The net phytoplankton in Kongsfjorden, Svalbard, July 1988, with general remarks on species composition of arctic phytoplankton

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Examination of 17 samples collected by a 20 µm meshed net in Kongsfjorden, Svalbard, 8–19 July 1988, showed a dominance of dinoflagellates and the chrysophyte *Dinobryon balticum* in the surface layers, whereas the diatom and the haptophyte *Phaeocystis pouchetii* abundance increased with depth. The diatom *Pseudo-nitzschia granii* appeared together with *P. pouchetii* through the whole water column, and *Actinocyclus curvatulus* was one of the few diatoms present also in the surface samples. Two samples, from 15 and 50 m, respectively, were cleaned of organic material and mounted in Naphrax for a more critical identification of the diatoms. We were able to group the species according to habitats, especially types of ice. The planktonic *Thalassiosira antarctica* var. *borealis*, *T. hyalina*, *T. nordenskioeldii*, *Bacterosira bathyomphala*, *Chaetoceros furcellatus*, *C. socialis* and *Fragilariopsis oceanica* were present mainly as resting stages representing a post-bloom situation. These species and *T. gravida* appear early in the season and may have started to grow already under the ice. *Fragilariopsis cylindrus* and *F. oceanica* seem to have a closer affinity to ice than *Thalassiosira* and *Chaetoceros* spp. although they are common in the plankton. Some *Nitzschia* species which are usually regarded as typical sea-ice diatoms and have thicker and older ice as the main habitat were present only in small cell numbers in the plankton samples. The last component, evidently introduced from Atlantic water in the Norwegian Sea, consisted of diatoms with a more oceanic distribution, e.g. *Fragilariopsis pseudonana* and a small form of *Thalassiosira bioculata*.

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Introduction

The study area

Kongsfjorden, or the Kings Bay, is located on the western coast of Spitsbergen transversed by the 79°N latitude. The term "bay" characterises the area better than "fjord" because there is no outer major sill or barrier separating it from the open coastal water. The maximum depth is ca 300 m (Fig. 1). The bay is usually covered by ice from October until May/June (Orvin 1934). The bay is surrounded by glaciers, among them Brøggerbreen, just south of Ny-Ålesund. Reddish sandstone is found near this glacier, and in summer the river Bayelva or Raudelva and many other rivers and streams near Ny-Ålesund are strongly discoloured by meltwater from Brøggerbreen (Hjelle 1993). Discharge of freshwater and sediments by the rivers into the bay results in (1) a patchy discolouration of the surface layer and a more or less pronounced salinity gradient in horizontal as well as vertical direction and (2) a reduced transparency of the stabilized surface layer. Warm Atlantic water is transported northwards along the western coast of Spitsbergen by the West Spitsbergen Current (Fig. 2). During spring and summer Atlantic water penetrates into Kongsfjorden on the southern side at water depths of 75–100 m, probably facilitated by the lack of an outer shallow sill (Elverhøi et al. 1983).

Previous phytoplankton investigations

The Halldal & Halldal (1973) phytoplankton investigation in Kongsfjorden in July 1971 focused on the light environment and the in vivo chlorophyll fluorescence but included also examination of species composition and cell concentra-

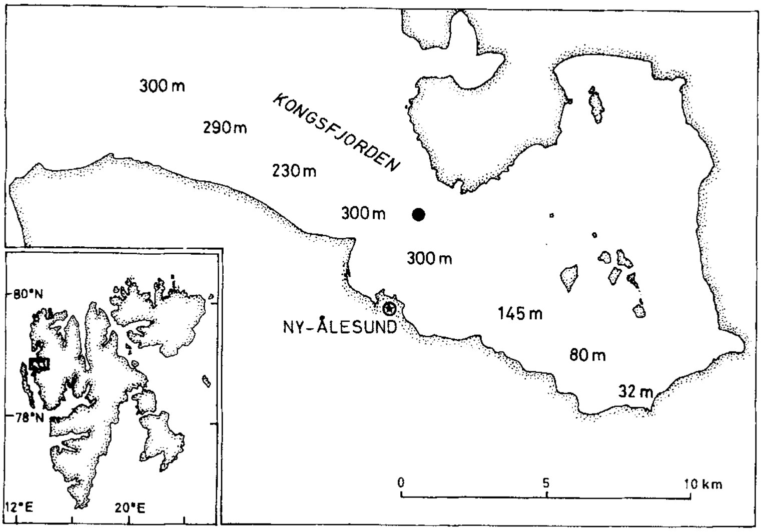


Fig. 1. Location of the study area. The solid circle gives the location of the sampling site.

tion in water samples collected at two stations. The phytoplankton was comparatively rich in coccolithophorids, a phenomenon regarded as an indicator of an Atlantic origin of the water masses.

Eilertsen et al. (1989) reported on maximum

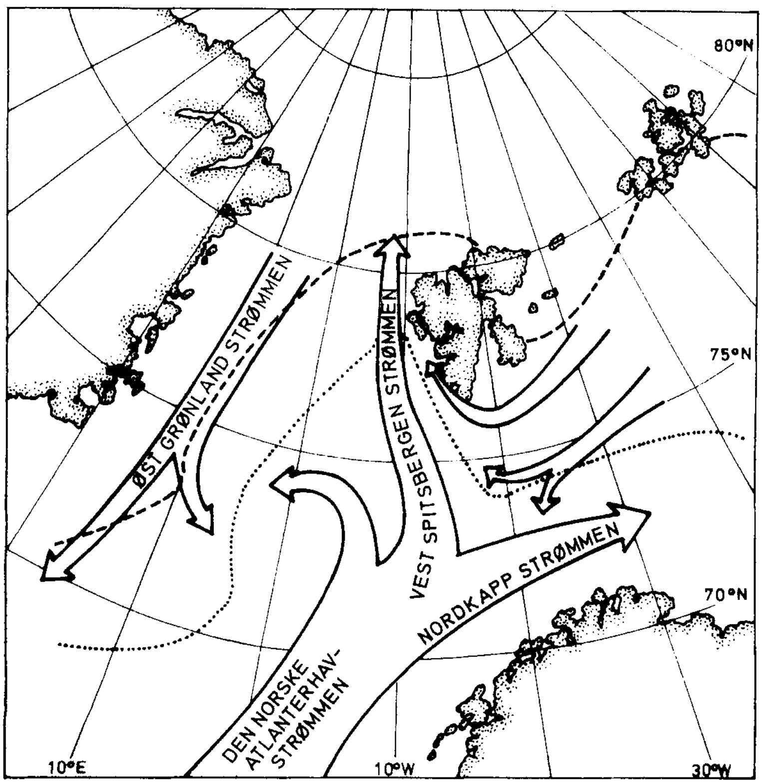


Fig. 2. Main current system. Dashed lines indicate ice cover in September; dotted lines indicate ice cover in March. Redrawn from Trætteberg (1982).

cell concentrations as cells per litre from Kongsfjorden. *Phaeocystis pouchetii* was the predominant species in May 1984 followed in abundance by *Chaeotoceros socialis*; both species were strongly reduced in cell numbers in June. *Phaeocystis pouchetii* was not recorded in July 1979 and *C. socialis* and a few other diatoms were present in fair numbers but outnumbered by "flagellates". Eilertsen et al. (1989) concluded that the spring bloom probably culminated at the end May/early June, that the first part of the bloom occurred under ice cover, and that the ice broke up and disappeared during May. In Hornsund, further south on the western coast (ca 77°N), from which the authors reported maximum cell concentrations from February through May, the bloom started in mid-March and lasted for nearly two months.

The investigations published by Okolodkov (1993, 1996) include a few samples collected by a 70 µm net in Kongsfjorden in June–July 1991 and July–September 1992. The phytoplankton was poor and *Protoperidinium depressum* was the only species mentioned from the area.

Ramsfjell's (1960) investigation from the Norwegian Sea in June 1952 included three stations in the coastal waters off Isfjorden, south of Kongsfjorden (78°20′N), while Paasche's (1960) four stations from the same area in June 1954 were located still further south, at and south of Sørkapp (ca 76°40′N). In 1952 the phytoplankton was more abundant at 25 m than at higher levels. *Phaeocystis pouchetii* was observed only at 25 m, and the cell counts from 25 m of *Chaetoceros furcellatus*, *C. socialis*, *Thalassiosira bioculata*, *T. gravida* and *T. nordenskioeldii* were considerably higher than from the surface layers, indicating later stages of the spring phytoplankton bloom.

Von Quillfeldt (1996) examined material collected between mid-July and end of August 1990 in Isfjorden and north of Kongsfjorden. Although the phytoplankton in general was poor, a great number of species were identified but with few reported as common, mainly some *Chaetoceros*, *Thalassiosira* and *Protoperidinium* species in addition to *Dinobryon balticum* and *Phaeocystis pouchetii*.

Although our investigation covers a short period of time and the possibilities for field work were hampered by lack of ship facilities, we consider the results worth publishing as a supplement to the investigations referred to above, especially since we are dealing with a remote marine area which may be regarded as a reference site as is presently the case in air pollution research.

Material and methods

The investigation was carried out during a two-week stay in Ny-Ålesund at the Research Station operated by the Norwegian Polar Institute. The sampling was performed from a 13-foot boat, 8–19 July, 1988, over the deepest part of Kongsfjorden (Fig. 1). The phytoplankton was collected by a 20 µm net, and water for measurement of the subsurface salinities and temperatures by a Nansen water bottle. A weight was attached to the mouth of the net which was lowered to the required depth and towed for 15–20 minutes. No winch was available and the net and the water bottle had to be operated by hand. The Nansen water bottle depths could be estimated fairly exactly but the lack of instrumentation hindered a precise estimate of the phytoplankton sampling depths.

The phytoplankton material consisted of 17 net samples, eight from the surface layer, one from each of approximately 5, 10, 15, 36 and 70 m and four from approximately 50 m. The samples were examined alive a few hours after the collection, with Leitz Laborlux microscopes equipped with phase contrast and bright field illumination. A few net samples, but no water samples, were preserved with neutralised formaldehyde and brought home for further examination. The two that showed the greatest diversity of diatom species and therefore regarded as representative for the whole material were acid-cleaned and mounted in Naphrax for light microscopy. To ensure correct identification, a few diatoms were also examined in the transmission electron microscope. A Nikon microscope with bright field, negative phase contrast and differential interference contrast equipment was used for photography.

Samples for salinity determination had to be brought home, restricting the number to seven, four from the surface and three from 36 or 50 m. The sea-surface temperature was measured on 12, 13, 16, 17 and 19 July, and also on 12, 13 and 19 between the surface and 50 m.

Results

Hydrography

The highest sea surface temperature, 9°C, was measured 12 July. One week later, after a change in the wind direction, the surface temperature, as well as the temperature gradient within the upper 5 m, had decreased. A de-stabilization of the upper surface layer was also indicated by a slight increase in the surface salinity (29.1‰–30.7‰, 12–19 July) whereas the salinity in 50 m was much the same on the two dates (34.4‰ and 34.3‰, respectively). The changes in temperature and salinity were too small, however, to allow any considerable variation in the water masses influencing the phytoplankton composition to have taken place during the collection period.

Phytoplankton

The number of diatom species recorded is biased. About half of those listed (Table 1) were not seen in water mounts but were found as cleaned valves in permanent mounts for which a comparatively great aliquot of the net samples had been used. The examination of the other groups had to be made on water mounts for which much smaller aliquots were used. Estimates of relative abundances of the respective groups were based on examination of water mounts, however, and showed that the dinoflagellates had more species appearing in fair abundances than any of the other groups. The most abundant species of the entire phytoplankton population were the haptophyte *Phaeocystis pouchetii* and the chrysophyte *Dinobryon balticum* (Fig. 3A and B).

Vertical distribution

The investigation started 8 and 9 July with net hauls from the surface layer dominated by *Dinobryon balticum* and dinoflagellates. Many of the dinoflagellates were large athecate or thecate heterotrophic forms and others were cyst-forming thecate forms. The diatom *Actinocyclus curvatulus* (Fig. 4C–E) occurred in considerable numbers and the freshwater and brackish water *Diatoma elongatum* and a few other diatoms were present in small cell numbers.

Since this composition could indicate a post-bloom situation, the interest was focused on the nature of the possible subsurface plankton. The first successful subsurface net haul (10 July, 15 m) contained *Dinobryon balticum* and most of the dinoflagellates present in the surface net haul taken the same day but possibly in smaller quantities. The greatest difference was, however, the presence of *Thalassiosira* (Figs. 5A–F, 6A) as well as *Phaeocystis pouchetii* colonies, the latter associated with the small diatom *Pseudo-nitzschia granii* (Fig. 6M and N). The chrysophyte *Apedinella spinifera* was also recorded from the deeper sample.

Phaeocystis pouchetii was even more abundant and the dinoflagellates even more scarce in a net sample collected 11 July in ca 35–40 m. Our only record of a coccolithophorid, *Coccolithus pelagicus* f. *pelagicus*, was made from this sample which in addition to diatoms also contained another haptophyte, *Chrysochromulina* sp., the chrysophyte *Meringosphaera mediterranea*, and the choanoflagellate *Bicosta spinifera*.

The sampling series of 12 July, consisting of net hauls from the surface, 5 m, 10 m and 50 m, illustrates the gross features of the vertical distribution: (1) dominance of dinoflagellates and *Dinobryon balticum* in the surface and the 5 m samples with some unhealthy *Phaeocystis pouchetii* colonies in the latter, and (2) a decrease of dinoflagellates, particularly of the athecate forms, together with an increase of *P. pouchetii* and diatoms between 10 and 50 m. The euglenophyte *Eutreptiella braarudii* and resting spores of the diatom *Chaetoceros furcellatus* (Fig. 3E and F) were also observed in the 50 m sample.

The second period of sampling, 16–19 July, showed more or less the same vertical distribution with *Actinocyclus curvatulus* (Fig. 4C–E) and the epiphyte *Licmophora* sp. as the only diatoms recorded in the surface samples.

Species composition (Table 1)

HETEROKONTOPHYTA

Bacillariophyceae

The first records of diatoms from the Spitsbergen area go back to the 19th century (Ehrenberg 1841; Cleve 1867; O'Meara 1874). A list of marine microalgae compiled from plankton investigations in Svalbard waters encompassed 108 diatom taxa compared to 60 dinoflagellates (Hasle & von Quillfeldt 1996). Approximately one third of these diatoms could be characterised as "arctic" in the

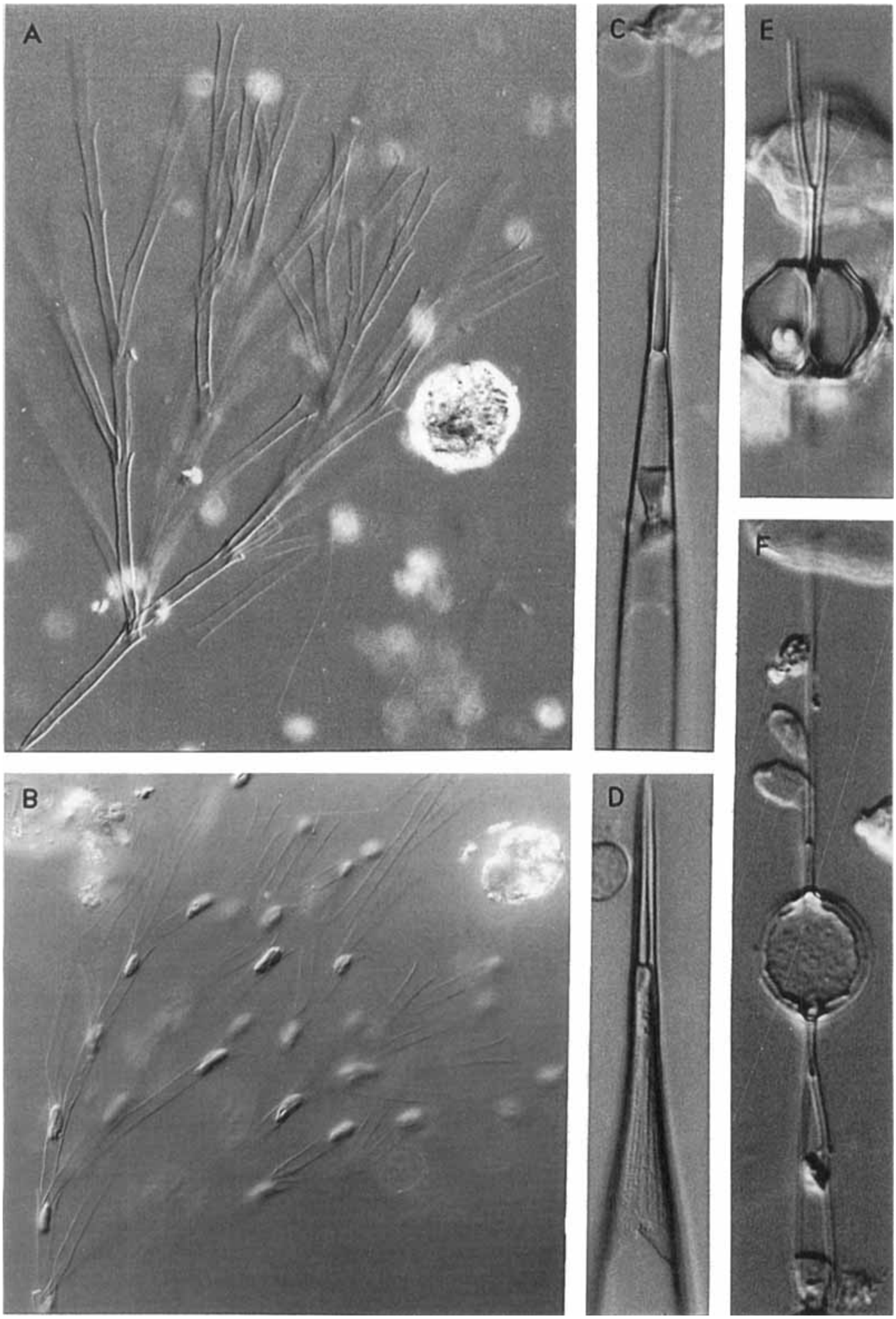


Fig. 3. A and B. ×500. Colonies of *Dinobryon balticum*, B. with the flagellate inside the loricae. C and D. *Rhizosolenia hebetata*, tip of valves, C. f. *semispina* ×1500, D. f. *hebetata* (the winter form) ×1000. E and F. *Chaetoceros furcellatus* resting spores ×2000, E. girdle view, F. valve view. All illustrations are light micrographs of permanent mounts.

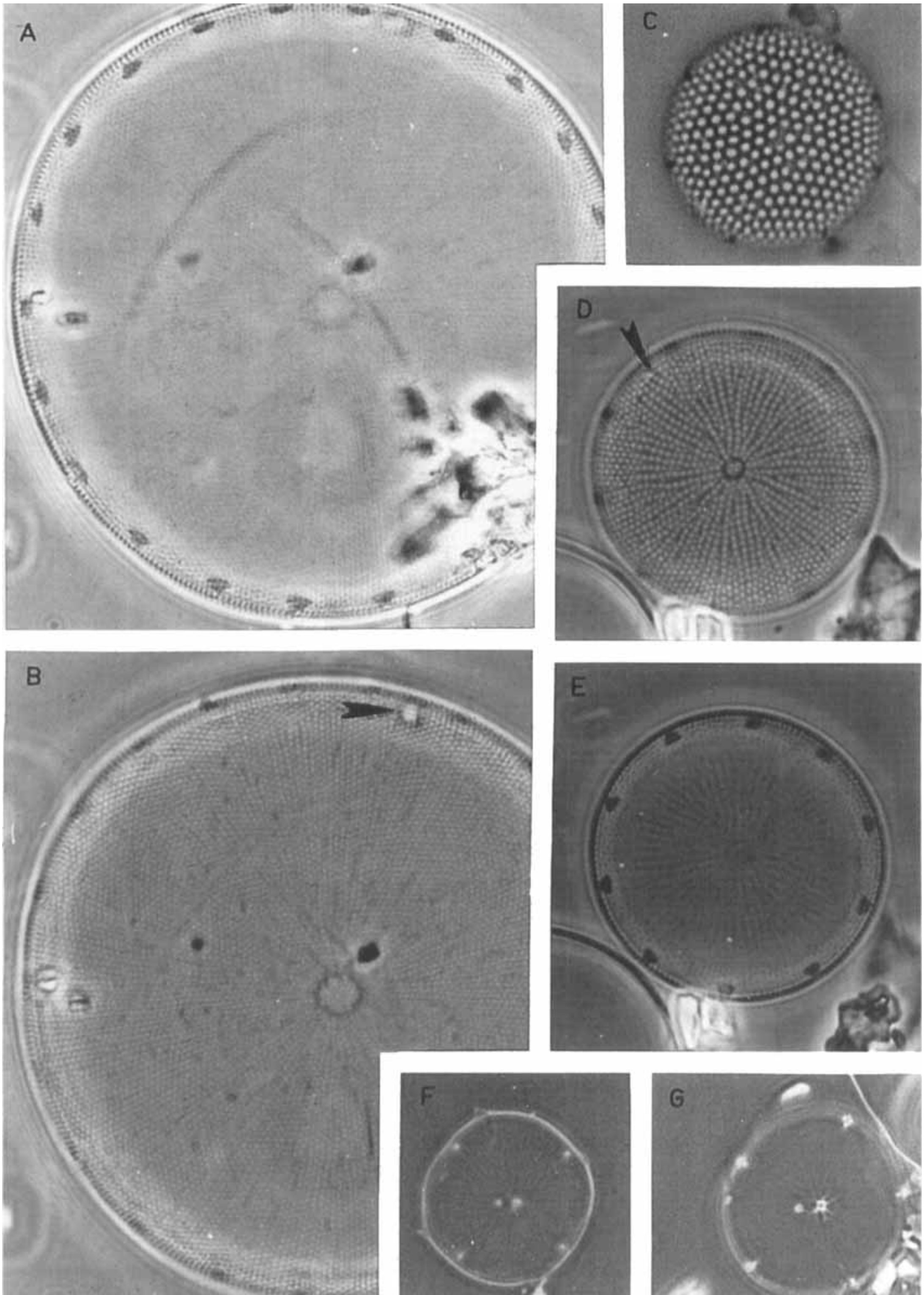


Fig. 4. All illustrations ×2000. A and B. Valve of *Actinocyclus subtilis* at two different foci, marginal ring of labiate processes (A), central annulus, pseudonodulus arrowed (B). C. Coarsely silicified valve of *Actinocyclus curvatulus* (?). D and E. Valve of *Actinocyclus curvatulus* at two different foci, central annulus, indistinct pseudonodulus arrowed (D), marginal ring of labiate processes (E). F and G. Valves of *Thalassiosira bioculata* var. *raripora*, in the centre labiate process to the left, strutted process to the right, longer tube of the marginal strutted processes pointing into the cell interior. All illustrations are light micrographs of permanent mounts.

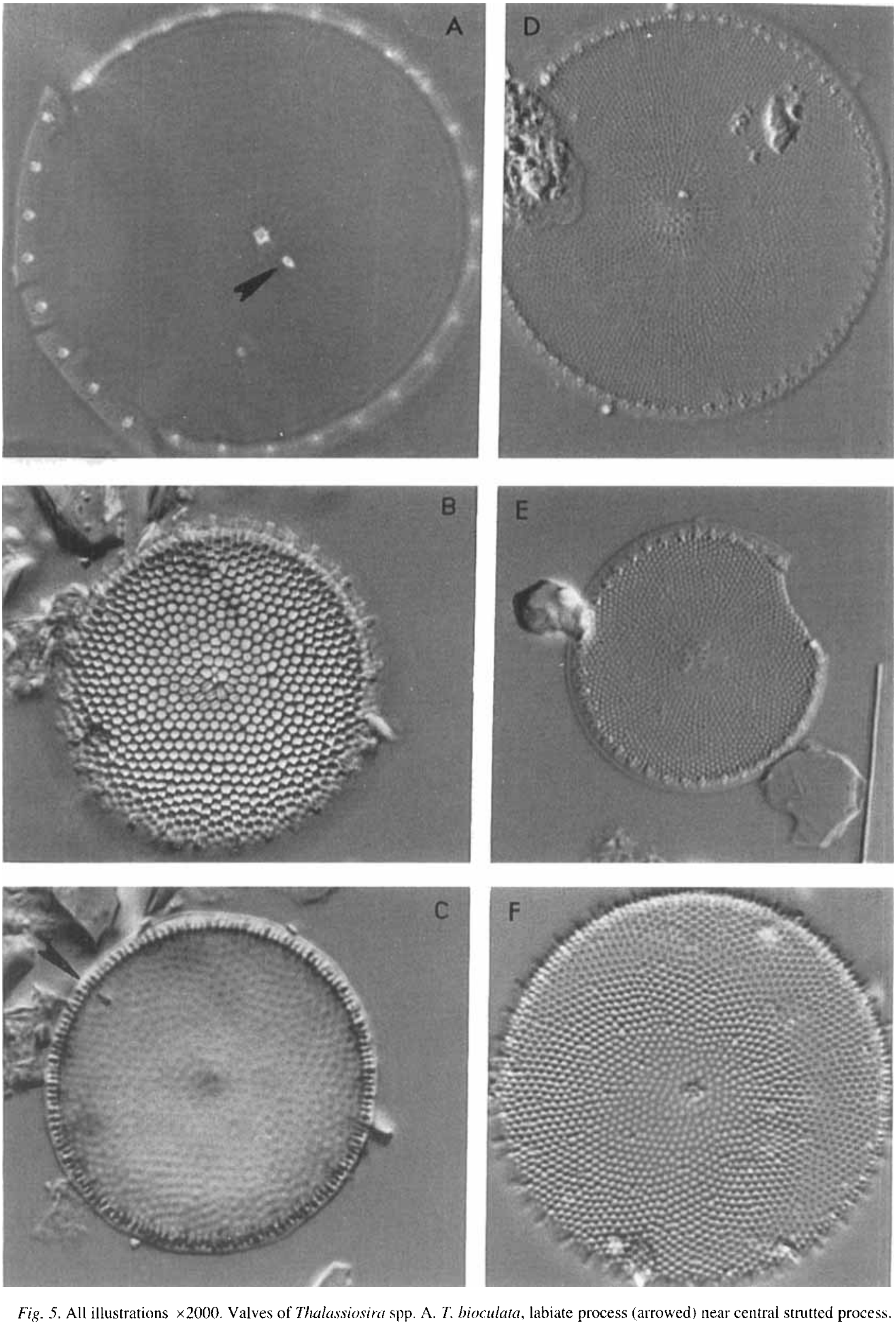


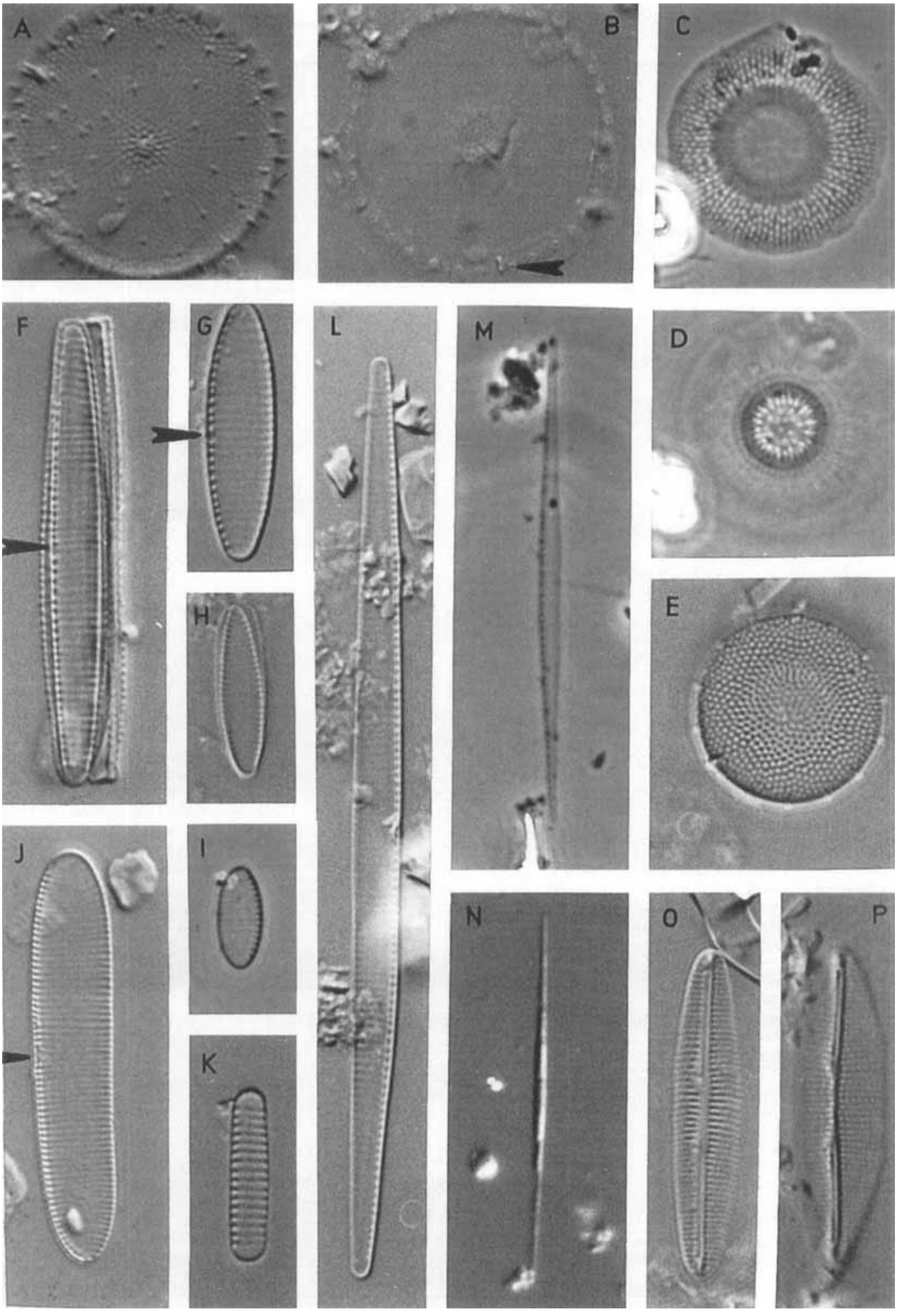
Fig. 5. All illustrations ×2000. Valves of *Thalassiosira* spp. A. *T. bioculata*, labiate process (arrowed) near central strutted process. B and C. *T. antarctica* var. *borealis* resting stage, at two different foci, few central strutted processes, labiate process inside view, arrowed (C). D and E. *T. hyalina*, vegetative cell (D), more coarsely silicified resting cell (E), many central and one marginal ring of strutted processes. F. *T. gravida*, many strutted processes in the centre, on valve face and along the margin. All illustrations are light micrographs of permanent mounts.

Table 1. List of species recorded in the net hauls from Kongsfjorden in July 1988. Classification after Van den Hoek et al. 1995. Explanation: cc = predominant, c = common, r = rare, [1] with resting spores.

Scientific names	Synonyms
HETEROKONTOPHYTA	
Chrysophyceae	
Dinobryon balticum (Schütt) Lemmermann cc	*D. pellucidum* Levander
D. belgicum Meunier	
D. faculiferum (Willén) Willén	*D. petiolatum* Willén
Meringosphaera mediterranea Lohmann	
Bacillariophyceae (= Diatomophyceae)	
Achnanthes sp. r	
Actinoccyclus curvatulus Janisch c	*Coscinodisus curvatulus* Grunow
A. subtilis (Gregory) Ralfs in Pritchard r	
Bacterosira bathyomphala (Cleve) Syvertsen & Hasle[1] r	*B. fragilis* (Gran) Gran, *Coscinodiscus bathyomphalus* Cleve
Berkeleya rutilans (Trentepohl ex Roth) Grunow r	
Chaetoceros borealis Bailey r	
C. convolutus Castracane	
C. decipiens Cleve	
C. furcellatus Bailey[1]	
C. mitra (Bailey) Cleve r	
C. socialis Lauder[1] r	
Chaetoceros sp., single-celled	
Cocconeis costata Gregory	
C. scutellum Ehrenberg	
Cylindrotheca closterium (Ehrenberg) J. Lewin & Reimann c	*Nitzschia closterium* (Ehrenberg) W. Smith
Diatoma elongatum (Lyngbye) Agardh r	
Diploneis spp.	
Fragilaria striatula Lyngbye r	
Fragilariopsis atlantica Paasche	*Nitzschia paaschei* Hasle
F. cylindrus (Grunow) Krieger in Helmcke & Krieger	*Fragilaria cylindrus* Grunow, *Nitzschia cylindrus* (Grunow) Hasle
F. oceanica (Cleve) Hasle[1] c	*Fragilaria oceanica* Cleve, *Nitzschia grunowii* Hasle
F. pseudonana (Hasle) Hasle	*F. nana* (Steemann Nielsen) Paasche *pro parte*, *Nitzschia pseudonana* Hasle
Grammatophora cf. *arcuata* Ehrenberg r	
Gyrosigma fasciola var. *tenuirostris* (Grunow) Cleve	
G. tenuissimum var. *hyperborea* (Grunow) Cleve	
Leptocylindrus danicus Cleve r	
Licmophora cf. *hyalina* (Kützing) Grunow	
Navicula directa (W. Smith) Ralfs	
Navicula spp.	
Nitzschia angularis var. *kariana* Grunow in Cleve & Grunow	
N. frigida Grunow r	
N. hudsonii Poulin & Cardinal r	
N. hybrida Grunow r	
N. lanceolata var. *pygmea* Cleve	
N. pellucida Grunow r	
N. scabra Cleve r	
Plagiotropis scaligera Grunow in Cleve & Grunow r	*Tropidoneis vitrea* var. *scaligera* Grunow
Pleurosigma intermedium W. Smith r	
P. stuxbergii Cleve r	
Pleurosigma spp.	
Porosira glacialis (Grunow) Jørgensen[1] r	
Pseudo-nitzschia delicatissima (Cleve) Heiden r	*Nitzschia delicatissima* Cleve, *Nitzschia actydrophila* Hasle
P. granii (Hasle) Hasle) c	*Nitzschia granii* Hasle
P. seriata f. *obtusa* (Hasle) Hasle r	*Nitzschia seriata* f. *obtusa* Hasle
Rhizosolenia hebetata Bailey f. *hebetata* r	
R. hebetata f. *semispina* (Hensen) Gran	
Synedra camtschatica Grunow r	
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen r	*Synedra hyperborea* Grunow
Tabularia spp.	

Table 1. contd.

Scientific names	Synonyms
Thalassiosira antarctica Comber var. *borealis* G. Fryxell, Douchette & Hubbard[1)]	
T. bioculata (Grunow) Ostenfeld r	
T. bioculata var. *raripora* Gaarder (provisional name)	
T. gravida Cleve cc	
T. hyalina (Grunow) Gran[1)]	
T. nordenskioeldii Cleve[1)] c	
Thalassiothrix longissima Cleve & Grunow r	
Trachyneis aspera (Ehrenberg) Cleve r	
Dictyochophyceae	
Apedinella spinifera (Throndsen) Throndsen	*Pseudopedinella spinifera* Throndsen
Dictyocha speculum Ehrenberg	
Pseudopedinella pyriforme N. Carter	
HAPTOPHYTA (=PRYMNESIOPHYTA)	
Chrysochromulina spp.	
Coccolithus pelagicus (Wallich) Schiller f. *pelagicus* r	
Phaeocystis pouchetii (Hariot) Lagerheim cc	
DINOPHYTA	
Alexandrium ostenfeldii (Paulsen) Balech & Tangen c	*Goniodoma ostenfeldii* Paulsen
Amphidinium sp.	
Amylax triacantha (Jørgensen) Sournia	*Gonyaulax triacantha* Jørgensen
Ceratium arcticum (Ehrenberg) Cleve var. *arcticum* r	
Cochlodinium spp.	
Dinophysis acuminata Claparède & Lachmann c	
D. norvegica Claparède & Lachmann	
D. ruudii (Braarud) Balech	*Phalacroma ruudii* Braarud
Gonyaulax parva Ramsfjell c	
G. spinifera (Claparède & Lachmann) Diesing	
Gymnodinium abbreviatum Kofoid & Swezy	
G. lohmannii Paulsen r	
Gymnodinium sp.	
Gyrodinium grenlandicum Braarud	
Gyrodinium sp.	
Peridinium faeroense Paulsen c	*Scrippsiella trochoidea* (Stein) Balech, *Scrippsiella faeroense* (Paulsen) Balech & Soares, *Peridinium trochoideum* (Stein) Lemmermann, *Glenodinium trochoideum* Stein
Phalacroma rotundatum (Claparède & Lachmann) Kofoid & Michener	*Dinophysis rotundata* Claparède & Lachmann
Prorocentrum balticum (Schiller) Loeblich III r	
Protoperidinium bipes (Paulsen) Balech	
P. brevipes (Paulsen) Balech c	
P. conicoides (Paulsen) Balech r	
P. islandicum (Paulsen) Balech	
P. cf. *ovatum* (Schütt) Balech	
P. pallidum (Ostenfeld) Balech	
P. pellucidum Bergh c	
P. cf. *quarnerense* (Schröder) Balech	
EUGLENOPHYTA	
Eutreptiella braarudii Throndsen	
CHLOROPHYTA	
Prasinophyceae	
Pyramimonas sp.	
ZOOMASTIGOPHORA	
Choanoflagellidea (=Craspedophyceae)	
Bicosta spinifera (Throndsen) Leadbeater	*Salpingoeca spinifera* Throndsen
Diaphanoeca sp.	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sense that they were either originally described from the Arctic, are restricted to the Arctic or appear in greatest abundances in the Arctic. Several of these diatoms often occur in mass concentration, e.g. *Thalassiosira nordenskioeldii* in the plankton ("enormous large masses, floating on the surface of the sea and colouring it for many miles", Cleve 1873, p. 7) and *Melosira arctica* ("communicating a brown tinge to the water in Melville Bay", Dickie 1852, p. cxcvi) or in decimetre-thick mats below multi-year ice in the central polar basin (Syvertsen 1991).

The prevalence of diatoms in arctic waters is most likely due to their prolific growth on sea ice and subsequent release into the water. The ice broke up in Kongsfjorden in May in 1988, and the little ice left in July could either be sea-ice floes or fragments of glacier-derived ice (Dowdeswell & Forsberg 1992). We have no sea-ice samples from Kongsfjorden in July 1988 and have to rely on information in the literature on arctic sea-ice diatoms in general.

Syvertsen (1991) differentiated between three types of sea ice in the Barents Sea, distinguished by thickness, age and seasonal distribution. Following Syvertsen's scheme the majority of diatoms identified in our investigation may have been living below or may have been released from the under-surface of the thinner, first year ice e.g. *Thalassiosira* spp. and *Bacterosira bathyomphala* (Fig. 6B–E). A smaller fraction, including *Nitzschia frigida* (Fig. 7J) may belong to the"first year sub-ice assemblage" of the thicker, first year ice. The only indication of any influence of the "multi-year sub-ice assemblage" present in the central polar basin under metre-thick ice on the plankton flora in Kongsfjorden in July 1988 was a single record of *Synedropsis hyperborea*. This species is epiphytic on *Melosira arctica*, the diatom forming the mats or rope-like extensions under the multi-year ice (Syvertsen 1991).

Fragilariopsis oceanica (Fig. 6F and G) was common in the "First year sub-ice assemblage" in the Barents Sea (Syversten 1991) but is also a successful member of the plankton in our material as well as in the type material ("floating on the surface of the sea together with Thalassiosira . . .", Cleve 1873, p. 23). This is true also for *F. cylindrus* (Fig. 6K), which belongs to the same assemblage and dominates in blooms in the ice-edge zone in the Barents Sea (Hasle 1990; Syvertsen 1991).

Fragilariopsis atlantica (Fig. 6J) was described by Paasche (1961), who reported it as widely distributed in arctic and polar waters in the Norwegian Sea in June 1954 and mainly in the western part in June 1959 at temperatures of about 2°C or less. It has also been found in the Denmark Strait outside the ice border (Hasle 1965) and in the North Pacific (pers. obs. GRH). We have no information about a possible association between this species and sea ice; this species was less common than the other *Fragilariopsis* species.

The *Nitzschia* species recorded (Table 1, Fig. 7D–J) are all reported as sea-ice diatoms (Poulin & Cardinal 1983; Medlin & Hasle 1990) and known from Svalbard as such (C. H. von Quillfeldt pers. com.), but unlike the two *Fragilariopsis* species they were rare in our plankton samples.

Actinocyclus spp. (Fig. 4A–E) seem to occupy a special position in arctic plankton. Syvertsen (1991) reported *Actinocyclus* cf. *curvatulus* from the upper surface of submerged ice floes in a monospecific assemblage. This is probably the species that has been found in great abundances in plankton samples collected in June in the Barents Sea (Hasle 1990) and in August north of Svalbard (unpubl. obs.) and which was the most abundant diatom in the surface samples in the present investigation.

Whereas the planktonic *Pseudo-nitzschia delicatissima* and *P. seriata* f. *obtusa* (Fig. 6L) were rare, *P. granii* was common wherever *Phaeocystis*

Fig. 6. N. Water mount ×1000, the rest ×2000. A. *Thalassiosira gravida*, process pattern as Fig. 5F. B–E. *Bacterosira bathyomphala*. B. Vegetative cell, many central and one marginal ring of strutted processes, marginal labiate process arrowed. C–E. Resting spore, C and D. Secondary valve with central conical protuberance, (C focused on marginal, D on central part of the valve), E. Primary valve. F–K. *Fragilariopsis* spp. F and G. *F. oceanica*, F. Whole vegetative cell, central larger interspace arrowed. G. More coarsely silicified valve of resting cell, central larger interspace arrowed. H–I. *F. pseudonana*, raphe along the right margin. J. *F. atlantica*, central larger interspace arrowed. K. *F. cylindrus*, raphe along left margin. L. *Pseudo-nitzschia seriata* f. *obtusa*, raphe along right margin. M and N. *P. granii*, M. Single valve, raphe along left margin, N. Whole cell with the two chloroplasts. O and P. *Berkeleya rutilans*, single valves with long central nodulus. Except for N, all illustrations are light micrographs of permanent mounts.

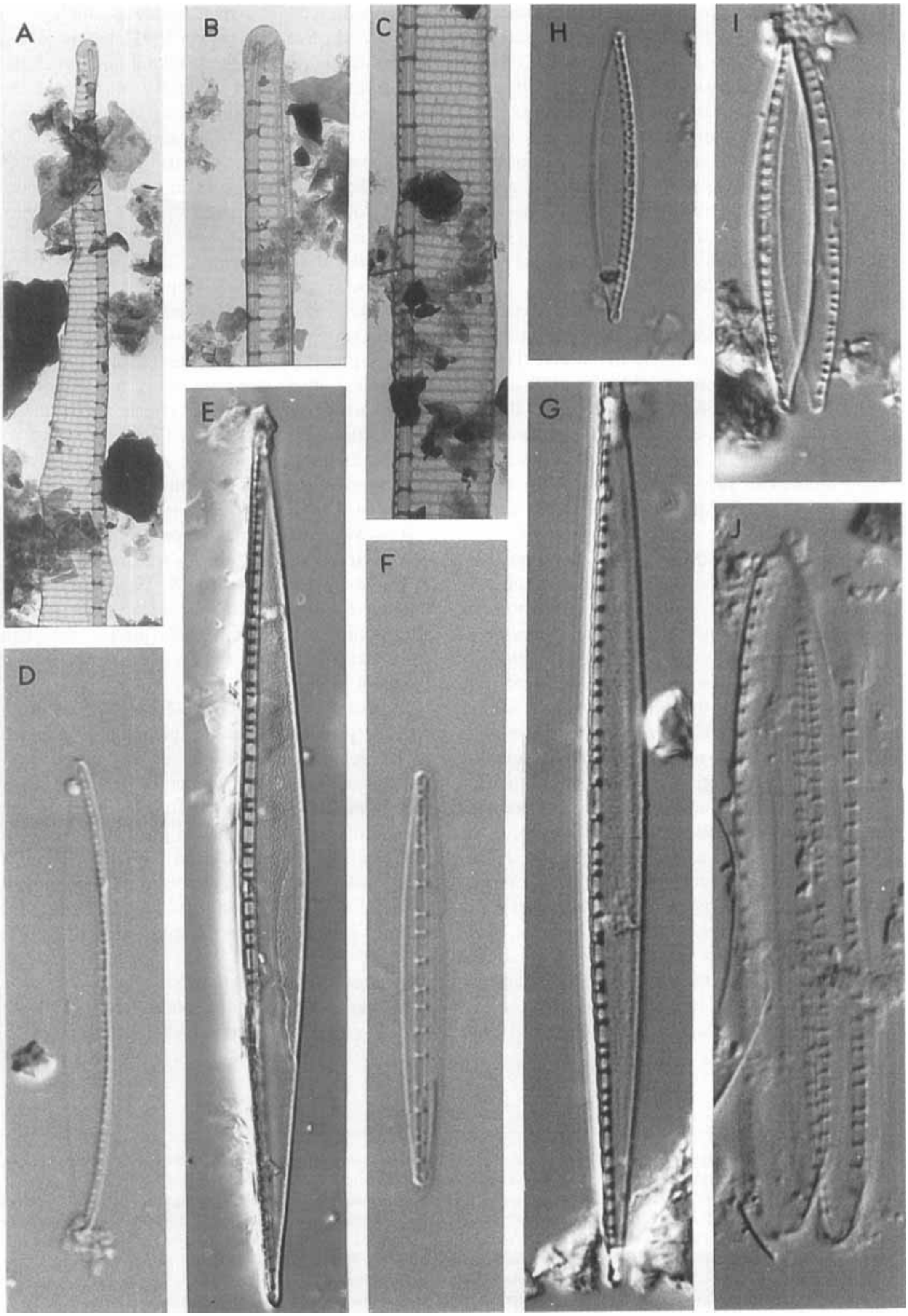

Fig. 7. A–C. Transmission electron micrographs of *Pseudo-nitzschia granii*, A. A half valve showing fibulae, striae and no central larger interspace ×6600, B. Valve end ×8300, C. Central part of the valve, striae with one row of areolae ×8300. D–J. *Nitzschia* spp. E. ×1000, H. ×1500, the rest ×2000. I and J. Whole cells, the rest single valves. D. *N. pellucida*. E. *N. scabra*. F. *N. angularis* var. *kariana*. G. *N. hudsonii*. H and I. *N. lanceolata* var. *pygmea*. J. *N. frigida*. All illustrations are light micrographs of permanent mounts.

was present, even in the net haul from 70 m. *Pseudo-nitzschia granii* is needle-shaped (Fig. 6M and N) and lives either attached to or inside the palmelloid colonies of *Phaeocystis*; it has not been observed in the typical stepped colonies of *Pseudo-nitzschia* but has the valve structure of the genus (Fig. 7A–C).

Fragilariopsis pseudonana (Fig. 6H and I) and a form of *Thalassiosira bioculata* (Fig. 5A) with the provisional name *Thalassiosira bioculata* var. *raripora* (Fig. 4F and G), are important components of the summer plankton in the Norwegian Sea, mainly in the Atlantic part (Paasche 1960; Ramsfjell 1960; Paasche 1961; Paasche & Rom 1962). *Thalassiothrix longissima* is a very long diatom, common in Norwegian Sea investigations but recorded in small cell concentrations. In Paasche's material it was found in Atlantic–Arctic waters, in Ramsfjell's material northeast of Iceland south of 75°N, and in the Barents Sea also in water characterised as "Atlantic" (Hasle 1990). Other large planktonic diatoms, e.g. *Chaetoceros borealis*, *C. decipiens* and *Rhizosolenia hebetata* f. *semispina* (Fig. 3C), occurred together with *T. longissima* in Atlantic water south of 72°N in May 1958 (Paasche & Rom 1962). A fragment of *T. longissima* (Fig. 9H and I) was found in a permanent mount of a net haul from 15 m whereas the other Norwegian Sea diatoms were more common.

The net samples contained also a small fraction of diatoms that were apparently detached from a substratum, e.g. *Cocconeis costata*, *C. scutellum* and *Berkeleya rutilans* (Fig. 6O and P) present on seaweeds in the area and *Licmophora* cf. *hyalina* (Fig. 8D) present in scrapings from the pier. *Cylindrotheca closterium* (Fig. 8A and B), which unlike these species and the following ones was very common in the net samples, may even so have been detached from sea-weeds. *Plagiotropis scaligera* (Fig. 8C) and *Trachyneis aspera* (Fig. 9A and B) are littoral species associated with sand (Round et al. 1990), the former described from Finnmark, North Norway, the latter probably having a wide distribution. *Pleurosigma stuxbergii* and *Gyrosigma tenuissimum* var. *hyperborea* (Fig. 9C and G) are well known from arctic sea ice although also found in plankton in the Arctic (Gran 1908; Poulin 1990), and *Pleurosigma intermedium* and *Gyrosigma fasciola* var. *tenuirostris* (Fig. 9D–F) are also found in the benthic environment (Cardinal et al. 1986) but probably with a wider geographical distribution.

HAPTOPHYTA (=PRYMNESIOPHYTA)

Phaeocystis pouchetii was the only haptophyte occurring in any quantities in our material. The first arctic record of *Phaeocystis* probably goes back to G. O. Sars, who in July 1878 near Jan Mayen experienced clogging of the plankton net by some gelatinous material (Gran 1902, p. 17). *Phaeocystis* started to appear in the literature as "a new pelagic alga" after findings between Lofoten and Varangerfjord in June and July 1882, near the Faeroe Is. in August 1890 and in Jan Mayen coastal waters in July 1892 (Pouchet 1892; Hariot 1893). It was described as *Tetraspora pouchetii* Hariot in Pouchet (1892) and transferred to the new genus *Phaeocystis* Lagerheim by Lagerheim (1893), who in a later paper gave detailed information about the single cells and the large, up to 2 mm, non-motile vegetative colonies (Lagerheim 1896) – a life cycle that about 60 years later was described as polymorphic with palmelloid colonies and flagellated cells (Kornmann 1955).

Phaeocystis globosa Scherffel was described from Helgoland, southern North Sea, where it appeared from end of March to July, sometimes as the predominant phytoplankter (Scherffel 1900). The main diagnostic character of the new species was the globular shape of the colonies. The distribution pattern was also regarded as a distinct character since at that time *Phaeocystis pouchetii* had only been recorded north of 60°N. Later studies of field samples as well as of cultures questioned the existence of two separate species (see Kornmann 1955). The increase of *Phaeocystis* blooms in the 1980s started a renewed interest in this question and investigations that in gross features supported Scherffel's statements. According to Baumann et al. (1994) the temperature tolerances of *P. pouchetii* and *P. globosa* are (−2°C–14°C) and (−0.6°C–22°C), respectively. Jahnke & Baumann (1987) found that the two species differed not only with respect to temperature tolerance, but also in the shape of the colonies. *Phaeocystis pouchetii* formed spherical to cloud-like colonies of delicate mucilage with cells arranged in groups of four, separated by wide zones of cell-free mucilage. The *P. globosa* colonies were globular or more irregularly shaped when getting older, with cells evenly distributed within the solid mucilage. Vaulot et al. (1994) regarded colony shape as not fully reliable, but emphasised pigment composition and genome

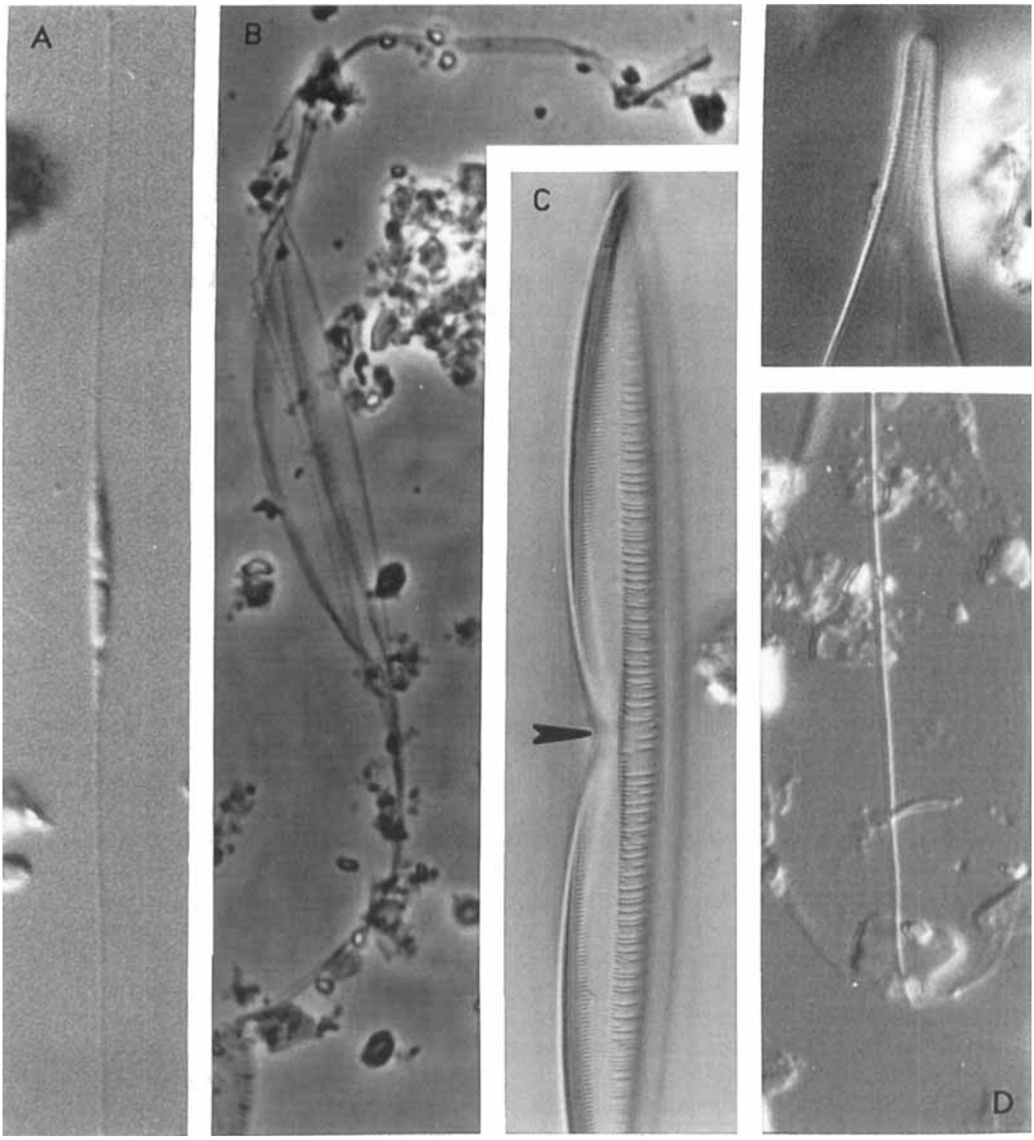

Fig. 8. A and B. *Cylindrotheca closterium*, A. Whole cell in water mount, two chloroplasts, ×1000, B. Cleaned material, two valves and very narrow bands, the two raphes in the middle, ×2000. C. *Plagiotropis scaligera*, valve view with typical striation, location of central nodulus arrowed, ×1000. D. Foot- and head-pole (at the bottom) of *Licmophora* cf. *hyalina*, ×2000. Except for A, all illustrations are light micrographs of permanent mounts.

size as taxonomic markers. However, none of the strains examined were referable to *P. pouchetii*. On the other hand, Medlin et al. (1994) recognised, by using sequence data from the nuclear-encoded ssu rRNA gene, the species status of *P. pouchetii* and *P. globosa* in consistency with the morphological and physiological characters.

As far as the temperature is concerned, both species could be present in Kongsfjorden. Colony morphology was the only character by which the species could be identified in the present study. The *P. globosa* type was not observed either from Kongsfjorden in July 1988 or from north of Svalbard in September 1979 (Heimdal 1983), and the species present was identified as *P. pouchetii*.

In Hornsund (ca 77°N) the maximum cell

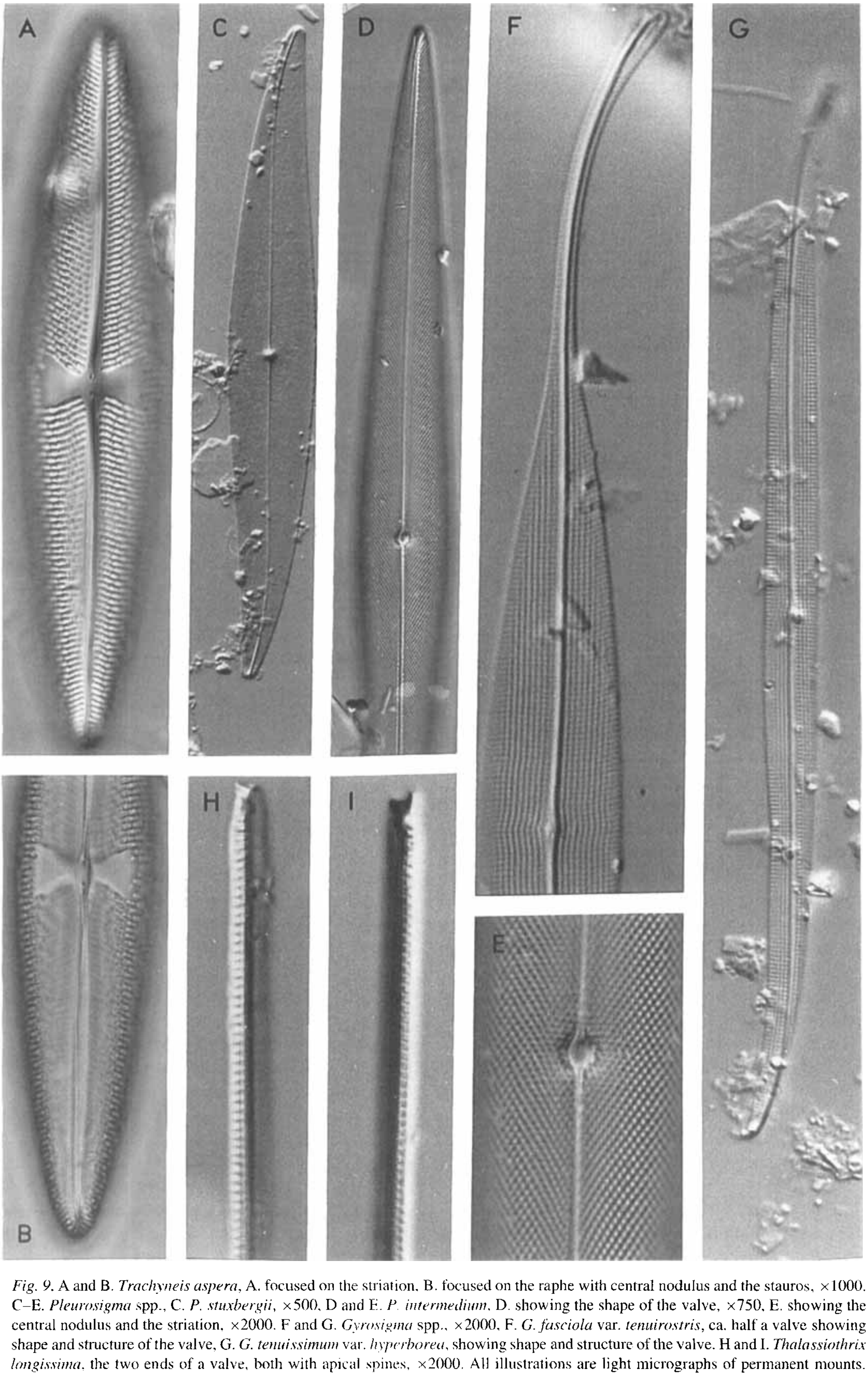

Fig. 9. A and B. *Trachyneis aspera*, A. focused on the striation, B. focused on the raphe with central nodulus and the stauros, ×1000. C–E. *Pleurosigma* spp., C. *P. stuxbergii*, ×500, D and E. *P. intermedium*, D. showing the shape of the valve, ×750, E. showing the central nodulus and the striation, ×2000. F and G. *Gyrosigma* spp., ×2000, F. *G. fasciola* var. *tenuirostris*, ca. half a valve showing shape and structure of the valve, G. *G. tenuissimum* var. *hyperborea*, showing shape and structure of the valve. H and I. *Thalassiothrix longissima*, the two ends of a valve, both with apical spines, ×2000. All illustrations are light micrographs of permanent mounts.

concentration of *P. pouchetii* was larger at the end of May than in April 1985; in Kongsfjorden (79°N) in 1986 the maximum cell concentration was ten times higher at the end of May than in mid-June while it was not mentioned at all from Kongsfjorden at the end of July 1979 (Eilertsen et al. 1989). Broch (1910) recorded *P. pouchetii* from Isfjorden (78°20′N) in July and August but not as a common and regularly occurring species. In Heimdal's (1983) investigation northwest of Spitsbergen it was found at the northernmost station only, ca 82°N, in late September. Our records of *P. pouchetii* in Kongsfjorden in July 1988 are thus consistent with the literature. The vertical distribution (see above) gives evidence that the bloom in the surface layer was past, and that we were dealing with a sinking population. The apparent better condition of the cells in 10–50 m than in 5 m, i.e., below the thermocline, and even in a net haul from 70 m, may indicate a continued subsurface growth during late summer.

DINOPHYTA

Findings of dinoflagellates in arctic net plankton have been reported since the beginning of the exploration of the arctic phytoplankton, by Moss (1879) and Vanhöffen (1897) from Greenland, by Cleve (1899) and Broch (1910) from Spitsbergen, by Meunier (1910) from the Barents and Kara Seas, from a single station in the Baffin Bay by Gran (1911), and more recently from as far north as 82°N, north of Spitsbergen by Heimdal (1983) and from northern Bering Sea (Gogorev & Okolodkov 1996). All these reports were from July–October, the one by Moss (1879) as late as November which included also dinoflagellate resting spores ("resting spores" of Peridinea in reticulated cases, Moss 1879, p. 126).

Examination of water samples demonstrated the presence of smaller thecate and athecate dinoflagellates in arctic waters (Braarud 1935; Paasche 1960; Ramsfjell 1960; Heimdal 1983). Schei et al. (1979) found in fact small athecate dinoflagellates and other flagellates and no diatoms in water samples from Van Mijenfjord, West Spitsbergen (ca 77°50′N) in the last week of July 1978.

The dinoflagellates were not identified to species by Halldal & Halldal (1973), and *Protoperidinium depressum* was the only one identified by Eilertsen et al. (1989) and Okolodkov (1996) from Kongsfjorden.

Broch's (1910) plankton survey of Isfjorden in July and August 1908 as well as the present one show a mixture of species with a wide geographical distribution, e.g. *Protoperidinium brevipes* (Fig. 11C) and *P. pellucidum* (Fig. 10F), species which may be regarded as brackish and/or arctic in distribution like *Amylax triacantha* (Fig. 12), and species mainly restricted to arctic waters like *Ceratium arcticum* (Fig. 11J).

Okolodkov & Dodge (1996) found that out of ca 250 planktonic dinoflagellate species recorded for the Arctic, only *Alexandrium ostenfeldii*, *Amylax triacantha*, *Ceratium arcticum* and *Dinophysis norvegica* could be classified as arctic-boreal in the meaning of being distributed north of the so-called Ortmann Line (average sea surface temperature 15°C in the Northern Hemisphere). *Dinophysis arctica*, *Protoperidinium islandicum*, *P. thulense* and *P. saltans* were assumed to be bipolar. They also pointed out that only two dinoflagellates, *Peridiniella catenata* and *Gymnodinium* cf. *punctatum* were associated with annual sea-ice.

A few of the dinoflagellates recorded are discussed in more details to point out possible taxonomic problems or biogeographical peculiarities.

Alexandrium ostenfeldii (Fig. 10A and B)

This species was described by Paulsen (1904) in his paper on plankton in the waters around Iceland. Although present as far south as NW Spain (Fraga & Sanchez 1985) and in the Oslofjord in August (Balech & Tangen 1985), it was one of the common dinoflagellates in Kongsfjorden as well as in our unpublished material from the Barents Sea and the waters north of Svalbard. It has an extremely thin-walled theca and was found almost without exceptions with a smooth-walled endocyst. The cell content of the endocyst was sometimes divided into several globular parts. These observations are consistent with Paulsen's mention of the cell content "coming out in a globular mass" and "the contents having divided while the cell was still moving".

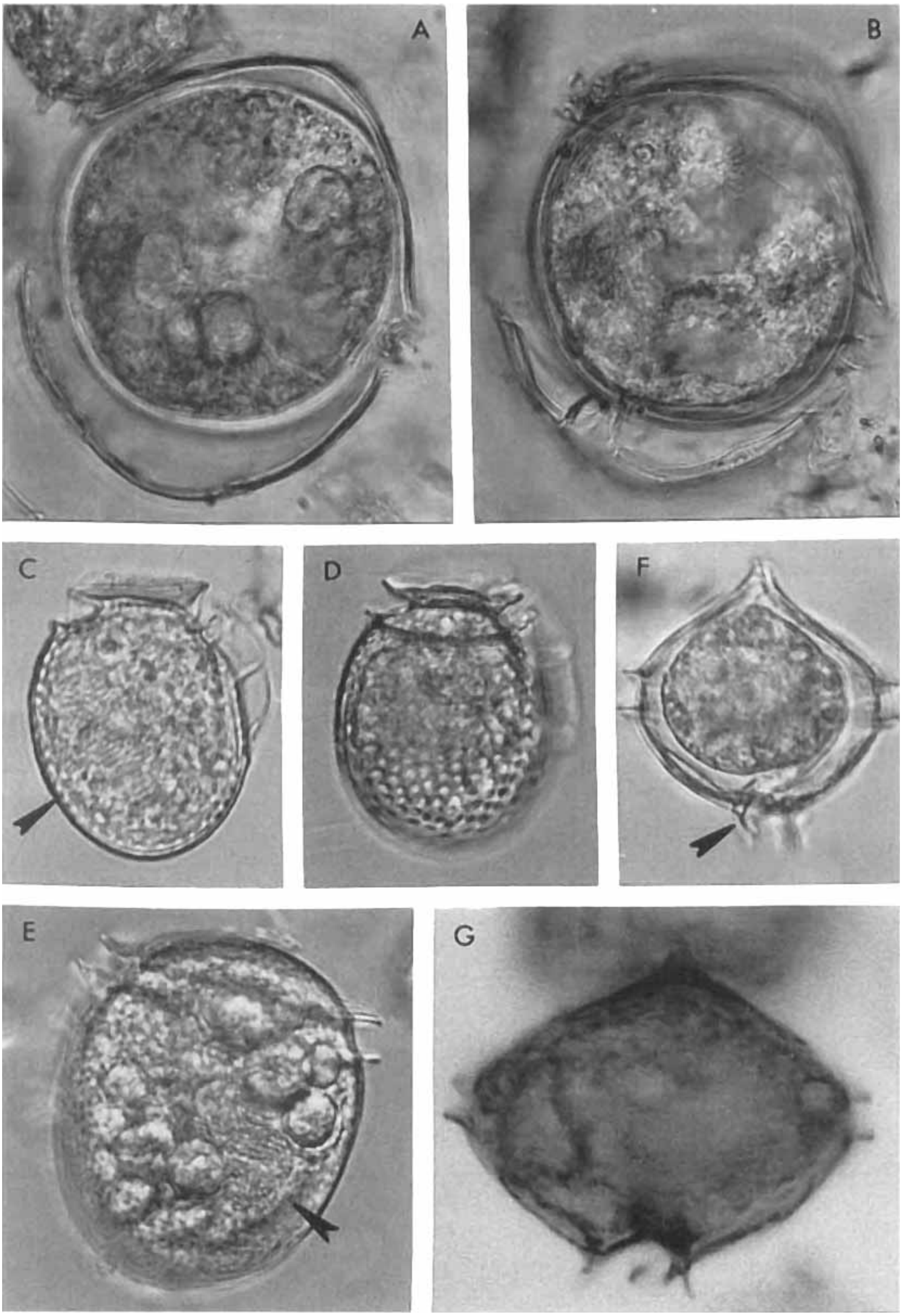

Fig. 10. All illustrations ×1000, water mounts. A and B. *Alexandrium ostenfeldii*, theca with cyst. C and D. *Dinophysis acuminata*, C. showing the nucleus (arrowed) in a more thin-walled specimen, D. a more thick-walled, heavily sculpered specimen. E. *Phalacroma rotundatum*, with the nucleus arrowed. F. *Protoperidinium pellucidum*, dorsal view, curved antapical winged spine arrowed. G. *Protoperidinium islandicum*, ventral view, coarse, winged antapical spines and a third spine or wing.

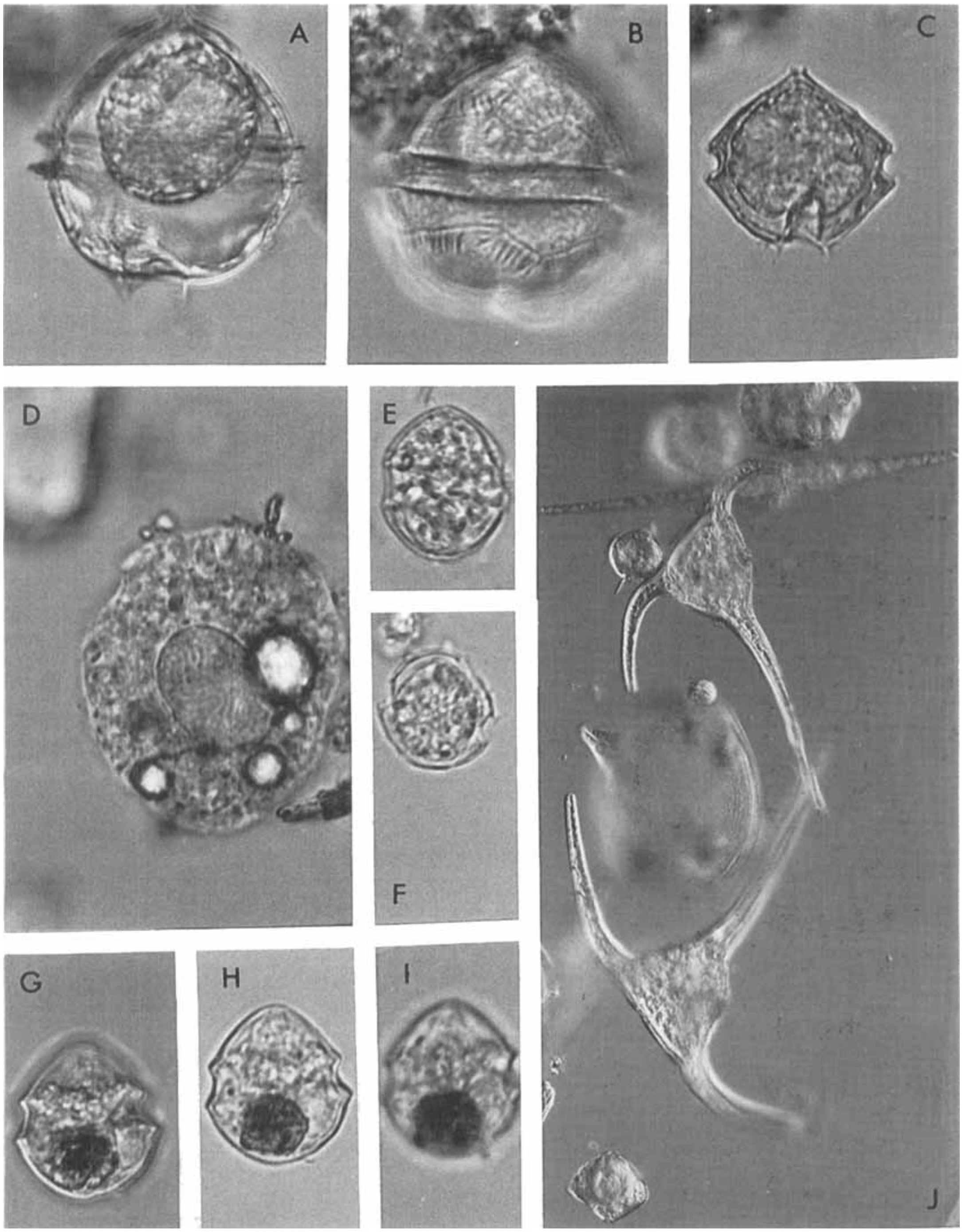

Fig. 11. J. ×ca. 250, the rest ×1000, all water mounts. A, B, D–I. Unidentified dinoflagellates. C. *Protoperidinium brevipes*. D. *Gymnodinium* sp. (?) with large nucleus. J. *Ceratium arcticum*.

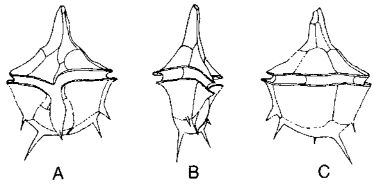

Fig. 12. Amylax triacantha. A. Ventral, B. Lateral, and C. Dorsal views, ×ca. 850, redrawn from Kofoid (1911). All illustrations are light micrographs of permanent mounts.

Dinophysis spp. (Fig. 10C and D)

The genus is well represented in arctic waters, possibly also by species peculiar to the region. Paulsen (1949) pointed out the great confusion concerning the taxonomy of the temperate and cold-water *Dinophysis* species. He suggested the new names (1) *D. granii* for the species which Gran (1902) had identified as *D. granulata* and Broch (1910) as *D. arctica*, (2) *D. subcircularis* for the dinoflagellate Jørgensen (1900a) identified as *D. acuminata* var. *granulata* and Paulsen (1911) as *D. arctica*, and (3) introduced *D. islandica* as a new species from NW Iceland without a valid description (Sournia 1973). Balech (1976) recorded *D. norvegica* and *D. acuta* from the Tromsø area, ca 70°N, but not *D. acuminata*. The *Dinophysis* taxa cited here from Paulsen (1949) were not mentioned in Balech's paper although the great morphological variability of *D. acuminata* was discussed in great detail. The species we have listed as *D. acuminata* Claparède & Lachmann is similar to the one Braarud (1935) illustrated as *D. arctica* Mereschkowsky and Paulsen (1949) as *D. granii*, possibly also *D. islandica* (e.g. Paulsen 1949, Fig. 11, P). It was one of the most common dinoflagellates in our samples. If it is a separate species, the correct name would be *D. granii* Paulsen; if it belongs to *D. acuminata* it differs from specimens in temperate waters by the lack of antapical protuberances and by the possesion of a heavy sculpturing of the cell wall (Fig. 10D).

The species we identified as *Phalacroma rotundata* (Fig. 10E) is most likely the one Paulsen (1949) illustrated as *Phalacroma irregulare* Lebour.

Amylax triacantha (Fig. 12)

This characteristic species was first described from Hjeltefjord, on the western coast of Norway (Jørgensen 1900b). It was illustrated and described as *Ceratium (?) hyperboreum* by Cleve (1900) from Spitsbergen. Meunier (1910) described the genus *Amylax* from the Kara Sea, and Sournia (1984) made the combination *Amylax triacantha*. Kofoid (1911) gave its distribution as "neritic, northern", being present also in the Baltic Sea. It is sometimes fairly abundant in the Oslofjord (pers. obs.), and a special variety was described from Belgian waters (Conrad 1939).

Protoperidinium islandicum (Fig. 10G)

The species was described from Islandic waters in July and August (Paulsen 1904, 1949). In contrast to the other *Protoperidinium* species listed here, the southern range of *P. islandicum* in the Northern hemisphere is most likely in Islandic waters. It has been recorded from several arctic localities, Isfjorden included (Paulsen 1949; Balech 1973). It has a superficial resemblance to another arctic dinoflagellate, *Protoperidinium monacanthum* (Broch) Balech, described from Isfjorden. But, while the latter has one long and another short, thin antapical spine, *P. islandicum* has two short, coarse, winged antapical spines and close to the left one a third spine or wing.

Discussion

The present investigation supports previous findings of dinoflagellates and *Dinobryon* as the prevalent members of the summer surface layer plankton. Most *Protoperidinium* spp. are heterotrophic and chloroplasts may be absent also in some *Gymnodinium* spp. (Steidinger 1996). *Dinobryon balticum* has been found capable of mixotrophy and of exploiting the bacteria-rich marine microaggregates (McKenzie et al. 1995), which may explain why it survives so well in oligotrophic cold waters after a spring diatom bloom. The reduced transparancy of the surface layer thus does not affect these organisms as much as photosynthetic algae. Some, e.g. *Amylax triacantha* and *Dinobryon balticum*, may have a preference for the low salinity found in the Baltic Sea and Oslofjord, although the salinity in Kongsfjorden is about 29–30‰.

Our single coccolithophorid record, viz. *Coccolithus pelagicus* f. *pelagicus*, contrasts Halldal

& Halldal's (1973) findings of the motile form *Coccolithus pelagicus* f. *hyalinus* (Gaarder & Markali) Kleijne in considerably great cell concentrations. The discrepancy is explained, however, by differences in methodology.

The recorded vertical distribution of *Phaeocystis pouchetii* and the presence of diatom species and their resting stages in the subsurface layers, in comparison with the relevant literature (Ramsfjell 1960; Eilertsen et al. 1989), reflect the composition of the spring bloom. Three or perhaps four components seem to be present in addition to *Phaeocystis pouchetii*, of which *P. pouchetii* may have a longer prolific season judging from the healthy cells found in the deeper layers. The most numerous component regarding number of species as well as cell concentration is exemplified by *Bacterosira bathyomphala* (Fig. 6B–E), *Thalassiosira antarctica* var. *borealis* (Fig. 5B and C), *T. hyalina* (Fig. 5D and E), *T. nordenskioeldii*, *Chaetoceros socialis* and *C. furcellatus* (Fig. 3E and F), all found with resting stages, and *Thalassiosira gravida* (Figs. 5F and 6A) as apparently the most abundant one. If ever related to ice, this component would belong to Syvertsen's (1991) "Plankton sub-ice assemblage". The second component consists of species which are associated with ice early in the season and continue to grow prolifically in the plankton, e.g. *Fragilariopsis cylindrus* and *F. oceanica*, the latter with resting stages (Fig. 6G). The next component, the listed *Nitzschia* spp., has evidently sea ice as the main habitat never forming a major part of the plankton. Net samples from Kongsfjorden in early June 1981 showed that *Nitzschia hybrida*, *N. angularis* var. *kariana*, *N. pellucida*, and *N. frigida* were present in the upper 7 m (pers. obs. GRH). This may be an indication that they were living in the water for a time earlier in the summer.

The last component is composed of species of a more oceanic distribution being introduced from further south by the West Spitsbergen Current, e.g. *Fragilariopsis pseudonana*, the small form referred to *Thalassiosira bioculata* and *Thalassiothrix longissima* living in Atlantic waters in the Norwegian Sea. Information gained by the present as well as unpublished observations places *Actinocyclus* spp. in a special group together with *Thalassiosira bioculata* and *T. poroseriata* (Ramsfjell) Hasle with respect to seasonal distribution in the Arctic. Whereas other planktonic diatoms scarcely appear in the surface layers in summer and autumn, those mentioned have been found at one time or another as the predominant species, occurring together with dinoflagellates and *Dinobryon* either far north in the Barents Sea or north of Spitsbergen (pers. obs. GRH). Syvertsen (1991) mentioned *Actinocyclus* cf. *curvatulus* as the diatom most commonly forming centimetre-thick mono specific assemblages on the upper surface of floes in pressure ridges and rafted ice during late summer and autumn in his material. On two occasions, however, he found *Thalassiosira bioculata* in similar habitats. The release of these "ice diatoms" will thus happen late in the season, and they may be so numerous or have a special mechanism that they can compete with dinoflagellates and *Dinobryon*.

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References

Balech, E. 1973: Cuarta contribucion al conocimento del genero *"Protoperidinium"*. *Rev. Mus. Argent. Natural. "Bernadino Rivadavia". Hidrobiol. 3(5)*, 347–368.

Balech, E. 1976: Some Norwegian *Dinophysis* species (Dinoflagellata). *Sarsia 61*, 75–94.

Balech, E. & Tangen, K. 1985: Morphology and taxonomy of toxic species in the *tamarensis* group (Dinophyceae): *Alexandrium excavatum* (Braarud) comb.nov. and *Alexandrium ostenfeldii* (Paulsen) comb.nov. *Sarsia 70*, 333–343.

Baumann, M. E. M., Lancelot, C., Brandini, F. P., Sakshaug, E., & John, D. M. 1994: The taxonomic identity of the cosmopolitan prymnesiophyte *Phaeocystis*: a morphological and ecophysiological approach. *J. Mar. Sys. 5*, 5–22.

Braarud, T. 1935: The "Øst" expedition to the Denmark Strait 1929. II. The phytoplankton and its conditions of growth. *Hvalrådets Skr. 10*, 1–173.

Broch, H. 1910: Das Plankton der schwedischen Expedition nach Spitzbergen 1908. *K. Sven. Vetensk.-Akad. Handl. 45(9)*, 25–64.

Cardinal, A., Poulin, M. & Bérard-Therriault, L. 1986: Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. *Nat. Can. 113*, 167–190.

Cleve, P. T. 1867: Diatomaceer från Spetsbergen. *Öfver. K. Vetensk.-Akad. Förh. 1864 10*, 661–669.

Cleve, P. T. 1873: On diatoms from the arctic Sea. *Bihang K. Sven. Vetensk.-Akad. Handl. 1(13)*, 1–28.

Cleve, P. T. 1899: Plankton collected by the Swedish expedition to Spitzbergen in 1898. *K. Sven. Vetensk.-Akad. Handl. 32(3)*, 3–51.

Cleve, P. T. 1900: Notes on some Atlantic plankton-organisms. *K. Sven. Vetensk.-Akad. Handl. 34(1)*, 1–22.

Conrad, W. 1939: Notes protistologiques. XIII. *Goniaulax triacantha* Jörg., var. nov. *subinermis*. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique 15(57)*, 1–3.

Dickie, G. 1852: Notes on the algae. Pp. cxci–cc in Sutherland, P. C. (ed.): *Journal of a voyage in Baffins Bay and Barrow Straits in the years 1850–1851*. Longman, Brown, Green, and Longman, London.

Dowdeswell, J. A. & Forsberg, C. F. 1992: The size and frequency of icebergs and bergy bits derived from tidewater glaciers in Kongsfjorden, northwest Spitsbergen. *Polar Res. 11*, 81–91.

Ehrenberg, C. G. 1841: *Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-Amerika*. Deutsche Akademie der Wissenschaften Berlin, Berichte. Pp. 202–209.

Eilertsen, H. C., Taasen, J. P. & Weslawski, J. M. 1989: Phytoplankton studies in the fjords of West Spitsbergen: physical environment and production in spring and summer. *J. Plankton Res. 11*, 1245–1260.

Elverhøi, A., Lønne, Ø. & Seland, R. 1983: Glaciomarine sedimentation in a modern fjord environment, Spitsbergen. *Polar Res. 1 n.s.*, 127–149.

Fraga, S. & Sanchez F. J. 1985. Toxic and potentially toxic dinoflagellates found in Galician rias (NW Spain). Pp. 51–54 in Anderson, D. M., White, A. W. & Baden, D. G. (eds.): *Toxic dinoflagellates*. Elsevier, N.Y., Amsterdam & Oxford.

Gogorev, R. M. & Okolodkov, Y. B. 1996: Species composition of the planktonic and sea-ice algae in the Chukchi Sea and Lavrentiya Bay (Bering Sea, August 1991). *Bot. Z. 81*, 35–41.

Gran, H. H. 1902: Das Plankton des Norwegischen Nordmeeres. *Rep. Nor. Fish. Mar. Invest. 2(5)*, 1–222.

Gran, H. H. 1908: Diatomeen. *Nord. Plankton 19*, 1–146.

Gran, H. H. 1911: Phytoplankton. *Rep. Second Nor. Arct. Exped. "Fram" 1898–1902. 27*, 1–28.

Halldal, P. & Halldal, K. 1973: Phytoplankton, chlorophyll, and submarine light conditions in Kings Bay, Spitsbergen, July 1971. *Nor. J. Bot. 20*, 99–108.

Hariot, M. P. 1893: Contribution a la flore cryptogamique de l'ile Jan Mayen. *J. Bot. 7*, 117–121.

Hasle, G. R. 1965: *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. III. The genus *Fragilariopsis*. *Skr. Norske Vidensk.-Akad. Mat.-Nat.vitensk. Klasse. N.S. 21*, 1–49.

Hasle, G. R. 1990: Arctic plankton diatoms: dominant species, biogeography. Pp. 53–56 in Medlin, L. K. & Priddle, J. (eds.): *Polar Marine Diatoms*. British Antarctic Survey, Cambridge.

Hasle, G. R. & Quillfeldt, C. H. von 1996: Marine microalgae. Pp. 375–382 in Elvebakk, A. & Prestrud, P. (eds.): *A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Norsk Polarinstitutt Skrifter 198*.

Hasle, G. R. & Syvertsen, E. E. 1990: Arctic diatoms in the Oslofjord and the Baltic Sea – a bio- and palaeogeographic problem? Pp. 285–300 in Simola, H. (ed.): *Proceedings of the 10th International Diatom Syvmposium*. Koeltz, Koenigstein.

Heimdal, B. R. 1983: Phytoplankton and nutrients in the waters north-west of Spitsbergen in the autumn of 1979. *J. Plankton Res. 5*, 901–918.

Hjelle, A. 1993: *Geology of Svalbard*. Polarhåndbok no. 7. Norsk Polarinstitutt, Oslo. 162 pp.

Jahnke, J. & Baumann, M. E. M. 1987: Differentiation between *Phaeocystis pouchetii* (Har.) Lagerheim and *Phaeocystis globosa* Scherffel. I. Colony shapes and temperature tolerances. *Hydrobiol. Bull. 21*, 141–147.

Jørgensen, E. 1900a: Protistenplankton aus dem Nordmeere in den Jahren 1897–1900. *Bergens Museums Aarbog 1900, 6*, 1–34.

Jørgensen, E. 1900b: Protophyten und Protozoën im Plankton aus der norwegischen Westküste. *Bergens Museums Aarbog 1899, 6*, 1–112, II–LXXXIII.

Kofoid, C. A. 1911: Dinoflagellata of the San Diego region, IV. The genus *Gonyaulax*, with notes on its skeletal morphology and a discussion of its generic and specific characters. *Univ. Calif. Publ. Zool. 8(4)*, 187–286.

Kornmann, P. 1955: Beobachtungen an *Phaeocystis*-Kulturen. *Helgol. Wiss. Meeresunters. 5*, 218–233.

Lagerheim, G. 1893: *Phæocystis*, nov. gen., grundadt på *Tetraspora Poucheti* Har. *Bot. Not. 1893(1)*, 32–33.

Lagerheim, G. 1896: Über *Phæocystis Poucheti* (Har.) Lagerh., eine Plankton-Flagellate. *Öfvers. K. Vetensk.-Akad. Förhandl. 53(4)*, 277–288.

McKenzie, C. H., Deibel, D., Paranjape, M. A. & Thompson, R. J. 1995: The marine mixotroph *Dinobryon balticum* (Chrysophyceae): phagotrophy and survival in a cold ocean. *J. Phycol. 31*, 19–24.

Medlin, L. K. & Hasle, G. R. 1990: Some *Nitzschia* and related diatom species from fast ice samples in the Arctic and Antarctic. *Polar Biol. 10*, 451–479.

Medlin, L. K., Barker, G. L. A., Baumann, M., Hayes, P. K. & Lange, M. 1994: Molecular biology and systematics. Pp. 393–411 in Green, J. C. & Leadbeater, B. S. C. (eds.): The haptophyte algae. *The Systematics Association Special Volume 51*. Oxford Science Publications.

Meunier, A. 1910: *Microplankton des Mers de Barents et de Kara*. Duc d'Orleans Campagne Arctique de 1907. Bulens, Brussels. 355 pp.

Moss, E. L. 1879: Preliminary notice on the Surface-Fauna of the Arctic Seas, as observed in the recent Arctic Expedition. *J. Linnean Soc. Zool. 14*, 122–126.

Okolodkov, Y. B. 1993: Dinoflagellates from the Norwegian, Greenland and Barents Seas, and the Faroe-Shetland Islands area collected in the cruise of r/v "Oceania", in June–July 1991. *Polish Polar Res. 14*, 9–23.

Okolodkov, Y. B. 1996: Net phytoplankton from the Barents Sea and the Svalbard waters (collected on the cruise of the research vessel "Geolog Fersman", in July–September 1992), with emphasis on the *Ceratium* species as indicators of the Atlantic waters. *Bot. Z. 81*, 1–8.

Okolodkov, Y. B. & Dodge, J. D. 1996: Biodiversity and biogeography of planktonic dinoflagellates in the Arctic Ocean. *J. Exp. Mar. Biol. Ecol. 202*, 19–27.

O'Meara, E. 1874: On diatomaceæ from Spitzbergen. *Q. J. Microsc. Sci. 14 N.S.*, 254–261.

Orvin, A. K. 1934: Geology of the Kings Bay region, Spitsbergen. *Skr. Svalbard Ishavet 57*, 1–195.

Paasche, E. 1960: Phytoplankton distribution in the Norwegian Sea in June, 1954, related to hydrography and compared with primary production data. *Rep. Nor. Fish. Mar Invest. 12(11)*, 1–77.

Paasche, E. 1961: Notes on phytoplankton from the Norwegian Sea. *Botanica Marina 2*, 197–210.

Paasche, E. & Rom, A.-M. 1962: On the phytoplankton vegetation of the Norwegian Sea in May 1958. *Nytt Mag. Bot. 9*, 33–60.

Paulsen, O. 1904: Plankton-investigations in the waters round Iceland in 1903. *Medd. Kom. Havunders. Ser. Plankton 1(1)*, 1–41.

Paulsen, O. 1911: Marine plankton from the East-Greenland Sea. III. Peridiniales. *Danmark-Ekspeditionen til Grønlands nordøstkyst 1906–1908 3*, 301–318.

Paulsen, O. 1949: Observations on dinoflagellates. *K. Dan. Vidensk. selsk., Biol. Skr. 6(4)*, 1–67.

Pouchet, M. G. 1892: Sur une algue pélagique nouvelle. *Comptes Rendus Hebdomadaires de la Société de Biologie 9. Série 4(2)*, 34–36.

Poulin, M. 1990: Family Naviculaceae: Arctic species. Pp. 137–148 in Medlin, L. K. & Priddle, J. (eds.): *Polar Marine Diatoms*. British Antarctic Survey, Cambridge.

Poulin, M. & Cardinal, A. 1983: Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebec, Canada). III. Cymbellaceae, Entomoneidaceae, Gomphonemataceae, and Nitzschiaceae. *Can. J. Bot. 61*, 107–118.

Quillfeldt, C. H. von 1996: Common diatom species in arctic spring blooms. 38 pp. in *Ice algae and phytoplankton in North Norwegian and arctic waters: species composition, succession and distribution*. Dr. scient. thesis, University of Tromsø, Norway.

Ramsfjell, E. 1960: Phytoplankton distribution in the Norwegian Sea in June, 1952 and 1953. *Rep. Nor. Fish. Mar. Invest. 12(10)*, 1–112.

Round, F. E., Crawford, R. M. & Mann, D. G. 1990: *The Diatoms, Biology & Morphology of the Genera*. Cambridge University Press, Cambridge. 747 pp.

Schei, B., Eilertsen, H. C., Falk-Petersen, S., Gulliksen, B. & Taasen, J. P. 1979: Marinbiologiske undersøkelser i Van Mijenfjorden (Vest-Spitsbergen) etter oljelekkasjen ved Sveagruva 1978. *Tromura, Naturvitenskap 2*, 1–50.

Scherffel, A. 1900: *Phaeocystis globosa* nov. spec. nebst einigen Betrachtungen über die Phylogenie nieder, insbesondere braunen Organismen. *Wissenschaftliche Meeresuntersuchungen. Neue Folge. Vierter Band. Abteilung Helgoland*, 1–29.

Sournia, A. 1973: Catalogue des espèces et taxons infraspécifiques de Dinoflagellés marins actuels. *Beiheft zur Nova Hedwigia 48*, I–X, 1–92.

Sournia, A. 1984: Classification et nomenclature de divers dinoflagellés marins (Dinophyceae). *Phycologia 23*, 345–355.

Steidinger, K. A. in Collaboration with K. Tangen 1996: Dinoflagellates. Pp. 387–584 in Tomas, C. R. (ed.): *Identifying Marine Phytoplankton*. Academic Press, San Diego.

Syvertsen, E. E. 1991: Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. Pp. 277–287 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Res. 10(1)*.

Trætteberg, A. 1982: Havis. Pp. 59–72 in Celius, H. & Rønning, O. I. (eds.): *Teknologi i Arktis*. Tapir, Trondheim.

Van den Hoek, C., Mann, D. G. & Jahns, H. M. 1995: *Algae. An introduction to phycology*. Cambridge University Press, Cambridge. 623 pp.

Vanhöffen, E. 1897: Die Fauna und Flora Grönlands. *Grönland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891–1893, 2*, 1–381.

Vaulot, D., Birrien, J.-L., Marie, D., Casotti, R., Veldhuis, M. J. W., Kraay, G. W. & Chrétiennot-Dinet, M.-J. 1994: Morphology, ploidy, pigment composition, and genome size of cultured strains of *Phaeocystis* (Prymnesiophyceae). *J. Phycol. 30*, 1022–1035.