon frequently observed below first year ice.

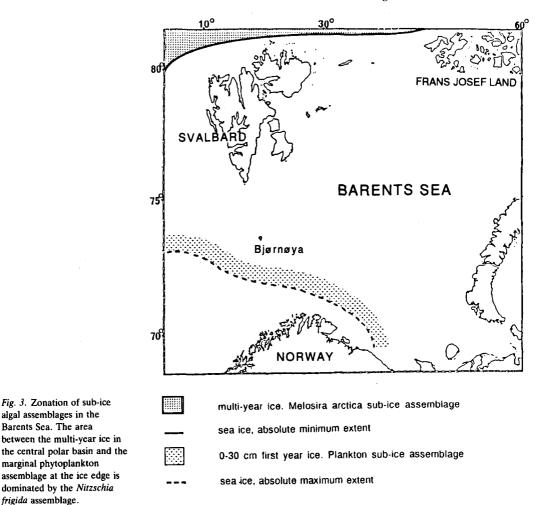
Brine channel assemblages are apparently not as prominent in the Barents Sea as has been reported from nearshore waters. When such assemblages have been found, they have either consisted of entrapped sub-ice algae or motile species from the interstitial assemblage. It has not been possible to distinguish any distinct algal assemblage using brine channels and cracks as a habitat.

Interstitial assemblages were common in the whole area investigated and consisted primarily of pennate diatoms from the genera Navicula, Nitzschia and Gyrosigma/Pleurosigma. These algae seemed to establish themselves simultaneously with the sub-ice assemblage and probably represent the moving of colonising motile species deeper into the ice matrix, in the pore water (here used for any water between ice crystals and in smaller holes in the ice) between ice crystals and platelets.

The sub-ice algal assemblages dominated the ice flora in the Barents Sea. In a S-N section through the ice from April-May onwards, there existed a characteristic zonation from the outer ice edge towards the multi-year ice in the central polar basin (Fig. 3). At the outer ice edge, where newly frozen nilas often dominated, few algae could be found on the ice under-surface.

Further towards the north, at an ice thickness of about 20 to 40 cm, there was everywhere a layer of algae about 0–3 mm thick, more or less attached to the platelets and ice crystals protruding down into the water. The algal layer was not film-like, but loose and more or less flocculent and easily disturbed by currents and ice movements. When mixed into the water, however, the algae seemed to quickly float up towards the ice under-surface again (or they were carried up by currents) where they adhered anew. In all observed cases the species composition was almost entirely planktonic, often reflecting the species found in the underlying water column (Fig. 4, Table 1).

Further into the ice, at a thickness above ca. 40 cm, the species composition gradually changed to become dominated by the pennate diatom *Nitz*-



schia frigida Grunow, forming arborescent colonies, probably in a mixture with the similar N. neofrigida Medlin and N. promare Medlin (Fig. 5, Table 1). Together with these dominant species, there were found a number of pennate diatoms forming ribbon-shaped colonies, such as Nitzschia cylindrus (Grunow) Hasle, N. grunowii (Cleve) Hasle, Navicula vanhoeffenii Gran, Achnantes taeniata Grunow and the peculiar Navicula pelagica Cleve with twisted colonies and seta-like detached girdle bands. The Nitzschia species, forming arborescent colonies, were always present, however, and most often dominating, especially in older annual ice. In addition, any other species in the area could be present in lower numbers.

In younger ice the assemblages formed a thin, smooth film on the ice under-surface, probably due to polysaccharides ("mucilage") which all diatoms exude. The diatom film was often disrupted by strong currents and ice movements and then parts of the film "rolled" off the ice and got twisted together to form long "ropes" hanging down into the water.

In older and thicker annual ice the film was more "moss-like" and the algae formed more or less spherical lumps in hollows and brine channel openings. The size of such lumps seemed to increase towards the north and with the age of the ice and could reach more than a decimetre in diameter.

In the northwestern part of the Barents Sea where the East Spitsbergen Current conveys ice from the central polar basin into the area, 2-4 m thick multi-year ice was encountered during late summer and autumn. These larger or smaller floes

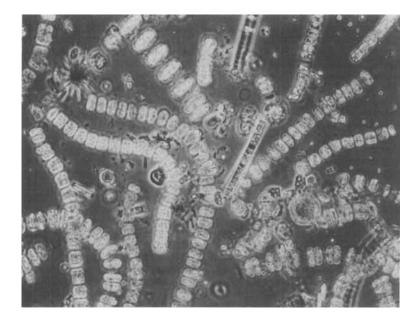


Fig. 4. Plankton sub-ice assemblage. First year ice. 30 cm. May 1985.  $\times$  ca. 160.

were often in various stages of deterioration, and in such instances contained only remnants of subice assemblages. Undisturbed multi-year ice. however, was often covered by decimetre-thick mats and thick rope-like extensions of sub-ice algae protruding down into the water. In the more decayed state of the ice the algal assemblages were hanging like Spanish moss from the Swisscheese-like matrix of the melting ice. When larger undisturbed floes broke up, tufts of sub-ice algae floated to the surface where they remained floating for a shorter or longer period before starting to sink. When the algae became entrapped on shallow ice-foots, the deep reddish-brown color turned to green and the algae died within a few days due to photooxidation.

In all investigated cases, this type of sub-ice

assemblage on the under-surface of multi-year ice consisted of one dominating species: *Melosira arctica* (Fig. 6, Table 1) and a few other species acting as epiphytes on the *Melosira* chains, namely *Chaetoceros septentrionalis* Östrup, clinging to the *Melosira* chains with its setae, *Synedra hyperborea* Grunow and *Pseudogomphonema arcticum* (Grunow) Medlin, both attached at one end by means of a polysaccharide pad. The most astonishing feature of this assemblage was the thickness of the mats (up to 30 cm and on one occasion close to one metre with algal chords more than two metres long).

One of the more curious observations during late summer and autumn was the centimetrethick, irregular assemblages of algae on the upper, more or less horizontal, sides of floes in pressure

Table 1. Sub-ice algal assemblages in the Barents Sea. An example of species composition and cell numbers in three distinct horizontal zones during spring and summer. Five most common species relative abundance.

Plankton sub-ice assemblage (76°22'N, 20°59'E) 20 cm first year ice		First year sub-ice assemblage (76°48'N, 24°37'E) 60 cm first year ice		Multi-year sub-ice assemblage (82°15'N, 26°51'E) 3 m multi-year ice	
Thalassiosira hvalina	1000	Nitzschia frigida	1000	Melosira arctica	1000
Thalassiosira hispida	211	Nitzschia grunowii	189	Svnedra hvperborea	480
Thalassiosira kushirensis	89	Pseudogomphonema arcticum	134	Pseudogomphonema arcticum	221
Bacterosira fragilis	32	Navicula vanhoeffenii	132	Chaetoceros septentrionalis	203
Porosira glacialis	21	Gyrosigma cf. arctica	48	Nitzschia grunowii	97

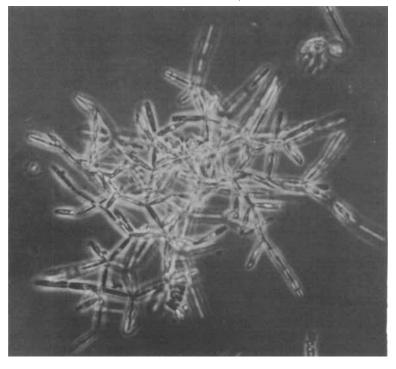


Fig. 5. Nitzschia frigida. First year ice, 50 cm. May 1985.  $\times$  ca. 130.

ridges and rafted ice. Characteristically, the ordinary *Nitzschia frigida* assemblage was growing on the under surface and sides of the submerged floes, while a different and almost unialgal assemblage was found on the upper surface. In most cases such monospecific assemblages consisted of *Actinocyclus* cf. *curvatulus* Janisch. On two occasions, however, an assemblage of *Thal-assiosira bioculata* (Grunow) Ostenfeld was found in similar habitats. In the latter case the normally chain-forming *T. bioculata* appeared as solitary cells, and in water samples the two species could hardly be distinguished. In other cases the ordinary *Nitzschia* or plankton sub-ice assemblages

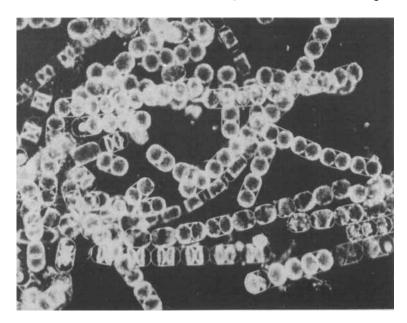


Fig. 6. Melosira arctica. Multiyear sub-ice assemblage. August 1984.  $\times$  ca. 160.

were extending all around the submerged floes in the pressure ridges.

On many occasions it was observed that the floes in the pressure ridges were dark brown on the side facing the current. The phenomenon was often observed when the water was turbid with terrigenous material. In such cases the fast ice under surface was also strongly coloured. In other instances, with phytoplankton blooms or detached sub-ice algae in the water, a similar phenomenon occurred. Closer inspection showed that particles in the water were entrapped between ice crystals and platelets on the ice. The crystals, giving the ice a shaggy appearance, occurred mainly when the ice was freezing. They were only from a few millimetres up to about two centimetres in size and seemed to grow out of the ice. Ice crystals and platelets were thus acting as a comb or sieve, filtering particles from the passing water. This mechanism seems to account both for the frozen-in bands of terrigenous material often found in the lower part of the ice and for the concentration of algae on submerged ice surfaces (Fig. 7).

It was also occasionally observed that during

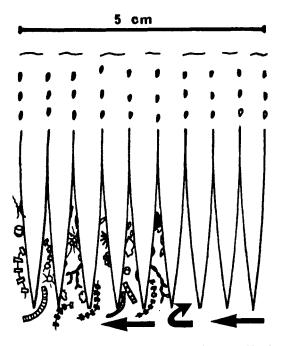


Fig. 7. Schematized drawing of platelets on the under side of the sea ice, acting as a "sieve" to particles and algae. Size of algae exaggerated.

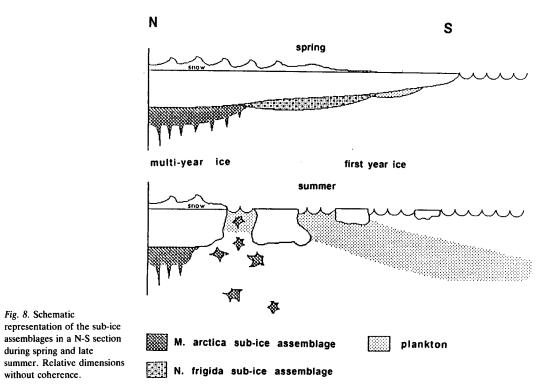
formation of "pancake ice", and in connection with small floes, wave action tended to concentrate frazil ice or falling snow on the margins of the floes, as upturned rims of crystals. When the rims had reached a certain height, the splashing of the waves continually filled the central part of the small floes with water. The seawater then percolated back into the sea through the upturned rims of ice crystals. In this way algal material in the water became concentrated on and between the crystals, and after a while the rims appeared distinctly brown in colour. However, it was never observed how these concentrated algal cells could develop further into any of the known types of ice assemblages.

#### Discussion

The present investigation indicates that every year, from early spring till the ice starts melting, there is a distinct, approximately circumpolar, zonation in the sub-ice assemblages (Figs. 3, 8). Three main types of assemblages may be distinguished in a S-N section through the ice: at the outer edge there is a broad zone (in the order of some tens of kilometres in width, varying geographically and interannually) where the sub-ice algal layer consists of actively growing planktonic species. Towards the north this assemblage gradually merges into a thicker layer of specialised subice algae, in most cases dominated by Nitzschia frigida. This zone of specialised ice algae covers most of the Barents Sea ice in late spring and summer. On the border towards the Polar Basin multi-year ice might be encountered, having another specialised sub-ice assemblage dominated by Melosira arctica.

This zonation appears to be the result of a succession of species, starting as soon as the ice is formed (light conditions permitting) and a mixture of algae from the water masses have mechanically become concentrated on the ice. The course of this apparent succession will depend on many factors, but it seems certain to result in the establishment of the N. frigida assemblage in first year ice and the M. arctica assemblage in the multi-year ice.

On the other hand, the characteristic zonation and apparent succession may be explained as resulting primarily from the composition of algae in the underlaying water masses in the various regions: it is reasonable to presume that at the



southern ice edge, Atlantic Water masses and water masses of mixed origin will contain a larger number of planktonic species than the truly Arctic Water further to the north which is likely to be strongly influenced by suspended ice algae. In the central polar basin sub-ice mats of M. arctica will probably exist year-round and cause a continual recolonisation of available ice in this area.

One of the interesting questions about ice algae is how they get into, or colonise, the ice. During this investigation, "combing" or "sieving" of the water by densely packed ice crystals has been observed repeatedly and seems to constitute an important mechanism for accumulation of algal cells (and any other particles suspended in the water) on the ice under-surface. It is evident from the accumulation of terrigenous material in the same fashion that morphological features such as chain formation or setae on the cells are not compulsory for becoming attached to the ice. On the other hand, such features might enhance the possibilities of becoming entrapped between the ice crystals. More important in this connection, however, might be the common occurrence of exuded polysaccharides, "mucilage", on the outer surface of algal cells, notably diatoms, which may help them to adhere to the ice. "Mucilage" of a syrup-like appearance is also a characteristic of the sub-ice algal mats. Exuded polysaccharides may also help prevent algal cells from being frozen into the ice. Sub-ice algae are seldom found frozen into the ice, except when they have been growing in a brackish water layer (band assemblages, see above). If ice crystals formed in the water column aggregate on the ice under-surface, however, a sub-ice algal layer will be covered and ultimately freeze into the ice. This does not, however, seem to be a regular occurrence in the Barents Sea.

From what has been said above, it is evident that the term "assemblage" is too broad in most cases, since we evidently deal with *communities*, that is, species which interact and have interacted for a long time. The only exception might be the newly accumulated sub-ice plankton at the ice edge.

It appears that resting spores in the traditional sense play no important role in winter survival. It seems likely that planktonic and ice algal species have similar physiological overwintering strategies, but the results are not conclusive as regards the site of survival. To fully elucidate these questions, year-round studies are needed. Our pointinvestigations in space and time have not given the data needed.

During the last twenty-five years of ice-algal studies, there has been an ongoing discussion in the literature concerning the ability of ice algae to induce or take part in the intense spring phytoplankton bloom at the ice edge. The investigations of some authors (Meguro et al. 1966, 1967; Grainger 1977; Hameedi 1978; Saito & Taniguchi 1978; Alexander & Chapman 1981; Schandelmeier & Alexander 1981; Legendre et al. 1981) seem to indicate a possible connection between the ice algae and the ice edge phytoplankton bloom. Others have pointed out that in their investigations the ice algae and phytoplankton blooms are clearly separated in time and species composition (Apollonio 1961; Horner & Alexander 1972; Clasby et al. 1973, Alexander et al. 1974; Matheke & Horner 1974; Horner 1977). The conflict was reviewed by Horner (1984) who concluded that the fate of the ice assemblages seems to vary from one geographical region to another. Apollonio (1985), however, states quite categorically that "it is now well recognized that the Arctic ice flora and phytoplankton are separate autotrophic systems" (Apollonio 1985, p. 168).

However, most investigations have been carried out in nearshore waters, with all the possible ambiguity caused by the influence of fresh water/ brackish water phytoplankton, neritic species and benthic bottom forms. The Barents Sea offers the possibility to study this question in an area which is predominantly "oceanic".

What is evident from the present investigation is that a zone of many kilometres in width contains a sub-ice phytoplankton assemblage, which may have been actively growing for as much as two months under stable conditions. Furthermore, it is sufficiently large to start an immediate phytoplankton bloom when the ice starts melting and a shallow, stabilised upper water layer gradually develops. Having grown as a sub-ice community for an extended period of time, the algae will have been subject to competition and succession. It is therefore likely that there is a certain group of algae (for example diatoms from the genera Bacterosira, Chaetoceros, Thalassiosira) which is successful in using this strategy and which will tend to dominate the spring sub-ice phytoplankton. Species which do not grow as sub-ice plankton in the early spring exist in low numbers in the water and will need time to become quantitatively important in the ice edge bloom. In addition, as the ice melts back, a steady input of sub-ice algae will be added to the bloom. A species like *Nitzschia frigida* seems to be able to stay in the plankton for some time, while others, like *Melosira arctica*, appear to sink quickly out of the euphotic zone when the ice melts.

The ice edge bloom is not merely a spring phenomenon but rather a more or less continual feature at the ice edge as long as it retreats during the summer season. One might therefore easily visualise a succession taking place in the bloom, starting with the inoculation of the sub-ice plankton and after a while becoming gradually more dominated by the true planktonic species originally found in low numbers in the water column.

A thorough understanding of the sub-ice assemblages of algae may be a key to understanding the whole ecosystem in the ice-covered parts of the Arctic seas. It seems unlikely that this considerable and easily accessible primary biomass should not play a major part in the Arctic food chain in itself, and not only act as an inducer of the ice edge phytoplankton bloom.

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