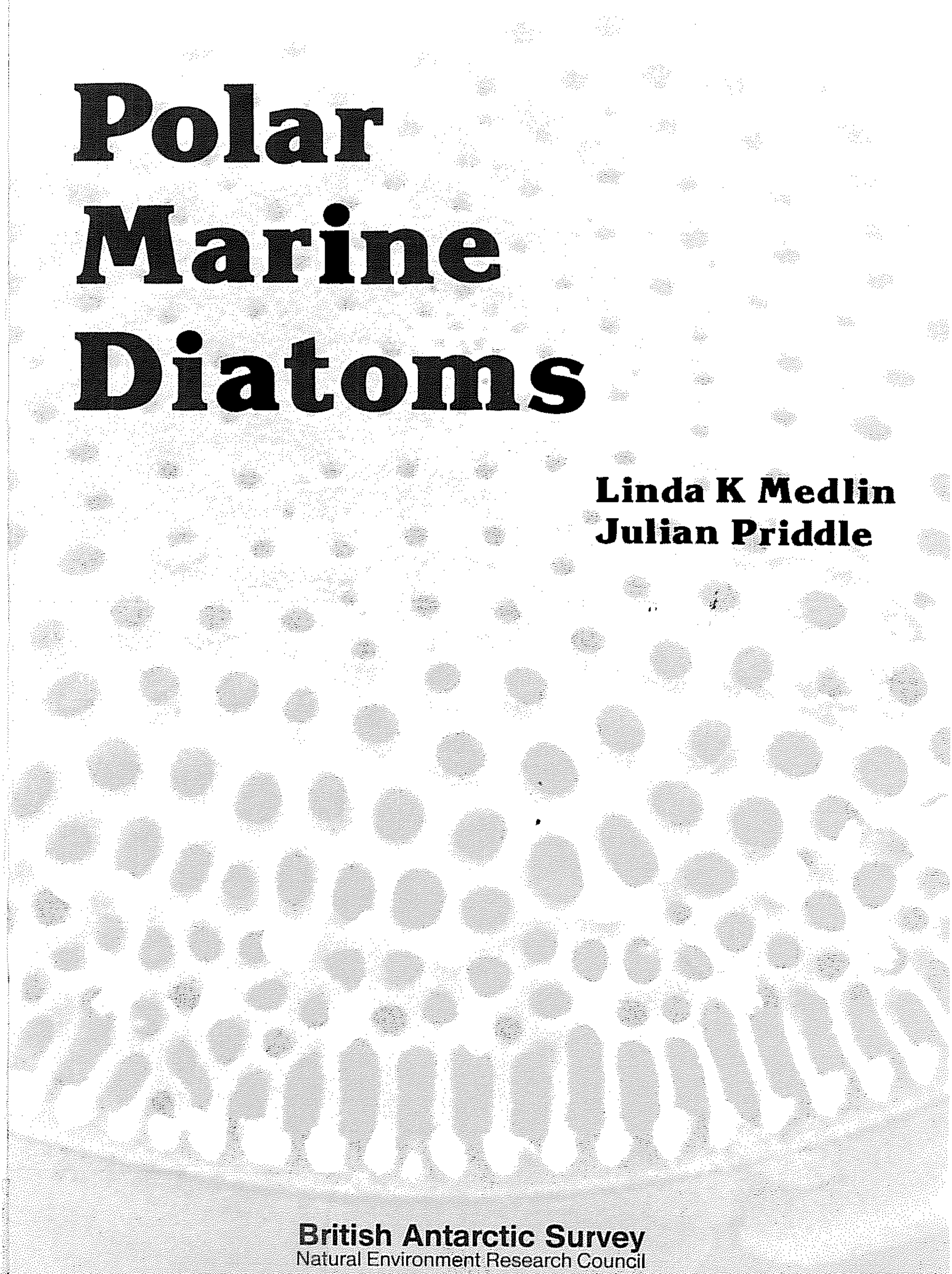


Polar Marine Diatoms

Linda K Medlin
Julian Priddle

British Antarctic Survey
Natural Environment Research Council

Published by the British Antarctic Survey,
Natural Environment Research Council,
High Cross, Madingley Road, Cambridge CB3 0ET, UK

First published 1990

ISBN 0 85665 140 0

COVER PHOTOGRAPH: DETAIL OF THE VALVE OF *THALASSIOSIRA* (SEM BY G. GIBBS AND R. W. JORDON)

INTRODUCTION

Diatoms form conspicuous elements of the microbial communities of many polar marine environments. They may achieve very high biomass in the plankton, where they commonly dominate the net phytoplankton and are the foundation of the pelagic food web. Microbial communities dominated by diatoms develop both underneath and within sea-ice, often reaching biomass which is high enough to give obvious brown colour to the undersides of floes, and the visual impression is more striking than the dense diatom blooms of the summer plankton. The siliceous frustules of diatoms in both communities ensures the preservation of these communities in the sediment record.

These algae have a long history of study in polar regions. Early investigations concentrated on the identification of species in samples brought back to Europe by the various polar expeditions. More recent research has expanded the scope of diatom studies to investigate their ecology and their role within the ecosystem. Polar environments are markedly seasonal and this impinges on plants as the most fundamental level of the food web. The imput of light energy for photosynthesis is concentrated into the short polar summer, where daily insolation may be higher than that at the equator, whilst the winter is a time where plant growth in the euphotic zone may be insufficient to counteract losses. The unusual environments within and under the sea-ice create unique conditions where diatoms are growing in very low illumination and in unusual chemical conditions.

This book examines diatoms in polar marine environments, and is subdivided into three parts. The environments and their communities are covered in the first section. The physical and chemical environment of the sea-ice is described followed by summary of the ecosystems associated with it and a detailed survey of ice-associated diatom communities. The problems of sampling in this very complex system are covered. Plankton environments are considered from the physical and ecosystem perspectives, with a more detailed description of the diatom communities being provided for the Arctic. Finally, there is a chapter on the palaeontological significance of diatoms in the sedimentary record of the polar oceans.

The second section of the book is a taxonomic guide to most of the important genera and species found in the polar marine phytoplankton and in sea-ice communities. Such information should not be regarded as the sole preserve of specialists. All biologists need to know their study organisms as well as what they are doing or where they are found. However, taxonomic information is often difficult to find and may even then be impossible to use. A glossary of terms is included to guide the non-specialist through the maze of current diatom terminology and to provide visual descriptions for terms used in the keys. Emphasis has been placed on a practical taxonomy based on light microscopy. Not all species are covered, and there are a few genera that could not be included. This taxonomic section should complement the earlier book "Handbook of the Common Plankton Diatoms of the Southern Ocean" by Priddle and Fryxell and we have only included those genera in this manual not treated there or if there has been a certain amount of revised nomenclature in a particular genus.

Finally, the bibliography contains not only references cited in the preceding chapters but also additional material, which the authors have identified as being of importance in the study of polar diatoms and their environments.

The idea for this manual arose from a meeting of polar diatomists held in Bristol in 1986, prior to the 9th International Symposium on Diatoms. The previous symposium had included a workshop on polar diatoms, which identified a need for closer collaboration in the fields of taxonomy and ecology. The production of this manual was suggested as a part of this collaboration and as a way of bringing the information to a wider audience. As well as including contributions from the participants in the Bristol meeting and a subsequent workshop in Bremerhaven in 1988, we have solicited contributions from specialists outside diatom research.

We would like to thank the organising committee and the participants of both colloquia for their help and encouragement in the publication of this manual. We are extremely grateful to all the authors for their contributions to the manual and for their patience in awaiting its publication. We thank Tim Colborn for drawing and redrawing the figures of *Rhizosolenia*, *Corethron*, and *Nitzschia* spp., Susan Escott, Gillian Lockett, Diane Spencer, Mary Taylor, Julie Thomson and Christine Thulbourn for their help with the preparation of the chapters, and David Thomas for access to his bibliography of polar diatom. Special thanks is extended to Bo Sundström, the late Horace Barber, E. Haworth, and D.G. Mann for allowing us to reproduce figures from their books and theses to Richard W. Jordan and Gill Gibbs for their scanning electron micrographs and to Grethe Hasle for permission to reproduce the plates from her papers on the Sections *Fragilariopsis*, *Nitzschiella*, and *Pseudonitzschia* of the genus *Nitzschia*.

LIST OF CONTRIBUTORS

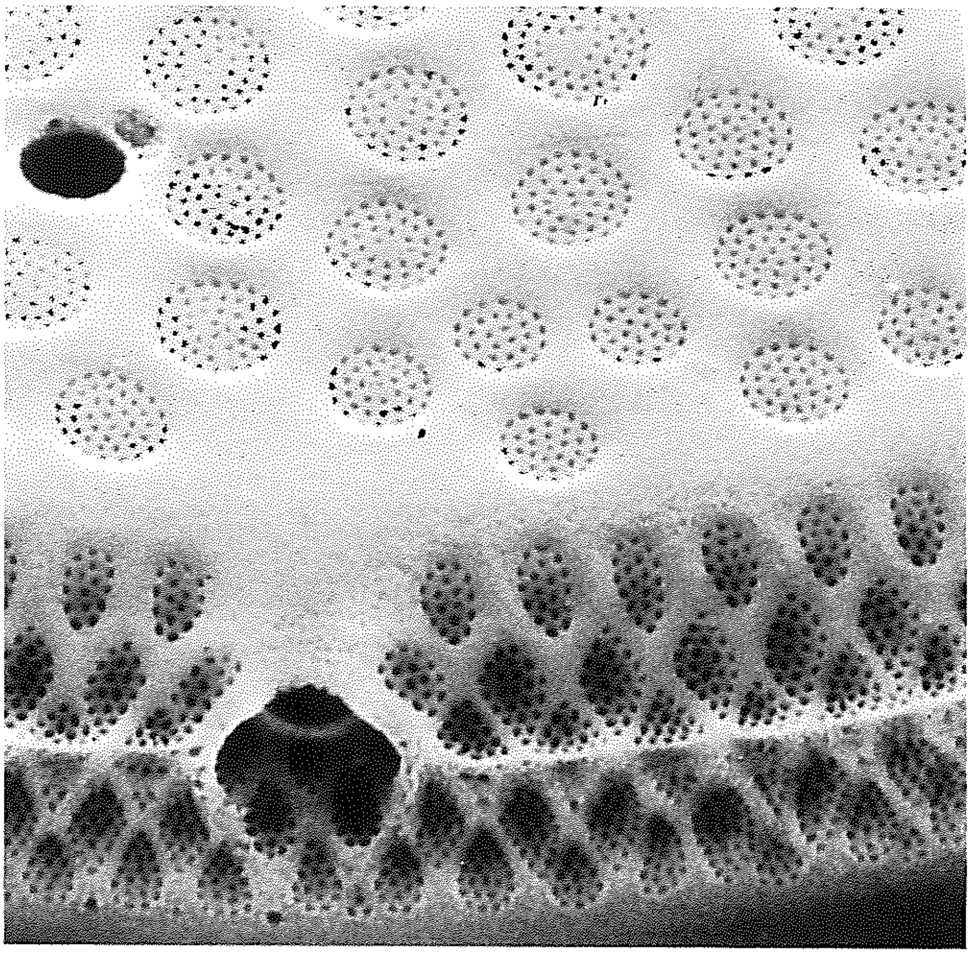
P. I. Bonham	University of Tasmania, Botany Department, GPO Box 252C, Hobart, Tasmania 7001, Australia
Eddy C. Carmack	Institute of Ocean Sciences, Sidney, British Columbia, V8L 4B2, Canada
Greta A. Fryxell	Texas A&M University, Department of Oceanography, College Station, Texas 77043, USA
Rainer Gersonde	Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstraße, D-2850 Bremerhaven, West Germany
Grethe R. Hasle	University of Oslo, Department of Biology, Marine Botany Section, P.O. Box 1069 Blindern, N-0316 Oslo 3, Norway
Rita A. Horner	4211 NE 88th St., Seattle, Washington 98115, USA
Jeffrey R. Johansen	Department of Botany, John Carroll University, Cleveland, Ohio 44118, USA
Richard W. Jordan	British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
Linda K. Medlin	University of Bristol, Botany Department, Bristol BS8 1UG, UK
T.B.B. Paddock	British Museum (Natural History), Cromwell Road, London SW7 5BD, UK
Michel Poulin	National Museum of Natural Sciences, Botany Division, Ottawa, Ontario K1A 0M8, Canada
Julian Priddle	British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
Egil Sakshaug	The Biological Station, University of Trondheim, Bynesveien 46, N-7018 Trondheim, Norway
Vernon A. Squire	Department of Mathematics and Statistics, University of Otago, P.O. Box 56, Dunedin, New Zealand
James H. Swift	Scripps Institution of Oceanography, La Jolla, California 92037, USA
Erik E. Syvertsen	University of Oslo, Department of Biology, Marine Botany Section, P.O. Box 1069 Blindern, N-0316 Oslo 3, Norway
David P. Thomas	Botany Department, University of Tasmania, GPO Box 252C, Hobart, Tasmania 7001, Australia

TABLE OF CONTENTS

ECOLOGY

TAXONOMY

Ecology



CHAPTER 1

SEA ICE:

ITS FORMATION, DISTRIBUTION AND PROPERTIES

Vernon A. Squire

In the Northern Hemisphere sea ice occupies some 15 million km^2 in March, the month of maximum extent, and some 8.4 million km^2 in August, the month of minimum extent. In the Southern Hemisphere there is greater seasonal variability. At its maximum extent (September) Antarctic sea ice covers approximately 20 million km^2, but in February at the end of the austral summer the ice recedes to its minimum of only 4 million km^2. Implicit in these statistics is a particularly important point, namely that Antarctic sea ice is predominantly less than a year old. Whereas some multi-year ice is found in Antarctica, for example in the Western Weddell Sea, the Bellingshausen Sea, the Amundsen Sea and to the east of Ross Ice Shelf, it is in the minority. In the Arctic and sub-Arctic seas the proportion of multi-year to younger ice forms varies markedly with location. In the central Arctic Basin, for instance, mainly multi-year sea ice is found. In the Bering Sea it is all first year. In the Greenland Sea a mix of first- and multi-year ice is found, with most of the older ice originating in the Arctic Ocean.

LIMITS AND DISTRIBUTION

Satellite remote sensing has revolutionised our ability to monitor sea ice limits and distribution in the polar regions. Hitherto, such data could only be based on the few expeditions which ventured into polar waters, and on observations from ships of opportunity or aircraft. Although we are still refining satellite instrumentation, especially in the sense of improving resolution, past and present sensors have enabled us systematically to map sea ice morphology and limits on seasonal and annual timescales for the first time. Satellite sensors operating at visual frequencies, although suffering from the severe drawback of not being able to 'see' in darkness or through cloud, have provided data on sea ice limits and distribution for many years. Sea ice limits for the Arctic and Antarctic are given in Fig. 1.1.

Of particular importance in the polar regions are the microwave sensors which see through darkness and cloud. These are categorised as passive (e.g. SMMR - scanning multichannel microwave radiometer) which measure naturally emitted incoming radiation, or active (e.g. SAR - synthetic aperture radar) which transmit energy and then receive the reflected signal from the surface. Future satellites such as the European Space Agency's ERS-l or the Canadian 'Radarsat' will be equipped with instruments of this kind.

A fine example of the use of satellite data to provide sea ice limits and distribution is the recent NASA publication on passive microwave observations of Antarctic sea ice distribution (Zwally and others, 1983). This book contains a collection of false colour images and other figures derived from the data produced by the electrically scanning microwave radiometer (ESMR) aboard the Nimbus 5 satellite. Seasonal and annual limits for Southern Ocean sea ice extent are presented, together with maps of brightness temperature and hence concentration. The algorithm used to derive ice concentration from brightness temperature is effective, despite ESMR being a single frequency instrument, because Antarctic sea ice is predominantly first year ice. Thus the ESMR receives microwave radiation from a surface made up of a mixture of only two materials (first year ice: emissivity $\epsilon = 0.92$, and sea water: $\epsilon = 0.44$), so that an appropriate algorithm to derive concentration unambiguously from brightness temperature is possible. However, this algorithm fails and errors are introduced when significant quantities of multi-year ice are present in the radiometric footprint.

In the Arctic, where the ice cover is often made up of several ice types, the single frequency ESMR device cannot give enough information to allow brightness temperature to be converted into ice type percentages. It can still give sea ice limits however (see Parkinson and others, 1987). Multi-channel devices such as SMMR are then used, although the precise algorithm to calculate the amount of multi-year, first year, young ice, and water in the footprint from brightness temperature at various frequencies and polarizations is a subject of current debate. The situation is confused further if meltwater is present on the ice surface.

FORMATION AND GROWTH

The addition of salt to water lowers its freezing point, θ_f. Neumann and Pierson (1966) provide an approximate equation which gives θ_f in °C as a function of salinity S in parts per thousand:

$$\theta_f = -0.003 - 0.0527S - 0.00004\,S^2 \qquad (1)$$

Salinity also affects an important temperature-dependent density change which has a pronounced influence on the way in which ice forms. Fresh water has a maximum density at about 4°C, and thus water cooler than this will float on slightly warmer water. This leads to rapid ice formation as the coldest water is at the surface. With higher salinities, the temperature at which maximum density occurs is depressed until, at $S \leq 22.7$, no density maximum occurs at temperatures above the freezing point (Fig. 1.2). Thus, for seawater of normal salinity, cooling always leads to an increase in density

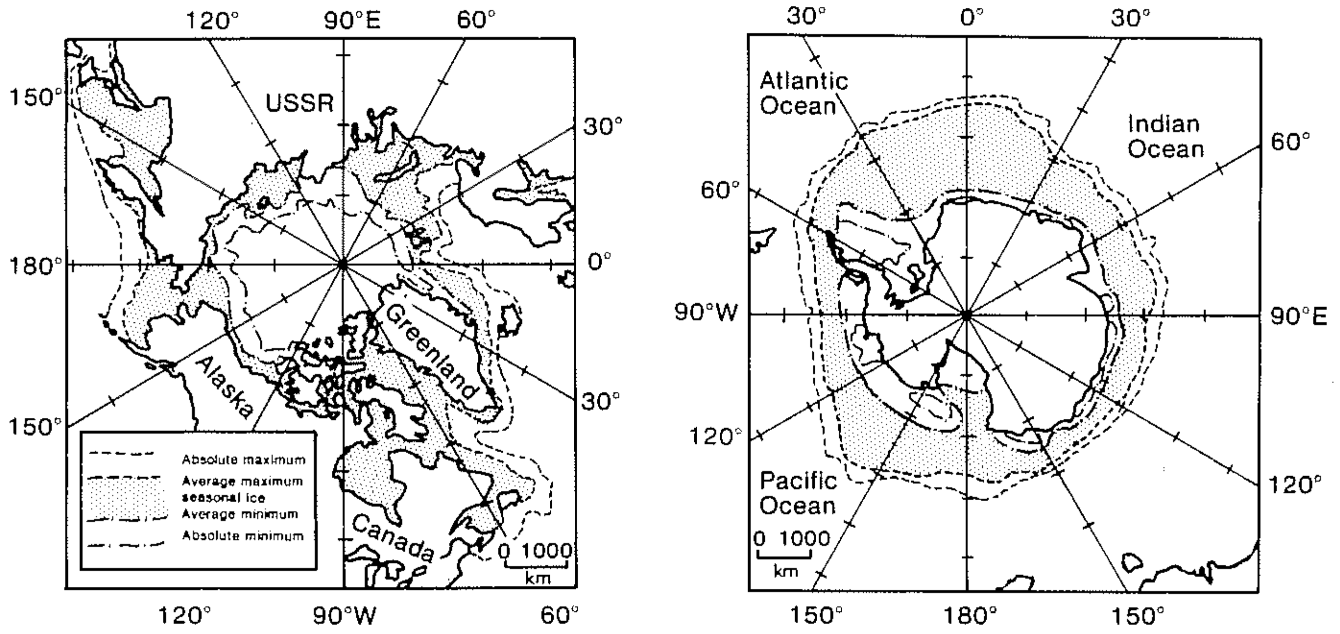


Fig. 1.1 Sea ice limits in the northern and southern hemispheres (after Central Intelligence Agency, 1978). The shaded areas are bounded by average maximum and minimum extents, and so represent the seasonal spread. Absolute maximum and minimum ice extents are also shown.

and hence to convective overturning in the upper water column. For seawater, therefore, it is necessary for a mixed layer of several metres thickness to reach freezing point before ice growth can proceed.

The first crystals to form in seawater are minute spheres of pure ice. These quickly develop into thin circular discs, and later into hexagonal dendritic stars which arise when the radius of curvature of the discoidal shape is too great to dissipate heat and solute into the surrounding liquid. In extremely calm conditions discs and stars would float with their c-axes vertical and, since ice growth is most rapid perpendicular to the c-axis, they would spread laterally across the horizontal surface of the water to form a continuous skim on meeting their adjacent partners. More usually, however, some crystals are trapped with their c-axes at an intermediate angle to the vertical. Furthermore, turbulence introduced into the upper ocean by wind and waves can often stir up the ice crystals to depths of up to several metres, favouring discoidal rather than stellar growth. 'Frazil' ice, the name given to a collection of these first ice crystals, develops into more consolidated ice under the control of the prevailing oceanographic conditions. With no wind or waves, a 1-10 cm layer of frazil ice will soon develop into an ice sheet with columnar fabric due to a geometric selection process which favours those crystals with vertical growth axis (c-axis horizontal). However, when wind and/or waves act, the frazil may form 'pancake' ice, or may be herded into a thick agglomeration known as 'grease' ice, which can consolidate into solid ice if the frazil is of sufficient concentration. Pancake ice is made up of small, roughly circular cakes of accumulated frazil separated by fairly ice-free water. The bumping and buffeting action of sea waves gives pancakes their characteristic raised edges. It is also possible for pancakes to form with grease ice between. Such situations consolidate into what is called a 'composite ice sheet'.

Once a continuous ice skim has formed, subsequent congelation growth is determined by the temperature gradient through the sheet, and by the fact that crystals can no longer grow laterally. The geometric selection process noted above will act, causing crystals growing in unfavoured directions to be eliminated over a transition zone of some 5 to 10 cm. Beneath this will occur a columnar zone where there will be pronounced crystal orientation parallel to the direction of heat flow, and a gradual increase in grain diameter with distance from the ice surface. With time the transition zone may diminish in thickness due to sublimation or recrystallisation into the overlying snow, leaving an ice sheet which is principally columnar. The columnar zone is the result of a dendritic interface where growing ice meets water. This interface, known as the skeletal layer, comprises a delicate layer, 1-3 cm thick, of thin ice platelets extending down into the melt. Between the many parallel platelets making up a single ice grain or crystal are grooves filled with highly concentrated brine. At the root of the groove, occlusion occurs to form brine cells or pockets (Fig. 1.3). Congelation growth beneath an ice sheet formed under more turbulent sea conditions, e.g. a consolidated pancake ice sheet or composite ice sheet, proceeds in a similar manner to that described previously after the turbulence has been damped by the presence of the ice cover.

It is in the skeletal layer, and just above, that one often finds (particularly in early spring) the characteristic yellow-brown colouration that is associated with growth of diatoms. Diatom colouration is also common in platelet ice. This type of ice, which is often seen in Antarctic waters, appears as a fragile array of thin plates arranged at random angles beneath the ice sheet. It is believed to be formed as a result of the relief of supercooling at the underside of the ice or in the water column.

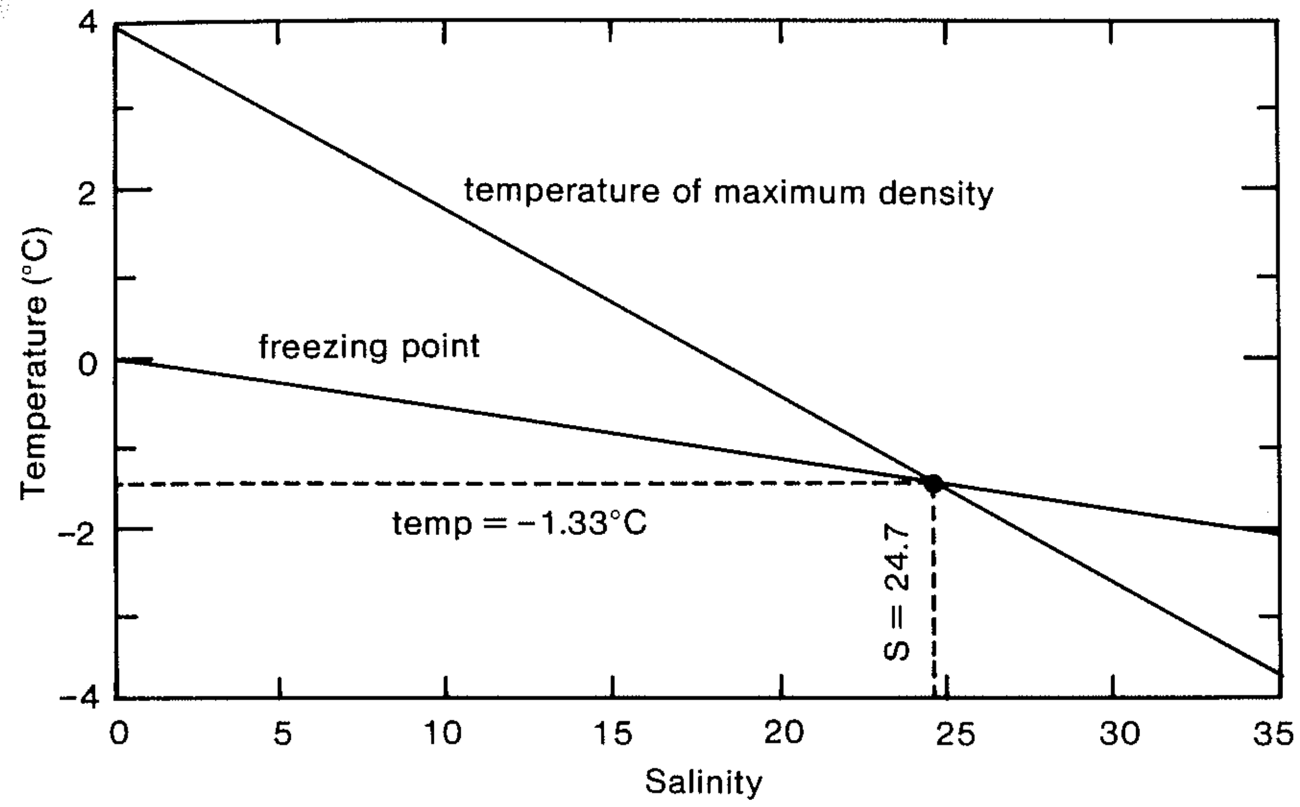


Fig. 1.2 Freezing point and temperature at which density is maximum for water of various salinities. The lines cross at a salinity of 24.7, the point which determines the two different modes of ice formation as described in the text.

Of great importance to the physical and biological properties of sea ice is the brine trapped inside its structure. As indicated above and in Fig. 1.3, within each crystal there is a cellular substructure of evenly-spaced, pure ice platelets with brine inclusions along their boundaries. As the platelets grow they reject brine at the skeletal layer. Most of this brine feeds thermohaline convection beneath the ice, but some is trapped within the crystal substructure as a network of long and narrow brine inclusions (width of the order of 0.05 mm). The platelet spacing, and hence the brine inclusion separation, generally increases with depth into the ice (viz. with decreased growth rate). The presence of brine cells within the ice grains, and the geometry and form of the skeletal layer, is an indication that sea ice grows under conditions of constitutional supercooling (see Weeks and Ackley, 1986, for a complete explanation). In contrast, freshwater ice has a planar interface and rejects all impurities back into the melt as it grows. The brine entrapped in sea ice is not passive. As the sea ice grows and the brine pockets become colder, solid salts precipitate out of solution and pocket walls move. The measured salinity of a brine inclusion at any time is therefore only weakly related to the salinity of the original water in which the ice is growing. These facts may have important consequences to living organisms within brine pockets, where salinities can reach 150; presumably a most inhospitable habitat.

Continued growth leads to various mechanisms of desalination, the most important of which is known as gravity drainage. Gravity drainage includes all mechanisms by which brine drains out of the sea ice under the action of gravity. The brine flows out along vertical, tubular brine drainage channels which are attended by a smaller tributary system of drainage tubes (Lake and Lewis, 1970). A horizontal section through a brine drainage network looks like a starburst pattern, with the arms of the star following grain boundaries. In 1.55 m thick sea ice, main brine channels were measured to be about 0.4 cm in diameter and one occurred every 180 cm^2. In thick ice the number of brine drainage channels appears to be related to average growth rate but not to grain size. Flow in drainage channels is oscillatory with (in general) the outflow being much longer than the upward flow. Eide and Martin (1975) measured an oscillation period of about an hour in young laboratory-grown sea ice, with 8-15 minutes inflow and 45 minutes outflow. This is an important result as it implies that brine drainage channels, which originally contained highly saline brine, are continually flushed with lower salinity sea water from beneath.

Production of frazil is greatest in ice edge regions and in large polynyas as might be expected. Away from such areas it has been found that some 95% of Arctic sea ice is columnar in structure. Where there is significant wind or wave action, however, up to a metre or so of stirred frazil ice can form before columnar congelation growth begins. In the Weddell Sea significant proportions of frazil ice have also been found, often forming several distinct layers within an ice core with each layer separated by a columnar zone. The origin of the high proportion of frazil crystals in Antarctic cores is unknown, although several possible mechanisms can be proposed: wind and wave induced turbulence; release of water with a pressure-depressed freezing point from beneath ice shelves; double-diffusive effects whereby two water masses at freezing point but with different salinities are brought into contact, and thermohaline convection be-

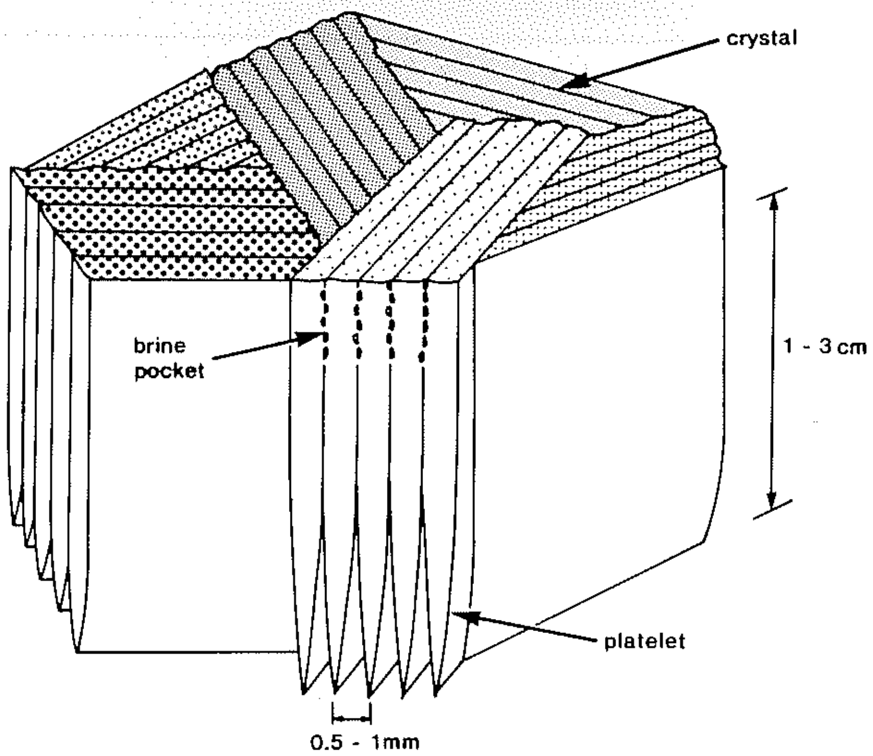


Fig. 1.3 Schematic of the skeletal layer of sea ice. Each grain (crystal) is made up of many parallel platelets separated by grooves filled with high salinity brine. Crystals are shaded to distinguish their boundaries. The platelets are typically between 0.5 and 1 mm apart, and extend some 1-3 cm into the melt. As the ice grows, brine between the platelets is occluded to form brine pockets.

neath growing ice. It is likely that different mechanisms dominate in different areas.

Two recent observations from the Winter Weddell Sea Project are pertinent to the present discussion. The first is that the alternate frazil/columnar structure seen in Weddell Sea cores may be due in part to over-rafting of floes. Many floes were drilled which had abrupt interfaces within their structure, often with large pockets (> 20 cm) of free brine between. Several over-rafts were possible for a single drill hole, and often the floes trapped underneath moved relative to the upmost floe; a most annoying feature when mid-sections of a hole just drilled would shift out of alignment as extension auger flights were fitted. Associated with the water between over-rafts was a greater abundance of krill, *Euphausia superba*, than would normally be seen during drilling, indicating that these flushed sea water pockets might be important to their grazing. Yellow-brown diatom-laden ice was also in evidence.

A second observation relates to ice conditions met as we steamed south. At the ice edge we encountered an extensive field of pancake ice composed of 10-20 cm cakes. The mean size of pancakes increased as we progressed south, with the cakes growing laterally from the frazil ice slurry in which they floated. At a certain point the slurry began to glue adjacent pancakes together to form floes of 20 m or so across which soon also bonded to form 100 m floes. Further south still the floes cemented together to form a continuous ice sheet. These observations are significant because they indicate that the high ocean waves of the South Atlantic can penetrate and travel though pancake ice for hundreds of kilometres and still have enough energy to provide an environment for frazil production and stirring between adjacent pancakes.

PHYSICAL PROPERTIES AND CHARACTERISTICS

A predominant factor influencing the physical properties of sea ice is its age. Young sea ice has an approximately linear vertical temperature gradient, is relatively saline, and its growth can be described by a simple function of cumulative freezing-degree days. As the ice thickens to, say, greater than a metre, thermal mass begins to play a significant role in determining its response to temperature variation at the upper surface, and the assumption of a linear temperature profile becomes inappropriate. Multi-year ice, defined as sea ice which has survived at least one summer's melt season, also has a very different temperature variation through its thickness, but in addition has a salinity profile which is the result of gravity drainage, meltwater flushing and other desalination mechanisms. Indeed the salinity of multi-year ice above the waterline is very near zero, and the salinity in its lower portions only increases to about 3 or 4. Idealised salinity profiles for first and multi-year ice are shown in Fig. 1.4, reproduced from Maykut (1985).

Deformation determines the topographical appearance of the upper and lower surfaces of sea ice. Such deformation may take the form of over-thrusting of one floe over an adjacent floe to create a rafted body of thickness equal to the sum of the component floes. Rafting is common in thin ice (especially finger rafting), but can also occur at greater thicknesses if the processes causing it are sufficiently intense. A second and equally important form of deformation results from changes in winds or currents which, due to differential stresses, can force a crack to open in the ice cover. The crack then widens into a lead, only to freeze over rapidly. With a subsequent wind change the lead closes and piles up (and pushes down) the newly grown ice to create a pressure ridge. Ridges may also be formed by shearing of two floes with thin ice between. In both cases they may weave sinuously across the ice cover for several kilometres. Ridges possess a part above the surface ('sail') and a deeper part beneath ('keel'). Subsequent snowfall will influence the development of the ridge by filling in voids. The degree and character of deformation in a particular area thus depends on local oceanography and meteorology, but also on the nearness of a coastline (which offers a immovable barrier) and ice conditions. The surface appearance of sea ice also depends on its age, with angular features such as ridges being smoothed out into rolling hummocks by differential melting over the summer.

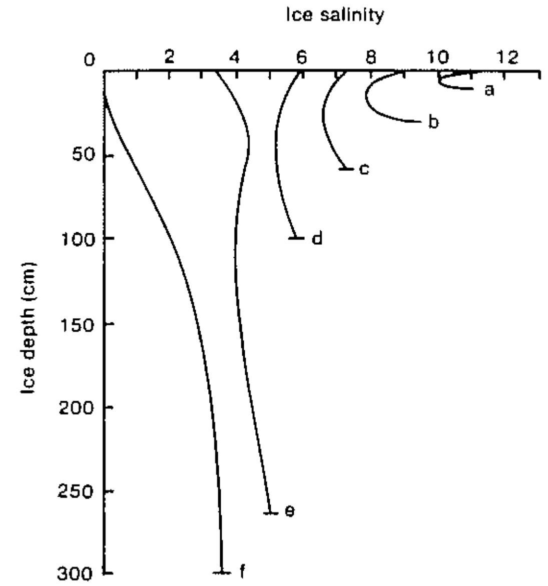


Fig. 1.4 Idealised salinity profiles in Arctic sea ice. Curves (a-d) are first year ice. Curve (e) illustrates the salinity profile typical of fairly undeformed multi-year ice, and curve (f) heavily deformed and hummocked multi-year ice. (After Maykut, 1985).

Many of the mechanical, electrical, thermal and optical properties of sea ice have been found to be related in some way to the fractional volume of brine trapped within the material. This quantity is known as the brine volume and is usually denoted by V_b. Empirical equations relating brine volume to temperature and salinity may be written down (Frankenstein and Garner, 1967), as follows:

$$V_b = S\left(\frac{52.560}{\theta} - 2.280\right) \qquad \text{for } \theta \text{ between } -0.5 \text{ and } -2.06°\text{C} \qquad (2)$$

$$V_b = S\left(\frac{45.917}{\theta} - 0.930\right) \qquad \text{for } \theta \text{ between } -2.06 \text{ and } -8.2°\text{C} \qquad (3)$$

$$V_b = S\left(\frac{43.785}{\theta} + 1.189\right) \qquad \text{for } \theta \text{ between } -8.2 \text{ and } -22.9°\text{C} \qquad (4)$$

where V_b is in parts per thousand. Equations (2), (3) and (4) enable brine volume profiles to be plotted from salinity and temperature data collected by coring sea ice.

The thermal properties of sea ice, viz. conductivity, diffusivity, specific heat and latent heat are all dependent on the temperature and composition of the ice. In addition, conductivity (and hence diffusivity) depends on the spatial distribution of pure ice, brine, air and solid phases within the sea ice structure. In pure ice thermal conductivity (k in W m^{-1} K^{-1}) is given approximately by

$$k = 9.828 \exp(-0.00570) \qquad (5)$$

where θ is now in °K. In this case k is only slightly dependent on direction. In sea ice thermal conductivity shows great anisotropy, although we shall not discuss this here since we are really only concerned with heat transfer vertically. Various models have been suggested to enable k for sea ice to be found, some based on realistic patterns of brine cell and air pocket layout, and some intended to provide a reasonably close value from salinity and temperature data alone. The model of Untersteiner (1961) falls into the latter category. In his model Untersteiner proposes that the thermal conductivity of sea ice is the same as that for pure ice plus a correction term which is proportional to S/θ. The constant of proportionality is, for salinity in parts per thousand and temperature in °C, 0.13 W m^{-1}. The specific heat, c of sea ice has also been found by Ono (1967) to follow a fairly simple expression involving θ, S and the specific heat of pure ice (c_i 2113 J kg^{-1} °C^{-1}) viz.

$$c = c_i + 7.53\theta + 18039.32\, S/\theta^2 \qquad (6)$$

Ono (1967) also derived an expression for the latent heat of fusion of sea ice in terms of θ, S and the latent heat of fusion of pure ice. Thermal diffusivity is found from conductivity, density and specific heat in the usual way.

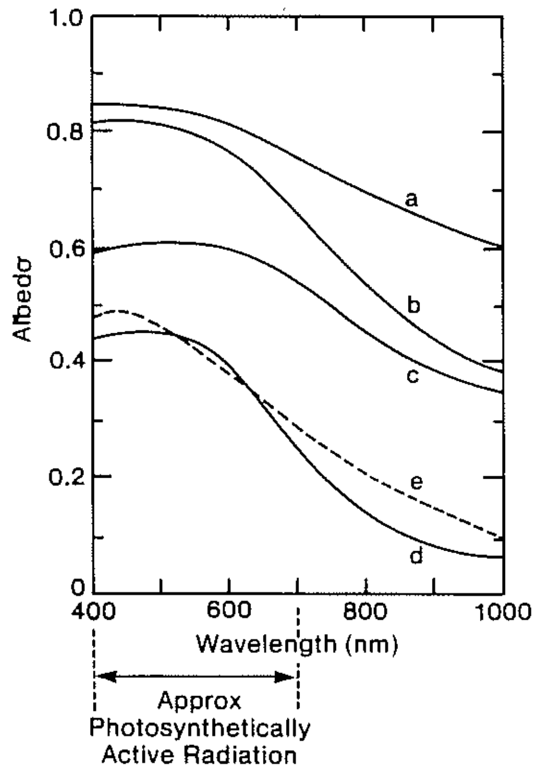


Fig. 1.5 Spectral albedos for bare Arctic sea ice and first year Antarctic sea ide (dashed): (a) frozen multi-year white ice; (b) melting multi-year white ice; (c) melting first year white ice; (d) melting first year blue ice; (e) first year Antarctic sea ice from McMurdo Sound. (After Perovich and others, 1986).

Two aspects of the optical properties of sea ice are important in the present context: albedo, defined as the ratio of reflected to incident short wave radiation; and extinction coefficient, which is a measure of how deep incident short wave radiation can penetrate into the sea ice. Each is a function of wavelength. Spectral albedo has been measured over various ice types in the Arctic, and modelling results compare favourably with these data. Two recent papers (Perovich and others, 1986; Grenfell and Perovich, 1986) present new data on spectral albedo and derive a theory which assumes the ice to be a three-phase mixture of pure ice, brine and vapour, and includes refractive effects at the air-ice and ice-water boundaries. These authors also calculate the extinction coefficient as a function of wavelength. In each case the calculations are done for various ice types. A plot of spectral albedo for various ice types is given in Fig. 1.5.

Although we have directed our discussion towards the physical properties of the sea ice itself, it is important to realise that the polar winter plays a crucial role in the development of biological matter; for some three months there is no direct sunlight and for five months chlorophyll is barely detectable in phytoplankton in the waters beneath the ice.

CONCLUSIONS AND BIOLOGICAL IMPLICATIONS

We briefly mention here aspects of the growth and physical properties of sea ice which are of biological relevance:

1. Growing sea ice rejects cold brine of greater salinity than the water from which it forms. This leads to thermohaline convection in the waters beneath and, particularly near a coastline, can cause a band of highly saline water to form under the ice.
2. Brine inclusions between the pure ice platelets making up sea ice crystals are highly saline.
3. Sea ice desalinates gradually with age, starting in the upper part of the ice layer.
4. Flow from vertical brine drainage channels is oscillatory, with the outflow significantly longer than the inflow. The saline brine drainage tubes are therefore gradually flushed with lower salinity sea water.
5. The spectral albedo and extinction coefficients for sea ice are important since they alter the visual light spectrum within and beneath the ice.
6. The polar winter is important. Diatoms begin growing with the onset of spring, primarily in the lowest 30 cm of ice as a yellow/brown layer. Their growth is small but important because it occurs when food supplies for plankton grazing animals are short.

ACKNOWLEDGEMENTS

Much of the material in section 3 is extracted from the excellent review on sea ice properties by Weeks and Ackley (1986). The author is grateful to the University of Cambridge and to the Natural Environment Research Council for support.

CHAPTER 2

ICE-ASSOCIATED ECOSYSTEMS

Rita Horner

Sea ice is present for all or varying portions of the year at high latitudes in both hemispheres. Physically, sea ice reduces solar input and wind mixing in the upper layers of the water column. These along with periodic freezing and thawing of the ice, affect the temperature and salinity structure of the underlying seawater. Biologically, sea ice provides a unique environment that is used by a wide variety of organisms, including bacteria to marine mammals. The best known of the ice-associated assemblages is that of the ice algae, although information on assemblages of ice fauna and bacteria is gradually accumulating.

FORM

The assemblages of microalgae associated with the sea ice in polar regions take a variety of forms (Horner and others, 1988) (Table 2.1). The best known is the interstitial assemblage that occurs in the bottom of the ice. In the Arctic, this assemblage is found in the bottom few centimeters (usually < 10) of congelation ice from about late March to early June, although timing varies depending on location and local weather conditions. This assemblage occurs in annual ice that may be up to 2 m thick. The dominant organisms are usually pennate diatoms, including species of *Nitzschia*, *Navicula*, and *Pinnularia*, but centric diatoms may be abundant in some places, such as the Gulf of St. Lawrence (Dunbar and Acreman, 1980), and microflagellates with a variety of taxonomic affinities may be dominant at some locations and times (Demers and others, 1984).

In the Antarctic, there may be a layer of unconsolidated ice crystals (platelet ice) up to 4 m thick (Dayton and others, 1969) at the bottom of the congelation ice. Cells are trapped between ice crystals or attached to them. This platelet ice assemblage may be present in McMurdo Sound (Bunt, 1963; Palmisano and Sullivan, 1983, 1985; Palmisano and others, 1985; Garrison and others, 1986; Palmisano and others, 1987a,b; Grossi and others, 1987). Bunt and Wood (1963) found attached diatoms including species of *Pleurosigma*, *Nitzschia*, and *Amphiprora*, plus non-attached species of *Biddulphia*, *Coscinodiscus* and *Asteromphalus*. Platelet ice has also been found at Mirny Station (Gruzov, 1977). Unconsolidated ice crystals have been reported from a number of places in the western Arctic (Larsen, 1980; Reimnitz and Kempema, 1987), but they have not been studied for ice algae. In Hudson Bay, ice algae were found in a layer of slushy frazil ice that may or may not have been attached to the harder ice above it (Runge and Ingram, 1986).

Ice algae are also found in the harder congelation ice in the Antarctic. *Amphiprora kufferathii* Manguin, *Nitzschia stellata* Manguin, and the epiphytic species *Fragilaria islandica* var *adeliae* Manguin were the dominant species at McMurdo Sound (Grossi and others, 1984; Grossi and Sullivan 1985). At Casey Station, *Entomoneis* spp. and *Nitzschia frigida* Grunow were found in brine channels in the bottom ca. 5 cm of the ice (McConville and Wetherbee, 1983; McConville and others, 1985), with *N. frigida* forming a network of cells that spanned the brine channels, but still allowed brine and seawater to flow along them (McConville and Wetherbee, 1983). Centric diatoms have been reported from the bottom of sea ice collected at Langhovde (69°13′S, 39°37′E), from near Ross Island (Watanabe, 1982), and from a variety of ice types collected in the vicinity of Palmer Station, Arthur Harbor (Krebs and others, 1987; Stretch and other, 1988).

In some areas of both the Arctic and Antarctic, there may be a sub-ice assemblage, consisting of algae floating directly beneath the ice or attached to the underside of the ice and forming strands that trail into the water column. In the Arctic, this assemblage has been reported from Pond Inlet (Cross, 1982), from the Barents Sea (E. Syvertsen, pers. comm., 1986), and from the central Arctic Ocean (Mel’nikov and Bondarchuk, 1987). At Pond Inlet, it consisted of a perforated sheet of algae floating against or partially adhering to the underside of the ice and may have been the interstitial assemblage separating from the harder congelation ice in late spring. At the ice edge in the Barents Sea, the sub-ice assemblage consisted mostly of centric diatoms either floating under the ice or attached to it by mucilage. In old annual ice, about 60 to 70 cm thick, *Nitzschia frigida* and *Gyrosigma* sp. are common (E. Syvertsen, pers. comm., 1986). Under multi-year ice, the sub-ice assemblage consists of a *Melosira arctica* community characterized by *M. arctica* (Ehrb.) Dickie and its associated epiphytes *Chaetoceros septentrionalis* Østrup, *Synedra hyperborea* Grunow, and *Pseudogomphonema arcticum* (Grun.) Medlin (Hasle and Syvertsen, 1985; E Syvertsen, pers. comm., 1986). In the central Arctic Ocean, the sub-ice assemblage consisted primarily of *M. arctica*, plus *C. septentrionalis*, *Gomphonema exiguum* Kütz. [= *Gomphonemopsis exigua* (Kütz.) Medlin], *Gomphonema septentrionale* Øst. (= *Pseudogomphonema septentrionale* (Øst.) Medlin], and small amounts of *Pinnularia quadratarea* (Schmidt) Cl., *Navicula pinnata* Pant., *N. kariana* (Grun.) Cl., *N. vitrea* (Cl.) Cl., *Nitzschia polaris* Grun., and *N. subtilis* (Kütz.) Grun. (Mel’nikov and Bondarchuk, 1987).

In the Antarctic, a mat-strand community was found at Casey Station (McConville and Wetherbee, 1983). This community consisted of tube-dwelling pennate diatoms [*Berkeleya rutilans* (Trent.) Grunow], plus ribbon-shaped colonies [*Entomoneis paludosa* var. *hyperborea* (Grun.) Poulin and Cardinal, *Nitzschia*

Table 2.1. Types of algal assemblage found in sea ice, their occurrence, production and biomass. Production and biomass figures are maximum except where noted.

Assemblage	*Occurrence*	*Location*	*Season*	*Production*	*Biomass*	*Reference*
Surface						
infiltration	at snow-ice interface infiltrated with seawater	Antarctic	winter, spring, summer	0.19 g C m^{-2} d^{-1}	407 mg chl *a* m^{-3}	Burkholder & Mandelli, 1965
pool	pools on ice surface	Arctic Antarctic	late spring early summer	363 µg C l^{-1} h^{-1}	2.8 × 10^6 cells l^{-1}	McConville & Wetherbee, 1983
Interior						
band	bottom ice algal layers frozen into the ice	Antarctic*	fall, winter	5 µg C l^{-1} h^{-1}	2.6 × 10^7 cells l^{-1}	McConville & Wetherbee, 1983
					77 mg chl *a* m^{-3}	Garrison & others, 1986
brine channels	in brine channels and cracks	Arctic Antarctic	spring spring		3 × 10^5 cells ml^{-1}	McConville & Wetherbee, 1983
Bottom						
interstitial	between ice crystals and platelets (includes platelet ice)	Arctic Antarctic	late winter, spring	14.9 mg C m^{-2} h^{-1} 81 µg C l^{-1} h^{-1}	30.5 mg chl *a* m^{-2} 52 × 10^7 cells 1^{-1}	Clasby & others, 1976 McConville & Wetherbee, 1983
					656 mg chl *a* m^{-3}†	Palmisano & Sullivan, 1983
					5320 mg chl *a* m^{-3}	Hoshiai, 1981
sub-ice	mats and/or strands loosely attached to the undersurface of the ice	Arctic Antarctic	spring, summer (?)		10^6 – 10^7 cells ml^{-1}	McConville & Wetherbee, 1983

* Only one report from the Arctic
† Average value

curta (V.H.) Hasle, *N. cylindrus* (Grun.) Hasle, and *N. kerguelensis* (O'Meara) Hasle] and stellate colonies (*Nitzschia* spp.) along with epiphytic pennate species (McConville and Wetherbee, 1983; McConville and others, 1985; D. Thomas, pers. comm., 1986). Strands of diatoms, including *B. rutilans*, *Nitzschia stellata*, and *Entomoneis kjellmanii* (Cl.) Poulin and Cardinal, have been found in November and December at Syowa Station (K. Watanabe, pers. comm., 1986, 1988). A strand community has also been reported from McMurdo Sound, but without a species list (Grossi and others, 1987).

Interior ice assemblages have been reported primarily from the Antarctic. The band assemblage is formed either by accretion of new ice under a previously formed bottom (interstitial) ice algal layer (Hoshiai, 1977; Ackley and others, 1979; K. Watanabe, pers. comm., 1986), or by the incorporation of planktonic algae at the time of first freezing of surface waters (R. Gersonde, pers. comm., 1986). This assemblage may be a remnant of an autumnal ice diatom bloom (Ackley and others, 1979; McConville and Wetherbee, 1983). *Nitzschia* spp. and unidentified flagellates were the most abundant organisms in this layer at Syowa Station (Hoshiai, 1977).

A second interior ice assemblage is that found in brine channels. It forms in spring when some melting occurs and the brine channels become interconnected forming a network in the ice. Brine channels in the interior of the ice contained species common to both the water column and the interstitial ice assemblages (McConville and Wetherbee, 1983).

Extensive ice algal populations have also been found throughout the interior of ice floes in the Weddell Sea pack ice (Ackley and others, 1979; Clarke and Ackley, 1984; Garrison and Buck, 1985, 1988). Ice in these floes is predominately frazil ice that forms rapidly during periods of high turbulence (Clarke and Ackley, 1984). However, congelation ice, composed of large, columnar crystals, and snow ice, formed when seawater floods the snow cover on a floe and freezes, may also be present. Cells are apparently incorporated into frazil ice either by nucleation of an ice crystal or by scavenging as a frazil ice crystal floats up through the water column (Ackley, 1982; Garrison and others, 1983). The highest concentration of cells is usually seen near, but not at, the bottom of the ice (Clarke and Ackley, 1984).

Ice platelets have been reported from depths of 250 m near the Filchner Ice Shelf (Dieckmann and others, 1986). These underwater ice platelets may be important in establisheing biological communities in and under fast ice and sea ice near Antarctic ice shelves because the platelets traverse large distances through the water column and could accumulate larger numbers of organisms than frazil ice crystals formed in the upper layers of the water column.

In addition to physical concentrating mechanisms, biological concentration must also occur. In the Weddell Sea, algae found in ice floes were able to survive in either the ice or the water column, but cells were more concentrated in the ice (Garrison and Buck, 1985). Gersonde (1986a) found *Nitzschia curta* (V.H.) Hasle to be the dominant species in both the ice and the water column, but other *Nitzschia* species consistently occurred in much higher concentrations in the water column. The occurrence of fewer species in the ice may indicate selective survival and/or growth of some species following their entrapment in the ice. Cells incorporated in the ice may survive there for one or more seasons (Garrison and Buck, 1985).

Two surface ice assemblages have been described. The infiltration assemblage occurs at the snow-ice interface when the snow on the ice surface is flooded with seawater. This may happen when the weight of the snow depresses the ice and seawater containing algal cells infiltrates the snow, as first described by Meguro (1962). This mixed diatom-flagellate assemblage occurs in layers ranging from 15 to 100 cm thick and can exist either as slush or frozen solid depending on ambient air temperatures (Burkholder and Mandelli, 1965). Large numbers of a "very small diatom" and moderate numbers of *Fragilariopsis curta* (= *Nitzschia curta*) and *N. seriata* Cleve, plus traces of other diatoms, dinoflagellates, small green flagellates, and *Phaeocystis pouchetii* (Har.) Lagerheim were found in the infiltration assemblage along the Palmer Peninsula (Burkholder and Mandelli, 1965).

The pool assemblage occurs on the ice surface in pools formed by thawing of the ice (McConville and Wetherbee, 1983), flooding of the ice, or a combination of flooding and melting. Other mechanisms that can lead to pool formation include wave action and pressure ridge build-up and breakdown. At Casey Station, this assemblage consisted of pennate diatoms, flagellates, and *Phaeocystis* sp. From late December to January, all species found in the pool assemblage were also found in the interstitial assemblage (McConville and Wetherbee, 1983).

SEASONALITY

Algae are present in sea ice whenever it occurs. In the Arctic, scattered cells are found throughout the ice thickness in winter (Alexander and others, 1974; Clasby and others, 1976; Horner, 1985) forming visible blooms in the bottom of the ice in late March-early April that last into June when the ice begins to melt. In winter, unidentified microflagellates are the most abundant organisms, but pennate diatoms are also present. The origin of the cells is not known, but there is some evidence to suggest that bottom and water column frazil ice may lift nematodes and benthic diatoms, as well as sediment, to the ice (Reimnitz and others, 1987). However, studies at Barrow and Narwhal Island, Alaska, indicate that few of the most abundant ice diatom species are found in the sediment either during or after the bloom in the ice (Matheke and Horner, 1974; Horner and Schrader, 1982).

The spring interstitial assemblage consists primarily of pennate diatoms, but autotrophic and heterotrophic flagellates from various phyla and autotrophic and heterotrophic dinoflagellates are present, as well as bacteria, ciliates, meiofauna, and meroplanktonic larvae (Horner and Alexander, 1972; Carey, 1985). The species composition of the flora may also change over the course of the bloom (Horner and Schrader, 1982).

A fall bloom in the ice has been reported from the Eskimo Lakes (Northwest Territories, Canada) (Hsiao, 1980) and from Narwhal Island (D.M. Schell, pers. comm., 1980). At the Eskimo Lakes, the population of about 3.9 x 10^3 cells m^{-2} consisted primarily of pennate diatoms. The Narwhal Island bloom contained concentrations of 1 x 10^8 cells m^{-2} and was similar in composition (pennate diatoms) and concentration to the earlier spring ice algal bloom in the same area (Horner and Schrader, 1982).

A marginal ice zone (MIZ) assemblage consisting of ice algae, both those found in the ice and those that have been released into the water column, and planktonic species in the water column, occurs in spring and may be present as long as the ice continues to recede. This may be until late August in the Barents Sea (E. Syvertsen, pers. comm., 1986). Relative contributions of the various components of this assemblage to species, standing crop, chlorophyll *a*, and productivity are not known.

In the Antarctic, ice algal assemblages are apparently present throughout the year depending on location (Garrison and others, 1986; Perrin and others, 1987; Watanabe and Satoh, 1987). At McMurdo Sound and other nearshore areas (Syowa, Casey, and Davis stations), sea ice starts to form in February-March. Algae grow on the underside of newly forming ice and on old ice that has survived the summer melt period. At Syowa Station, an autumnal bloom of ice algae is a relatively regular feature with chlorophyll *a* concentrations reaching about 1000 mg m^{-3} (Hoshiai, 1977). Autumnal blooms may occur elsewhere as well, but are not well-documented (Garrison and others, 1986). If the autumnal bloom becomes incorporated into the ice as an interior band assemblage, its presence could affect the development of the bottom interstitial assemblage by reducing light levels and may also contribute to the growth of brine channels and the colonization of melt pools by increased heat absorption (McConville and Wetherbee, 1983).

As in the Arctic, in nearshore areas the highest concentrations of ice algae occur in late spring in the bottom 20 cm of the ice, the interstitial assemblage. Chlorophyll *a* in this assemblage may reach 656 mg m^{-3} (= 309 mg m^{-2}) (Palmisano and Sullivan, 1983). This bloom lasts until late December or January when ablation removes it from the ice.

In oceanic areas, e.g. the Weddell Sea, the ice algae form primarily interior and surface assemblages (Garrison and others, 1986). Biomass (as chlorophyll *a*) is less than in the interstitial assemblage. In internal band assemblages, chlorophyll *a* ranges about from 4 mg m^{-3} in late summer or late winter to about 77 mg m^{-3} in spring (Ackley and others, 1979; Clarke and Ackley, 1984; Garrison and Buck, 1982; Garrison and others, 1986), Chlorophyll *a* concentrations in infiltration assemblages range from about 50 mg m^{-3} in late winter and spring in the Weddell Sea (Clarke and Ackley, 1984; Garrison and others, 1986) to about 407 mg m^{-3} along the western side of the Palmer Peninsula in February (Bürkholder and Mandelli, 1965) and 670 mg m^{-3} in Lützow-Holm Bay in January (Meguro, 1962). Bürkholder and Mandelli (1965) calculated that the infiltration assemblage could fix about 0.19 g C m^{-2} d^{-1} or about 0.5 × 10^6 tons of carbon per day in the approximately 2.6 x 10^6 km^2 of this kind of brown ice that surrounds the Antarctic continent in summer.

TROPHIC STRUCTURE

In addition to the algal component, sea ice also supports populations of bacteria (Iizuka and others, 1966; Horner and Alexander, 1972; Sullivan and Palmisano, 1981, 1984; McConville and Wetherbee, 1983; Grossi and others, 1984; Kottmeier and others, 1987) and faunal components ranging from colourless flagellates, foraminiferans and ciliates, to copepods, amphipods, krill, and fish (Sutherland, 1852; Nansen, 1906; Apollonio, 1961; Andriashev, 1968; Fenchel and Lee, 1972; Horner and Alexander, 1972; Whitaker, 1977; Buck, 1981; Bradstreet and Cross, 1982; Cross, 1982; Carey and Montagna, 1982; Grainger and Hsiao, 1982; Pett and others, 1983; Hamner and others, 1983; Kern and Carey, 1983; Gulliksen, 1984; Carey, 1985; Garrison and others, 1986; Spindler and Dieckmann, 1986; Spindler, 1988; Daly and Macaulay, 1988; Marschall, 1988; Stretch and others, 1988). Seabirds and mammals are also important in the ice ecosystem, using the ice in a variety of ways, including as a substrate on which to rest or bear young, for shelter, and for transportation (Fay, 1974). In addition, the luxuriant algal production, both in the ice and in the water column at the ice margin, either directly or indirectly, provides an abundant source of food for these birds and mammals.

There are relatively few studies on bacterial populations in the ice, especially in the Arctic. Horner and Alexander (1972) reported finding bacteria during their studies on heterotrophy and concluded that most of the uptake of organic substrates was by bacteria or colourless flagellates, but provided no quantitative data. Bacterial populations in surface ice samples collected from the Beaufort Sea in April had $< 10^4$ cells ml^{-1}, or about the same number as in the underlying seawater (Kaneko and others, 1977), but counts of viable cells were much lower in the ice (Kaneko and others, 1978).

In the Antarctic, the first report of bacteria in sea ice is that of Iizuka and others (1966). They isolated species of *Brevibacterium* and *Achromobacter* from surface meltwater near Syowa Station. In the Weddell Sea pack ice, Marra and others (1982) reported about 10^9 bacterial cells l^{-1} at the depth of the chlorophyll maximum in the ice, or about 700 mg C m^{-3}. In the water column, there were about 10^8 cells l^{-1} or about 0.7 mg C m^{-3}.

McConville and Wetherbee (1983) found large, Gram-negative rod-shaped epibacteria and cocci that were primarily attached to the surface of some of the dominant diatoms, especially the sheaths of *Berkeleya* and the valves of *Entomoneis*. Bacterial cell densities of 4×10^5 to 2×10^7 ml^{-1} were found. The highest bacterial numbers and the shortest turnover times of ^{3}H-labelled amino acids coincided with assemblages having the highest primary production and heterotrophic activity was mostly associated with fractions > 2 µm in size.

The most extensive study of bacteria associated with sea ice is that of Sullivan and his co-workers (Sullivan and Palmisano, 1981, 1984; Grossi and others, 1984; Kottmeier and others, 1984, 1987; Sullivan, 1985) in McMurdo Sound. Bacterial cells were present in concentrations of 1.02×10^{12} cells m^{-3} with 47% of the numbers and 93% of the biomass found in the bottom 20 cm of ice (Sullivan and Palmisano, 1984). Mean bacterial cell concentration was 1.4×10^{11} cells m^{-3} or 9.8 mg C m^{-2}, but this was only 0.1% of the ice algal standing crop at the same time. Bacterial cell numbers were positively correlated with chlorophyll *a* concentrations and dividing cells were common. Coccoid, rod, fusiform, filamentous, and prosthecate cells were present with about 70% of them being free-living and 30% being attached to either algal cells or detritus.

Kottmeier and others (1987) showed that bacteria grow and accumulate in both the bottom layer of hard congelation ice and in the loosely consolidated ice platelet layer, but bacterial biomass was less than 1% of the algal biomass and bacterial production was only about 9% of algal production in the sea ice. Correlations between bacterial production and growth rates and algal biomass, production, and growth support the contention that bacterial growth is coupled to algal metabolism as suggested earlier by Grossi and others (1984).

Pigmented, heterotropic bacteria that form gas vacuoles were recently found in sea ice for the first time (Staley and others, 1989). Highest concentrations of these bacteria were found in conjunction with the highest chlorophyll *a* concentrations, again suggesting that bacterial growth is linked to algal metabolism.

Although animals, primarily protozoans, have been known from sea ice since the 1850s (Sutherland, 1852), studies on the fauna associated with sea ice have lagged behind those of the algae, and a number of investigators believed that little or no grazing occurred in the ice (Meguro and others, 1967; Bunt and Lee, 1970; Whitaker, 1977). The first comprehensive description of fauna associated with sea ice is that of Andriashev (1968). He divided the fauna into two major ecological groups: 1) the ice fauna that live, at least temporarily, in the lower part of the ice, and 2) the sub-ice fauna that do not live in the ice, but are trophically linked to it.

Carey (1985) reviewed the literature on Arctic ice fauna. He proposed the term sympagic, meaning with ice, because the ice meio- and macro-fauna included organisms from both the benthos and plankton and this term could be used to refer to fauna from a variety of habitats and ice types.

The sympagic microfauna is composed of organisms < 62 µm in size, primarily protozoans, including heliozoans, ciliates, and colorless flagellates. This group is not well-known, in part because many of the organisms are delicate and may be lost during collection and preservation of samples (Garrison and Buck, 1986). The meiofauna, ranging in size from 62–500 µm, includes nematodes, harpacticoid, cyclopoid, and calanoid copepods, rotifers, and larvae of benthic invertebrates such as polychaetes, pelecypods, gastropods, tunicates, turbellarians, and cirripedes. The macrofauna, animals > 500 µm, consists primarily of gammarid amphipods (Carey, 1985).

The sub-ice fauna includes a number of fish, such as *Pagothenia borchgrevinki* in the Antarctic and *Boreogadus saida*, *Arctogadus glacialis*, and *Ammodytes hexapterus* in the Arctic (Andriashev, 1968; Carey, 1985). Krill must also be included in the sub-ice fauna because they are known to accumulate under the ice and to feed on ice diatoms (Andriashev, 1968; Hamner and others, 1983; Daly and Macaulay, 1988; Marschall 1988; Stretch and others 1988), probably switching from filter feeding on phytoplankton to grazing on ice algae (Marschall, 1988).

The presence of a complex food web within, and associated with, sea ice is well-known (Andriashev, 1968; Horner, 1976; Carey, 1985; Garrison and others, 1986) (Fig. 2.1), although all the links have not been established among the various components. There are virtually no quantitative data available on the ice-based food web, and spatial and temporal coverage is sparse (Carey, 1985).

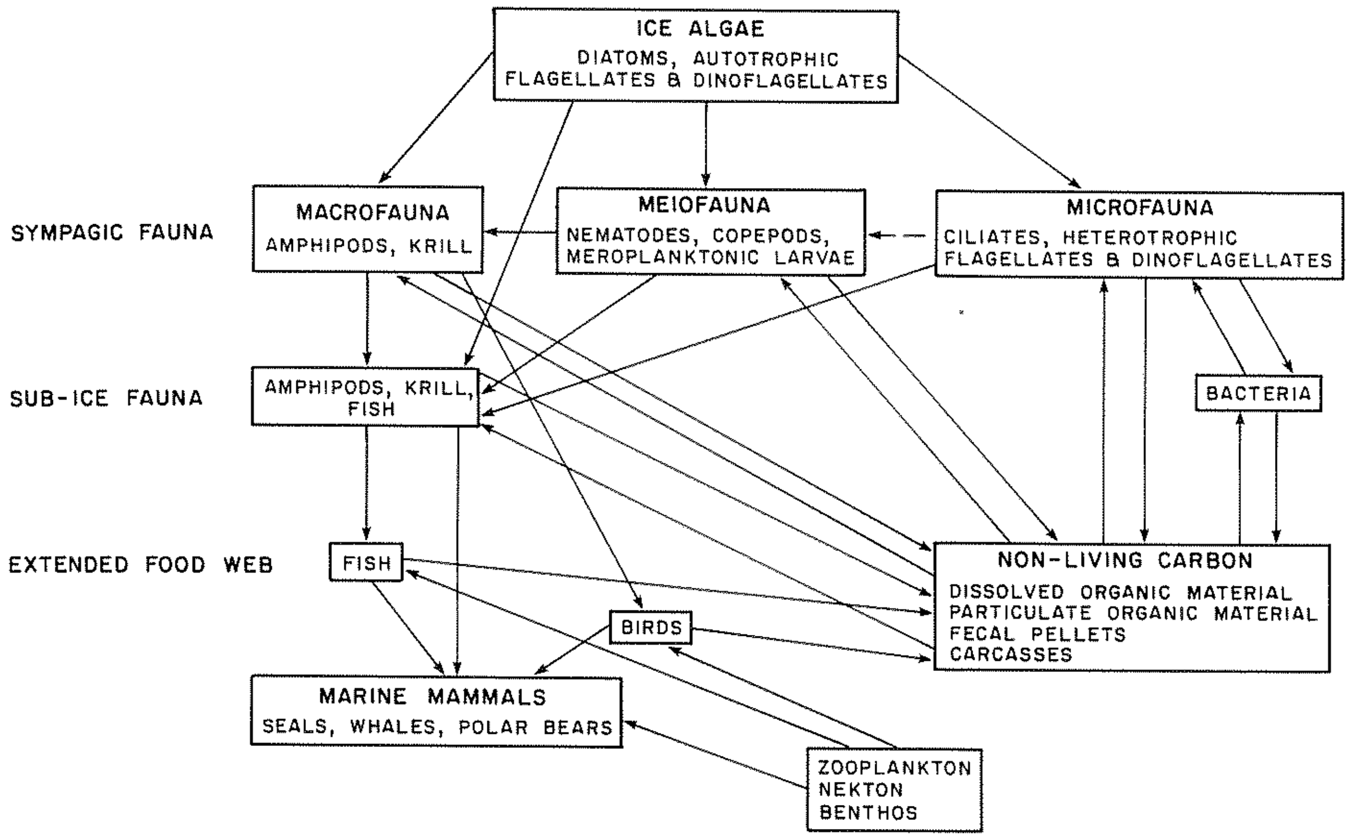


Fig. 2.1 Proposed food web illustrating the major trophic relationships among sea ice biota and their relationship to an extended food web (modified from Carey, 1985). Solid arrows = observed; broken arrow = hypothesized.

Ice algae are a regular and significant source of food for females of the calanoid copepods, *Calanus glacialis*, *Metridia longa*, and probably *Pseudocalanus* sp. in Hudson Bay throughout the time of the ice algal bloom. Feeding takes places in or near a slush ice layer loosely associated with the hard congelation ice (Runge and Ingram, 1988). Amphipods and juvenile krill are known to feed on ice algae and lysianassid amphipods in the Arctic feed on meiofauna and other crustaceans early in the spring before the peak of the ice algal bloom (Carey and Boudrias, 1987), but the food sources of many of the other faunal species seen and collected from beneath the ice are not known. The fish may feed on ice algae or on faunal components of the ice biota, but they may also be grazing on the amphipods and other sub-ice fauna.

Some of the animals found near the undersurface of the ice may be there for reasons other than for feeding. Some species may be attracted by the higher light intensities at the undersurface of the ice, while zooplankton may be concentrated by the ice barrier (Carey, 1985). Some species, including benthic and pelagic amphipods, may use the ice as nursery grounds and larvae of benthic species close to metamorphosis may aggregate on the relatively solid ice substrate (Carey and Montagna, 1982; Carey and Boudrias, 1987). The young of some species, such as *Boreogadus saida* and *Ammodytes hexapterus*, may use the holes and crevices in the ice as refuges from predators.

The downward transport of organic material, including ice diatoms and fecal pellets, may provide a source of food for pelagic and benthic organisms. In the Arctic, particles from the ice reach the sea floor throughout the winter and spring in shallow water areas, not just during the melt period (Pett and others, 1983; Carey, 1985, 1987) but the flux is low. Carey (1987) estimated that only about 1-10% of the carbon production from the ice algae reaches the bottom in shallow water so significant amounts of organic carbon and nitrogen do not reach the benthos. Much of the ice algal production that is lost may be due to advection or *in situ* grazing, particularily by amphipods (Carey, 1987).

In the Antarctic, the same dominant species occur in fecal material and in the ice and water column at Syowa Station, suggesting that carbon fixed at the surface could be transported downward by sinking fecal pellets (Fukuchi and Sasaki, 1981). Other data from the same site, including low phaeopigment:chlorophyll *a* and carbon:chlorophyll *a* ratios, and decreased fecal pellet fluxes during the ice algal bloom, however, suggest that ice algal cells and aggregates sink without strong grazing pressure (Sasaki and Hoshiai, 1986). The presence of ice diatoms in the sediments also suggests that these organisms can sink directly (Gersonde and Wefer, 1987).

Seasonal variation in downward flux of organic material occurs under Antarctic fast ice (Matsuda and others, 1987). For example, the POC:chlorophyll *a* ratio changes such that fresh algae are dominant from November through February, while detrital material is more abundant in winter. In addition, the chlorophyll *a* flux, varying from 4500 µg m^{-2} in summer to 3 µg m^{-2} in winter, suggests that both ice algae and phytoplankton sink directly to the sea floor. Thus, the depth of the water, temporal patterns, local weather and ice conditions, the rate of particle sinking, and the nature of the pelagic organisms, e.g. whether they are large or small (Niebauer and others, 1981; Sasaki and Hoshai, 1986), all influence the availability of organic material from the ice to either the pelagic or benthic faunas.

DISCUSSION

Unicellular algae are found in sea ice whenever ice is present. The origin of these cells and the mechanics of their incorporation into the ice are not always known. About 500 species from nine algal classes, including Bacillariophyceae, Chlorophyceae, Chrysophyceae, Cryptophyceae, Dictyochophyceae, Dinophyceae, Euglenophyceae, Haptophyceae and Prasinophyceae, have been reported from sea ice. Diatoms are usually dominant, but other organisms may be more abundant at some times and places. Production, in terms of carbon uptake, or biomass, in terms of chlorophyll *a* concentrations and cell numbers, may be extremely high. Bacteria are also common in sea ice and their production is apparently coupled with ice algal growth and production.

Sympagic faunal assemblages are also present, ranging in size from microfauna < 62 μm in size to macrofauna > 500 μm. A sub-ice fauna trophically linked to the ice biota includes fish and krill, while an extended food web includes seabirds and mammals. Pelagic and benthic animals may also derive nourishment either directly or indirectly from the ice biota. All linkages in the ice-associated food web are not known, but the presence of ice algae in spring when little or no primary production occurs in the water column provides an early source of carbon for a variety of animals. Thus, the ice assemblages extend the short growing season for several months and reduce the extreme seasonal fluctuations of primary production found at high latitudes.

ACKNOWLEDGEMENTS

This manuscript benefitted from discussions with K. Daly. A.G. Carey, Jr. critically read the manuscript and provided new information about the ice fauna and particle flux.

CHAPTER 3

ICE DIATOMS: THE ARCTIC

Michel Poulin

Microscopic algae have the physiological ability to colonise numerous habitats, from hot springs to sea ice. In the latter environment, Bacillariophyceae (diatoms) usually predominate but many other algal classes are represented: Chlorophyceae, Chrysophyceae, Craspedophyceae, Cryptophyceae, Cyanophyceae, Dictyochophyceae, Dinophyceae, Euglenophyceae, Prasinophyceae, and Prymnesiophyceae. Basically we can observe three categories of floristic assemblages according to the position of the maximum biomass in the ice column: surface assemblages (Fukushima, 1961; Meguro, 1962), interior assemblages (Hoshiai, 1969; Ackley and others, 1979), and bottom assemblages (Bunt, 1963; Meguro and others, 1967a). The bottom ice assemblages are differently constituted in the Arctic or Antarctic regions. In the Arctic, microalgae are incorporated into the ice as it forms in the fall. They occupy brine pockets and channels in the lower sections of the ice as well as the ice-water interface, and they are mainly dominated by benthic/pennate diatoms (Meguro and others, 1967a; Alexander and others, 1974; Hsiao, 1980; Grainger and Hsiao, 1982; Hsiao, 1983; Poulin and others, 1983; Horner, 1985).

TAXONOMIC STUDIES

The current taxonomic knowledge of sea ice microflora is the result of a research effort undertaken for a century and a half. Ehrenberg (1841, 1853) first reported the occurrence of microscopic algae from the north Atlantic and the Canadian Arctic Archipelago, accompanied by succinct species lists. A few decades later, Cleve (1873) identified about 140 diatom taxa from the North Atlantic Ocean and the Davis Strait. In 1874, O'Meara drew up a list of diatoms observed until then in Svalbard (=Spitsbergen), Norway. Cleve and Grunow (1880) produced an excellent study on the Arctic diatoms, especially from the Kara Sea, U.S.S.R. They identified 110 previously known taxa and described 24 new ones. During the expedition of the "Vega", Cleve (1883) identified 102 diatoms collected from sea ice near Cape Vankarem, U.S.S.R. He produced a list with species descriptions, totalling 446 taxa recorded for the Arctic latitudes. Grunow (1884) surveyed the microscopic flora of Zemlya Frantsa Iosifa (=Franz Josef Land), U.S.S.R., and he described 47 sea ice diatoms. In 1895, Østrup identified diatoms sampled from sea ice off East Greenland and described 59 new taxa. These last four reports constitute the basic, fundamental references which concentrate most of the relevant information on diatoms inhabiting or in close association with sea ice. The literature is very old and some taxonomic treatments in these works may disagree with our current understanding of certain taxa.

Cleve (1896) further identified many pelagic diatoms collected between Baffin Bay and Davis Strait and later in 1898 identified diatoms from freshwater and sea ice near Zemlya Frantsa Iosifa, U.S.S.R. He drew up a comprehensive list of 427 diatom taxa likely to be encountered in the Arctic region. He also produced species lists for taxa encountered between Greenland and Svalbard (Cleve, 1899), and those observed north of Jan Mayen Island, Norway (Cleve, 1900). Gran (1897) studied diatoms collected in Karajak fjord (West Greenland), and in 1904b he reported on pelagic diatoms of the Arctic Ocean as well as those on ice floes. In 1949, Usachev collated the Russian studies and recorded a total of 142 diatom taxa from Kara and Laptev Seas (U.S.S.R.), of which 24 were considered as typically cryophilic (Table 3.1).

Table 3.1. Bottom sea ice diatoms considered as typical cryophilic taxa by Usachev (1949).

Melosira arctica (Ehrenb.) Dickie
Thalassiosira bioculata (Grun.) Øst.
Chaetoceros septentrionalis Øst.
Fragilaria islandica Grun.
Fragilaria cylindrus Grun.
Synedra hyperborea var. *rostellata* Grun.
Diploneis litoralis var. *clathrata-arctica* Cleve
Navicula derasa Grun.
Navicula detersa (Grun.) Gran
Navicula directa (W. Sm.) Ralfs
Navicula gelida Grun.
Navicula superba (Cleve) Gran
Navicula transitans Cleve
Navicula trigonocephala Cleve
Navicula valida Cleve & Grun.
Pinnularia quadratarea var. *constricta* Østr and var. *stuxbergii* Cleve
Pinnularia semiinflata Østr.
Pleurosigma stuxbergii Cleve & Grun.
Amphiprora gigantea var. *septentrionalis* Cleve
Amphiprora kjellmanii Cleve
Gomphonema exiguum var. *arctica* Cleve (+ var. *pachyclada* Cleve?)
Gomphonema kamtschaticum var. *groenlandicum* Østr.
Nitzschia laevissima Grun.
Nitzschia polaris Grun.

All these previous works are used as a taxonomic base for recent studies on sea ice assemblages. Today, little effort is made to complement past taxonomy, with research interest oriented toward more ecological and eco-physiological aspects. At northern latitudes, bottom ice assemblages are largely represented by pennate diatoms as recorded in Table 3.2 (Meguro and others, 1966; Horner and Alexander, 1972; Alexander and others, 1974; Dunbar and Acreman, 1980; Hsiao, 1980; Grainger and Hsiao, 1982; Hsiao, 1983; Poulin and others, 1983; Horner, 1985). The taxonomy and nomenclature in these recent studies is essentially the same as those in the studies from the turn of the century.

The basis for diatom identification has improved over the years with the advent of new techniques, such as scanning or transmission electron microscopy. These new tools have clarified valvar features and improved definitions of taxa. This has often resulted in taxonomic or nomenclatural changes, hopefully leading to a contemporary taxonomy. In spite of these developments, the research effort of the past 20 years in sea ice assemblages has generally not encompassed new developments in taxonomy. Exceptions to this include taxonomic studies by Poulin and Cardinal (1982a, 1982b, 1983) from Hudson Bay, Canada, by Heimdal (1970) and Syvertsen (1984) on the morphology of *Navicula* species, by Medlin and Round (1986) on the taxonomic status of some arctic species of *Gomphonema* and by Poulin (1990, In press) on *Stenoneis* and a *Gyrosigma* species, respectively.

Table 3.2. Percentage of pennate diatoms forming sea ice assemblages at different northern geographical locations.

Locations	*Latitude*	*Percentage*	*References*
Arctic regions		85	Horner, 1985
Barrow, Alaska	71 N	89	Horner, 1976
Narwhal Island, Alaska	70 N	91	Horner and Schrader, 1982
Arctic Canada		89	Hsiao, 1980
		86	Hsiao, 1983
Davis Strait	60–64 N	64	Booth, 1984
Frobisher Bay (1971-78)	64 N	90	Hsiao, 1979c
Frobisher Bay (1979-81)	64 N	88	Grainger and Hsiao, 1982
Eskimo Lakes	69 N	90	Hsiao, 1979b
Eclipse Sound	72 N	92	Hsiao, 1979a
Robeson Channel	81 N	98	Dunbar and Acreman, 1980
Barrow Strait	74-75 N	96	Dunbar and Acreman, 1980
Hudson Bay	58 N	99	Dunbar and Acreman, 1980
	55 N	90	Poulin and others, 1983
	55 N	83	Hsiao and others, 1984
St. Lawrence			
Gulf	46–49 N	57	Dunbar and Acreman, 1980
Estuary (1979)	49 N	50	Demers and others, 1984
Estuary (1980)	49 N	0	Demers and others, 1984

DISTRIBUTIONS

In the Arctic, bottom sea ice assemblages start to form at the beginning of the fall. The source of the algae is still questioned and many hypotheses have been suggested for their occurrence in the ice: 1) members of the fall phytoplanktonic community, 2) seeding from drifting pack ice, and 3) resuspension of sediments during fall storms. Cells are incorporated into the ice as it forms (late September/October); they are few in number and scattered through the entire thickness of the ice so that no visible layer of organisms is present. Microflagellates are usually the most abundant organisms in new ice, but pennate diatoms are also present. Algal cells remain scattered throughout the ice in winter, with biomass (indicated by chlorophyll content or cell numbers) being low and variable throughout the ice from January to mid-March. By this time, the algae become concentrated in the bottom few centimetres as a result of increasing air temperatures causing brine drainage and an active migration of cells through the brine channels in the ice. Growth begins in response to increasing light levels and continues throughout the spring, although adverse weather conditions may interrupt or slow growth during this time. By early April, at the bottom of the ice, a brown or golden brown layer about 3-5 cm thick is visible with the highest productions occurring in mid to late May. At the same time, the ice containing the algae becomes softer and begins to deteriorate. The algae probably contribute to its disintegration by selective absorption of solar energy. Weak water movements gradually wash the algal layer away, and by early June, the brown layer is no longer visible.

Ice algae are encountered in annual sea ice in all regions where sea ice is a common phenomenon of the environment. In higher latitudes of the northern hemisphere, the algal ice assemblages, consisting primarily of pennate diatoms ($\leq$ 83%), are widely distributed throughout the arctic zone, while in lower latitudes, centric diatoms form the major part of the ice assemblage (Table 3.2). Dunbar and Acreman (1980) found a significant difference in biomass indicators between the Gulf of St. Lawrence and their three arctic locations with striking differences in the proportion of centric and pennate forms (Table 3.3). The arctic stations were mainly dominated by the three following pennate diatoms, *Diploneis litoralis*, *Navicula kjellmanii*, and *N. peregrina* while in the Gulf, the main centrics were *Chaetoceros debilis*, *Porosira glacialis* and *Thalassiosira nordenskioeldii*. In the St. Lawrence Estuary, Demers and others (1984) observed a sea ice flora dominated by microflagellates and the centric diatom *Cyclotella striata*. This change in species composition is explained by different light regimes associated with variations in the ice thickness. The thin ice of the Estuary/Gulf of St. Lawrence allows better light penetration favouring the growth of a light-adapted assemblage. By contrast, thicker ice found in northern latitudes favours the development of a shade-adapted assemblage (Dunbar and Acreman, 1980; Demers and others, 1984). The variations in the light intensity also explain the results of Hsiao (1980) and Grainger and Hsiao (1982) who reported primarily planktonic organisms in the upper part of the ice and benthic diatoms in lower sections. During the fall when the ice is relatively thin, the light penetrates easily and allows the development of the light-adapted planktonic algae. On the other hand, at the end of the spring, the light is fairly attenuated by the thicker ice and this favours the growth of benthic diatoms associated with the ice.

Table 3.3. Dominance of ice diatom species at different times and different northern geographical locations.

Locations	*Species*	*References*
Alaska		
Barrow 1972	*Nitzschia frigida*	Horner and Alexander, 1972 Horner, 1981
Barrow 1973	*Navicula marina*	Horner, 1981
Beaufort Sea	*Nitzschia cylindrus*	Horner, 1981
	Nitzschia frigida	
Stefansson Sound	*Nitzschia cylindrus*	Horner and Schrader, 1982
	Nitzschia frigida	
Narwhal Island	*Nitzschia cylindrus*	Horner and Schrader, 1982
Arctic Canada	*Nitzschia cylindrus*	Dunbar and Acreman, 1980 Hsiao, 1980
	Nitzschia frigida	Dunbar and Acreman, 1980 Hsiao, 1980
	Nitzschia grunowii	Dunbar and Acreman, 1980
	Nitzschia polaris	Hsiao, 1980
	Navicula quadripedis	Hsiao, 1980
Davis Strait	*Navicula transitans* var. *derasa*	Booth, 1984
	Nitzschia frigida	
Fobisher Bay	*Achnanthes taeniata*	Grainger and Hsiao, 1982
	Cylindrotheca closterium	
	Navicula directa	
	Nitzschia frigida	
	Nitzschia grunowii	
	Nitzschia longissima	
	Nitzschia tergestina	
Hudson Bay	*Navicula pelagica*	Poulin and others, 1983
	Nitzschia cylindrus	Gosselin and others, 1985
	Nitzschia frigida	
St. Lawrence Gulf	*Chaetoceros debilis*	Dunbar and Acreman, 1980
	Porosira glacialis	
	Thalassiosira nordenskioeldii	
St Lawrence Estuary	Microflagellates	Demers and others, 1984
	Cyclotella striata	

To some extent, the community structure in the different ice layers reflects the growth conditions prevailing at the time the algae were incorporated into the ice. In lower latitudes and in estuarine conditions, ice formation is affected by tidal movements and thus, the floristic composition in the ice may be completely different from the high arctic sea ice assemblage. This estuarine ice assemblage may show a higher proportion of freshwater and pelagic forms (Dunbar and Acreman, 1980; Demers and others, 1984) and because of our ignorance about the area where the ice formed, it becomes difficult to determine the reasons for its peculiar assemblage. The ice fields, which are drifted at the mercy of the tides, are colonized by algal cells of unknown origins, i.e. the algae may have been incorporated into the ice at different localities in the estuary resulting in a composite bottom sea ice assemblage.

In the Arctic, the vertical distribution of the bottom sea ice assemblage is ascribed to the photo-oxidation of the photosynthetic pigments in the upper sections of the ice (Apollonio, 1961), to the occurrence of an upward increasing gradient of the osmotic pressure in the brine isolating the algae in the lower sections (Meguro and others, 1967a), or to the increasing number of brine pockets in the lower strata of the ice (Lake and Lewis, 1970; Grant and Horner, 1976) ensuring a larger surface area for colonisation.

On a global view of the North Hemisphere, the same taxonomic composition is found in sea ice sampled in Alaska (Horner and Schrader, 1982), Canada (Hsiao, 1980; Poulin and Cardinal, 1982a, 1982b, 1983), and U.S.S.R. (Usachev, 1949). Thus, the bottom sea ice flora has a circumpolar distribution, but the dominant species will vary from one region to another (Table 3.3).

Although some endemism has been reported in the literature (Hsiao, 1980, listed 11, 24, and 44 species apparently endemic to Eskimo Lakes, Eclipse Sound and Frobisher Bay, respectively), it seems likely that many, if not most endemic taxa, will be found to be more widely distributed when the sea ice diatom flora becomes better known and taxonomic work on the more difficult groups is done. For the Canadian Arctic, Hsiao (1980) identified the eighteen most frequently encountered ice diatom taxa (Table 3.4), some of them being considered as typical cryophilic taxa according to Usachev (1949).

Table 3.4. Most frequent ice diatom taxa encountered in the Canadian Arctic (after Hsiao, 1980).

Amphiprora kjellmanii var. *kariana* (Grun.) Cleve
Amphiprora kjellmanii var. *striolata* (Grun.) Cleve
Amphora laevis var. *laevissima* (Greg.) Cleve
Cylindrotheca closterium (Ehrenb.) Reimann & Lewin
Gomphonema exiguum var. *pachycladum* (Bréb.) Cleve
Navicula directa (W. Sm.) Ralfs
Navicula quadripedis Cleve-Eul.
Nitzschia cylindrus (Grun.) Hasle
Nitzschia frigida Grun.
Nitzschia gruendleri Grun.
Nitzschia hybrida Grun.
Nitzschia laevissima Grun.
Nitzschia polaris Grun.
Nitzschia tergestina (Kütz.) Ralfs
Pinnularia quadratarea var. *stuxbergii* (Cleve) Cleve
Pleurosigma clevei Grun.
Pleurosigma stuxbergii Cleve & Grun.
Thalassiosira nordenskioeldii Cleve

CHAPTER 4

TECHNIQUES FOR SAMPLING SEA-ICE ALGAE

Rita Horner

Sampling is one of the most difficult problems in the study of ice algae. Part of the problem is the structure of the ice. In the Arctic, most of the ice is composed of congelation ice, i.e., ice crystals whose c-axes are parallel to the ice-water interface (also called columnar ice) (Maykut, 1985; Squire, this volume). In the Antarctic, however, layers of frazil (platelet) ice crystals may occur between layers of congelation ice (Weddell Sea-Maykut, 1985) or may form layers up to 4 m deep on the underside of the ice (McMurdo Sound - Dayton and others, 1969; Mirny - Morecki, 1965). A similar situation may occur in the Arctic where slush ice up to 2.5 m thick can occur beneath congelation ice in coastal areas (Larsen, 1980; Reimnitz and Kempema, 1987). These variations in the ice structure then, may add to the difficulties in choosing an adequate sampling technique for the ice algae. As a result, many techniques have been used, but not all of them have been equally successful or adequately described in the literature. This is an attempt to describe the sampling methods that have been used and to point out some of their strengths and weaknesses.

The most commonly used ice sampler has been a surface-operated coring device usually known as a SIPRE (for Snow, Ice, Permafrost Research Establishment) corer (Apollonio, 1965; Horner and Alexander, 1972; Alexander and others, 1974; Hoshiai, 1977; Ackley and others, 1979; Dunbar and Acreman, 1980; Hoshiai and Fukuchi, 1981; Takahashi, 1981; Pett and others, 1983; Palmisano and Sullivan, 1983; Clarke and Ackley, 1984; Grossi and others, 1984; Grossi and Sullivan, 1985; Palmisano and Sullivan, 1985a; Sullivan and others, 1985; Gosselin and others, 1985, 1986; Takahashi and others, 1986). This coring auger cuts a core 7.6 cm in diameter and 0.75 to 0.9 m long. It consists of heavy-walled stainless steel tubing with specially formed and shaped double helical stainless steel flighting welded to it (Fig. 4.1). A stainless steel cutting shoe with tungsten carbide bits enables the corer to cut through snow, ice, and permafrost. A T-shaped handle attached to the driving head is used for hand coring, but a small 1-5 horsepower gasoline engine may be used for more rapid coring. When 1 m long aluminum extension rods are added, a core through the entire ice thickness can be retrieved.

Unfortunately, the bottom of the ice where most of the ice algae are found, at least in the Arctic, is often relatively soft and is easily broken when the corer breaks through the bottom of the ice. As a result, an unknown part of the sample may be lost. Booth (1984) sampled ice floes in Davis Strait and used a fibrescope to watch the underside of the ice as the corer cut through. She did not observe any loss of the bottom ice, but this may have been because of the hardness of the ice.

If ice cores obtained with surface coring techniques are to be used for physiological experiments such as ^{14}C uptake, then care must be taken to minimise exposure of the cells to the high light intensities and subfreezing air temperatures at the surface. It is not known what, if any, physiological damage might be done to the cells adapted to the relatively low light intensity and higher water temperature found beneath the ice. Care must also be taken to ensure that incubators used for laboratory studies mimic conditions normally experienced by the ice algae (Palmisano and Sullivan, 1982). Further, if the ice cores are allowed to melt, then the cells are not living under their normal environmental conditions.

Ice samples collected with SIPRE corers have been used to determine primary productivity both in laboratory incubators (Alexander and others, 1974; Palmisano and Sullivan, 1982) and *in situ* (Booth, 1984), and to

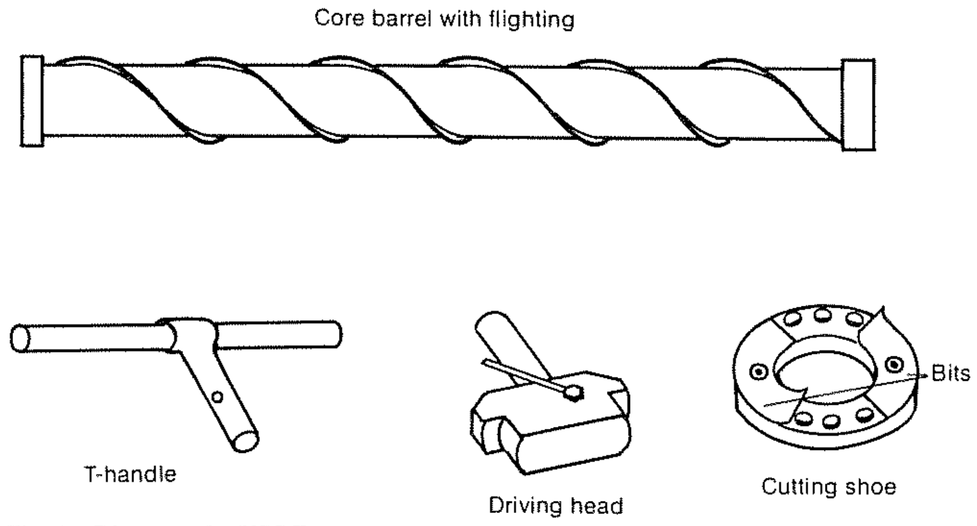


Fig. 4.1 Diagram of a SIPRE corer.

Geographical variations can be observed on a small and large scale with patchy distributions of the bottom sea ice assemblages correlated with light attenuation caused by increased snow cover. Situations prevailing in offshore coastal environments tend to follow this same patchy distribution but the floristic composition may not be necessarily different. At the mouth of freshwater effluents, the physical conditions of the water bodies establish peculiar oceanographic situations. In southeast Hudson Bay, Poulin and others (1983) reported that the salinity of the underlying surface waters establishes a salinity gradient in the ice which emerges as a major environmental factor controlling the spatial distribution and the abundance of the species responsible for the particular horizontal distribution of the ice diatom flora. The presence of a high number of ice diatom taxa corresponds to maximum salinities of the surface waters as well as in the ice. A decrease in salinity is followed by a progressive loss of ice diatom taxa. Thus, the taxonomic impoverishment gradient represents the tolerance of the diatoms to a decreasing salinity gradient.

Seasonal and annual variations in species dominance and floristic composition are also observed in the bottom sea ice diatom flora; the main genera present, in terms of number of species, are *Navicula*, *Nitzschia*, and *Pinnularia* (Table 3.5). Some species succession was noted during the season in Alaska: *Nitzschia cylindrus* was the dominant taxon in April and early May; by mid-May the community shifted to a multi-species dominance including *Gomphonema exiguum* var. *arctica*, *Navicula directa*, *N. transitans*, *Nitzschia frigida*, and *Pinnularia quadratarea* (Horner, 1985). This shift in the species composition may be due to different environmental conditions favouring species tolerant of reduced salinity, high level of nitrates, or higher light intensity.

The variability in species composition between years is also considerable. At the time of ice formation, algal cells trapped during the freezing process will give a sea ice assemblage that reflects the physical conditions of the water at the time the ice formed. The floristic composition then depends on the oceanographic characters of the underlying waters, which vary from year to year. At Barrow, Alaska, the bottom ice flora was dominated by the pennate diatom *Nitzschia frigida* in 1972, whereas the next year, *Navicula marina* was the major component of the ice diatom assemblage (Table 3.3).

It is important to understand that the species composition of bottom ice assemblages varies considerably depending upon the time of the year (seasonal distribution), the station locations (spatial distribution), and the sections of the ice core sampled (vertical distribution). Variability is also expressed year to year. In a sense, the northern distribution can be considered as circumpolar with probably few endemic taxa. More taxonomic works need to be done in order to better identify the floristic elements of this bottom sea ice assemblages in the Arctic.

Table 3.5. Relative dominance of ice diatom genera (Pennales) according to their number of taxa recorded from the literature.

References	*In decreasing order of importance*		
	1	*2*	*3*
Meguro and others, 1966-1967b	*Navicula*	*Pinnularia*	*Pleurosigma*
Horner, 1976	*Navicula*	*Nitzschia*	*Amphiprora*
Dunbar and Acreman, 1980	*Amphiprora/Diploneis*	*Navicula*	*Nitzschia*
Hsiao, 1980	*Navicula*	*Nitzschia*	*Pinnularia*
Grainger and Hsiao, 1982	*Navicula*	*Nitzschia*	*Pleurosigma*
Hsiao, 1983	*Navicula*	*Nitzschia*	*Pinnularia*
Poulin and Cardinal, 1983	*Navicula*	*Nitzschia*	*Pinnularia*
Booth, 1984	*Navicula*	*Nitzschia*	*Pleurosigma*
Horner, 1985	*Navicula*	*Nitzschia*	*Pinnularia*

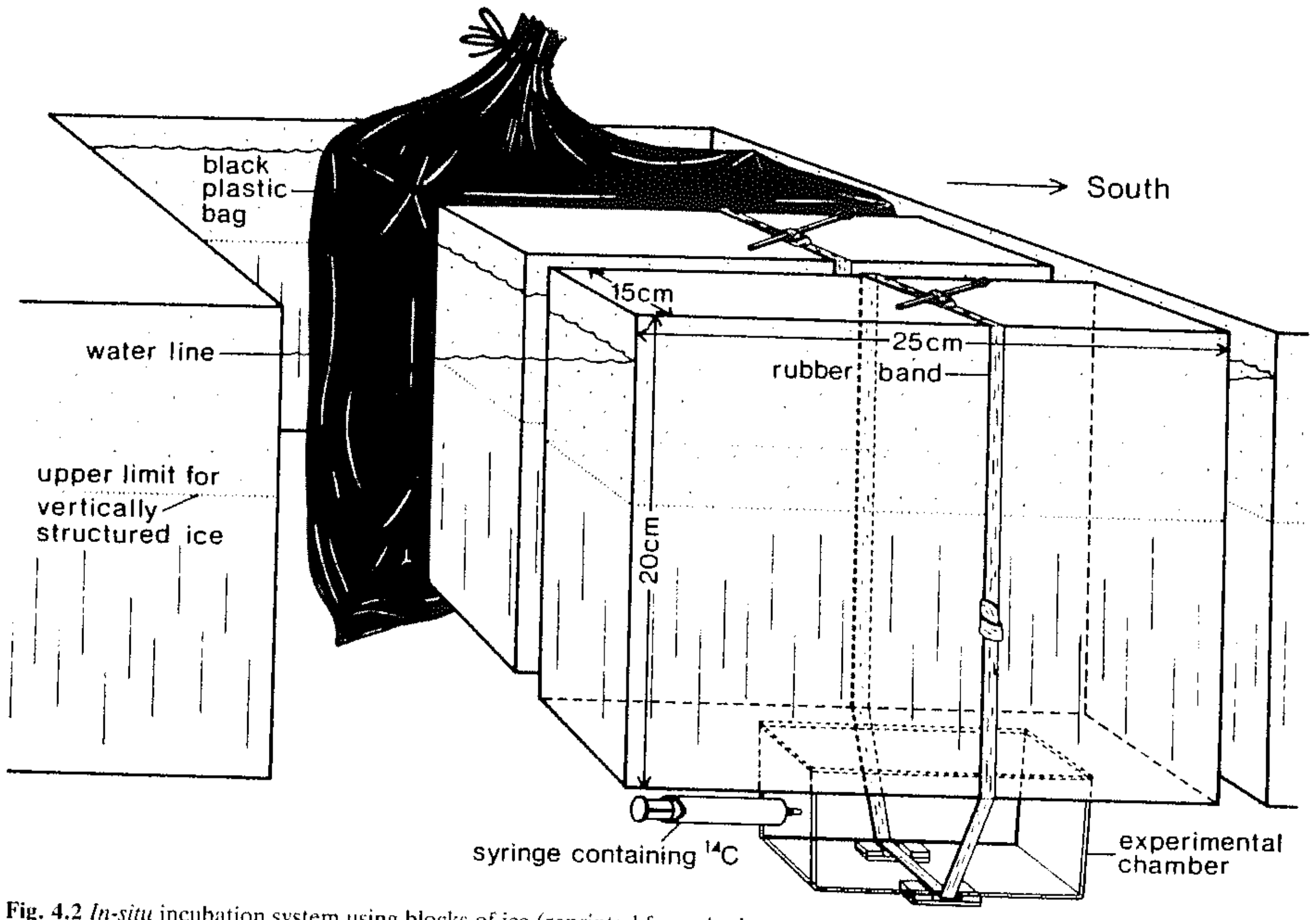


Fig. 4.2 *In-situ* incubation system using blocks of ice (reprinted from Andersen, 1977)

determine chlorophyll *a*, species composition, cell numbers, and salinity and nutrient concentrations. When ice cores have been used to determine salinity and nutrient concentrations, the samples are usually allowed to melt before analyses are done. This dilutes the interstitial water where the cells are living with freshwater from the ice crystals so that accurate measurements of the salinity and nutrient concentrations are not obtained. One possible solution for this is to allow the core samples to drain so that interstitial water is collected, but the ice does not melt completely. However, it is not known how much dilution might still occur. Another solution is to collect interstitial water directly by removing a short core from the ice and collecting the water that drains into the core hole. This method was used by Garrison and Buck (1986) to show that serious losses of organisms occur when the cells are subjected to rapid and extreme changes in salinity as ice cores are melted. Nutrient concentrations could also be measured in this interstitial water (called pore water by Garrison and Buck, 1986).

Other surface sampling techniques have included cutting blocks of ice and attaching plastic incubation boxes to the underside of the ice (Andersen, 1977). After the incubation box was attached and ^{14}C injected, the whole block of ice was returned to its original position in the ice (Fig. 4.2). Dark experiments had the ice plus incubation chamber enclosed in black plastic bags. This technique would work best where the ice is not very thick. Poulin and Cardinal (1982a,b, 1983) cut 2-3 cm sections from blocks of ice for samples used to describe the floristic composition of the ice algae in Manitounuk Sound, Hudson Bay. Blocks of ice have also been used to determine biomass (chlorophyll *a*) and species composition in relation to light and rate of freezing of the ice in the St. Lawrence estuary (Demers and others, 1984). Booth (1984) used a SIPRE corer to collect her samples, but placed them in plexiglass chambers that were then suspended under the ice (Fig. 4.3). She avoided exposing the samples to high light intensity by keeping them in dark plastic bags during manipulations before putting them back under the ice.

In order to avoid the problems encountered using surface coring techniques, Clasby and others (1973) devised a simple combination sampler-incubation chamber (Fig. 4.4) that could be placed directly into the undersurface of the ice by SCUBA divers. Primary productivity measurements could then be made *in situ*. Following incubation, the ice core was cut from the ice with a heavy metal spatula and the sampler capped with a core cap and returned to the surface. These chambers, also used to collect samples for estimation of pigment concentration, cell numbers, species composition, and nutrient and salinity determinations, worked well in the relatively soft bottom ice at Barrow, Alaska. They did not work well near Prudhoe Bay, Alaska (R. Horner, pers. obs.), perhaps because of the shallowness of the soft unconsolidated ice layer where the algae were living. As a result, the chamber was redesigned (Schrader and others, 1982) (Fig. 4.5) to permit more secure attachment to the ice and to reduce sampling loss that may occur during core extraction and capping. A similar chamber was used at Australian Antarctic stations

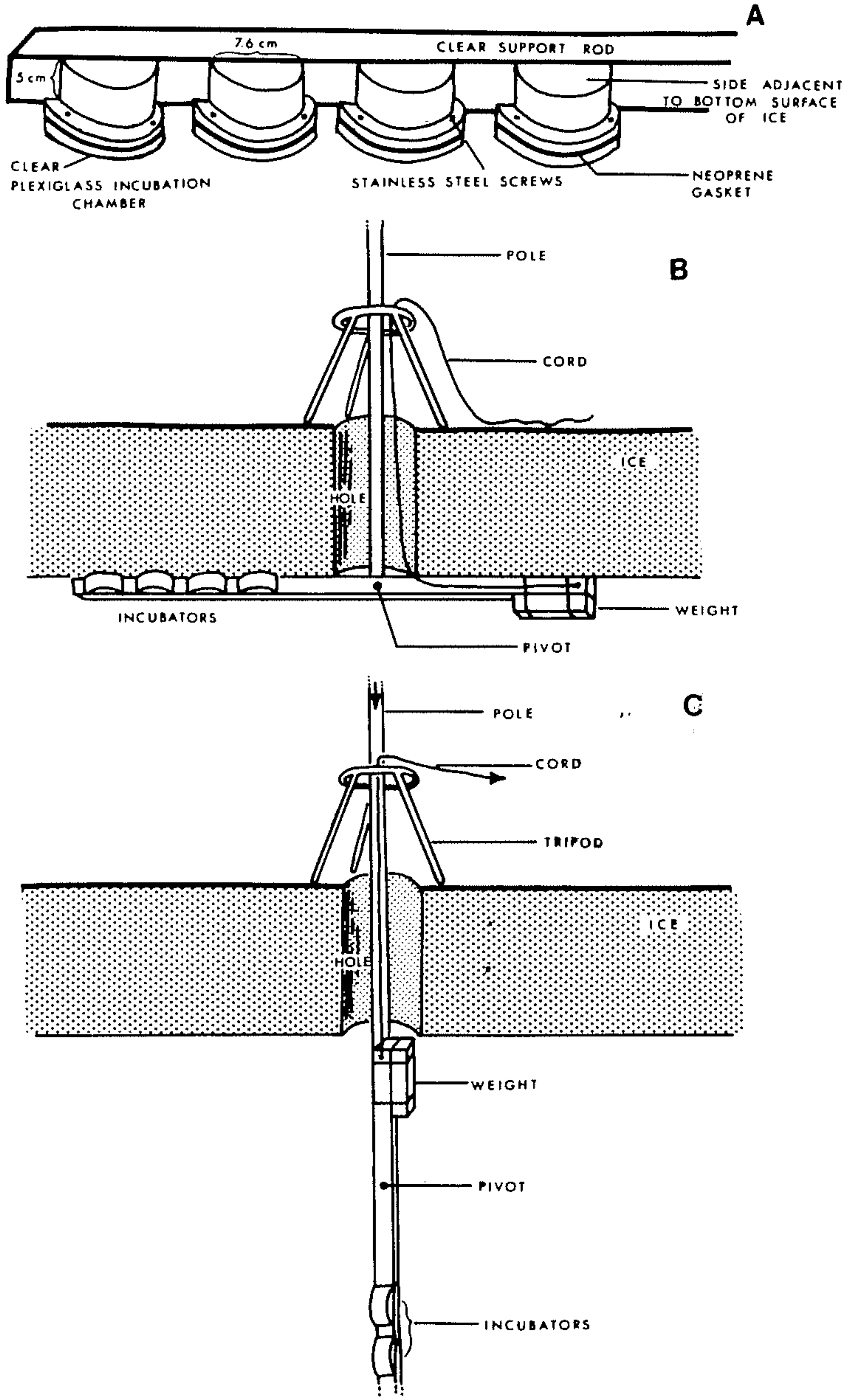


Fig. 4.3 *In-situ* incubation system using ice cores collected with a SIPRE corer (reprinted from Booth, 1984)

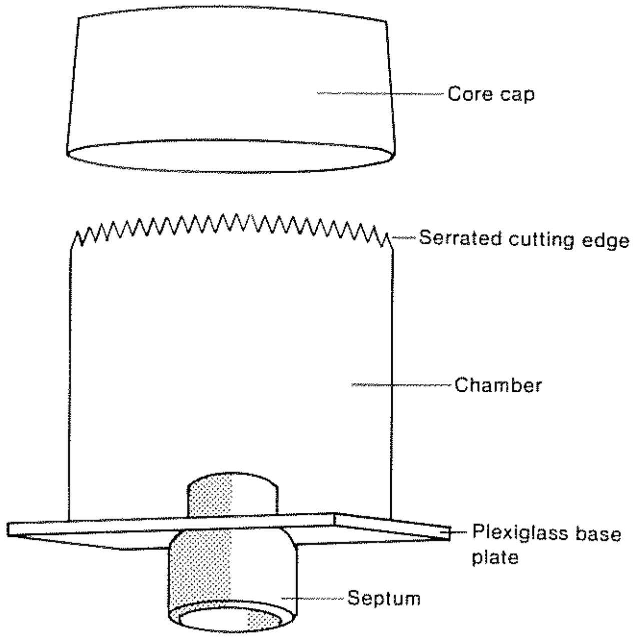


Fig. 4.4 Original *in-situ* combination sampler-incubation chamber (Clasby and others, 1973).

(McConville and Wetherbee, 1983; McConville and others, 1985).

These chambers offer improvements over surface sampling techniques, but there are still problems. It is difficult to ensure that there is adequate mixing of the isotope in the chamber because of the matrix of ice crystals. It is also possible that an unknown amount of the isotope may diffuse upward into the ice above the chamber during incubation and not be retrieved. This latter problem was solved by McConville and Wetherbee (1983) who cut the ice core sample off before ^{14}C inoculation and added a plexiglass cap to the chamber, thus ensuring that all the added isotope would be recovered at the end of the incubation period. McConville and Wetherbee (1983) also enlarged the chamber and lengthened the steel pins that hold the chamber in the ice, thus making the chamber usable in areas where the bottom layer of the ice is relatively thick. The enlarged chamber was also used to collect ice crystals scraped off the underside of the ice to be used for *in situ* productivity incubations. These *in situ* combination sampler-incubation chambers did not work at McMurdo Sound where there is often a thick layer of frazil ice (C.W. Sullivan, pers. comm.).

Sampling at McMurdo Sound has been more difficult because of the layer of frazil ice that is often found underneath the congelation ice. Bunt (1963) found that it was not feasible to design appropriate sampling gear, so divers manually dislodged large quantities of ice crystals that were retrieved when they floated to the surface in the dive hole. Divers have also forced a van Dorn water sampling bottle through the ice, closing it manually (Bunt and Lee, 1969).

A modified syringe device was used by Grossi and others (1984) and Palmisano and others (1985). This sampler consisted of a polypropylene funnel 9 cm in diameter to which three 50 ml syringes were attached by a common port. The funnel was pushed into the ice by a diver and the ice-seawater sample was pulled into the syringes. The sample was mostly water with only a few ice crystals. Cells actually attached to ice crystals could have been dislodged and thus increased the number of cells in the sample (interstitial) water, or could possibly have been lost. Either way, the samples could have been biased. Jars of various kinds and sizes have also been used in both the Arctic and Antarctic to collect ice crystals that have been dislodged from the underside of the ice (Sullivan and Palmisano, 1984; Sasaki and Watanabe, 1984; Palmisano and Sullivan, 1985b; R. Horner, pers. obs.).

In the Arctic, a specially designed 2 litre epontic sampler was used to collect interstitial water from the ice and microalgae from the ice-water interface (Rochet and others, 1985; Gosselin and others, 1986; Legendre and others, 1986; Maestrini and others, 1986). The samples were free of ice. This sampler is composed of a disk (piston) that slides back and forth in a 20 cm diameter hollow cylinder (Fig. 4.6). A rod ca. 6 cm long is welded to the outside of the piston. When the piston is at the upper part of the cylinder, the cylinder is closed and contains no water. When the rod hits a hard surface (e.g., the underside of the ice), the piston moves downward and the cylinder fills with water. Suspending wires are attached to the upper edges of the cylinder (M. Gosselin, pers. comm., 1986). This sampler is deployed by cutting a hole in the ice and sawing two parallel tracks 25 cm apart. The sampler is lowered through the hole and positioned under the ice by pulling the suspending wires along the parallel tracks. The sampler is attached to a winch and pulley system mounted on a tripod and is thus firmly attached to the underside of the ice. The block of ice above the sampler is freed by cutting through the ice perpendicular to the parallel tracks. The ice block and sampler are then lifted free using the winch and pulley system (Maestrini and others, 1986).

Algae in the interstitial water flowing from the ice and in the upper 2 cm of the water column are collected in the cylinder. The sample is trapped *in situ* and is protected from surface light. The sample can be transferred to other containers and transported to a shore laboratory for experimental procedures (Maestrini and others, 1986). The advantages of this technique are that the samples can be collected from the upper surface of the ice and they can be used for analysis or experimentation without melting the ice. A 2 dm^3 sample can be collected in 1-2 h by two people (M. Gosselin, pers. comm., 1986). However, this sampler may not collect cells actually attached to ice crystals unless the cells are dislodged by the movement of the interstitial water flowing out of the ice, or in some other manner.

Another sampling device used by M. Gosselin (pers. comm., 1986) is a suction or slurp gun that is used by a diver. This device consists of a plexiglass cylinder with a nozzle on one end and containing a piston made of neoprene that can be withdrawn to collect a sample. Similar suction guns are available from SCUBA gear shops. An advantage of the suction gun is that samples can be collected from a number of sites close together in a relatively short time. Horner, Alexander, and their coworkers tried using a suction gun, but had trouble with sample loss, perhaps because the piston was also made of plexiglass and water leaked from the cylinder (R. Horner, pers. obs.). They used the device primarily to collect amphipods from the underside of the ice.

Sediment traps have been used under ice in shallow, nearshore areas (Pett and others, 1983; Carey and

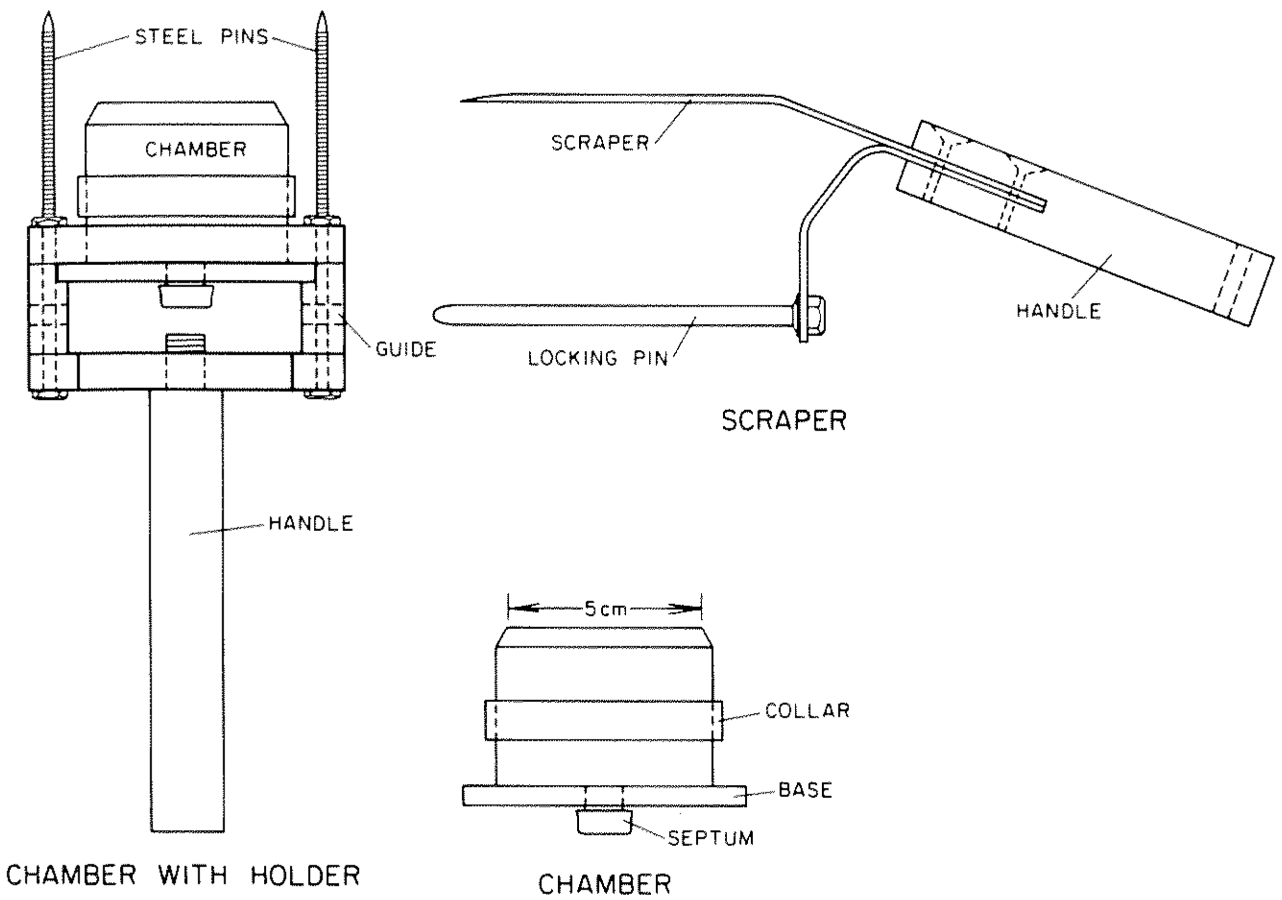


Fig. 4.5 Redesigned *in-situ* combination sampler-incubation chamber (reprinted from Schrader and others, 1982).

others, 1984; Carey, 1987) and in deep water (R. Gersonde, pers. comm., 1986) to determine particle flux to the sediments. Deployment times for the shallow water traps ranged from 13 to 55 days (Pett and others, 1983) and from 5 to 7 days (Carey and others, 1984; A.G. Carey, Jr., pers comm., 1986; Carey, 1987). The efficiency of sediment traps depends on trap design, placement, length of deployment, and dynamics of water flow around the trap (Pett and others, 1983; Gardner, 1980a, b). In addition, resuspension of bottom sediments, horizontal advection, and *in situ* grazing may affect the efficiency of the trap. Ice algal samples found in sediment traps can be useful indicators of the fate of ice algae through sinking or utilization by zooplankton, as seen by their occurence in faecal pellets, and perhaps even of the origin of ice algae, at least in shallow water, if cells can be resuspended from bottom sediments and caught in the traps.

A variety of sampling devices have been used in studies on ice algae. Some of them work well, others not so well; some work better in some types of ice than in others. Adequate descriptions and figures of newly devised sampling gear are not always given in the literature. In addition, the kind of ice, e.g. congelation, platelet, grease, etc., and the age of the ice are not always described completely. This makes it difficult for other investigators to determine what kinds of samples were used, or how they were obtained. Therefore, it is imperative that sampling gear, the kind of ice being sampled, and the experimental methods used be described adequately.

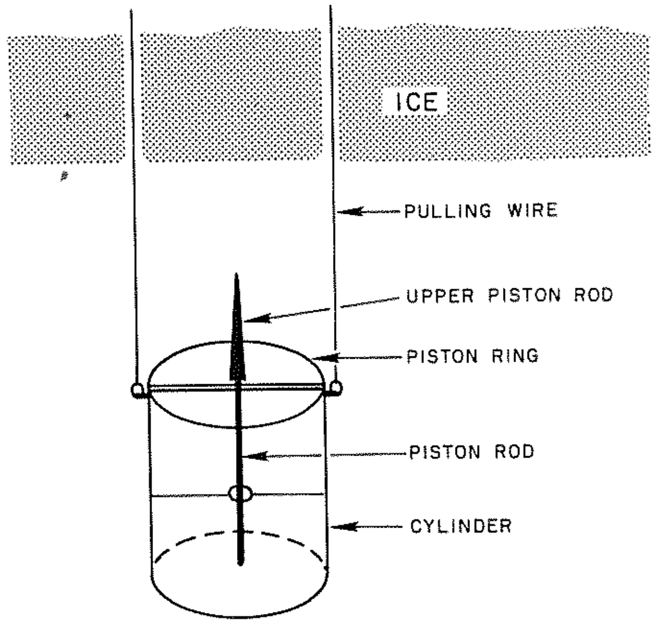


Fig. 4.6 Specially designed 2 litre epontic sampler (designed by Harold D.G. Smyth, GIROQ, Pavillon Vachon, Université Laval Quebec G1K 7P4 and drawn from sketches provided by M. Gosselin, pers. comm., 1986).

CHAPTER 5

THE ANTARCTIC PLANKTONIC ECOSYSTEM

Julian Priddle

The Southern Ocean covers an area of appproximately 36 million km^2, bounded at the poleward edge by the Antarctic continent and its ice-shelves but delimited at lower latitudes by an oceanographic feature - the sub-Antarctic Front (Antarctic Converegence). This configuration of a more-or-less continuous belt is unique in the World Ocean, and covers the area between 55° and 75°S. As with the Arctic Ocean, the Southern Ocean is persistently cold whilst other components of the physical environment exhibit marked seasonal changes. Annual variation of incoming solar radiation increases in amplitude with increasing latitude (Holm-Hansen and others, 1977; Sakshaug, this volume) and sea-ice cover undergoes similar season-to-season changes. Half of the Southern Ocean experiences annual ice cover (Squire, this volume) whilst only the most northerly 40% is perennially ice-free.

The apparent high abundance of marine life in an environment which is so inhospitable for humans is often surprising to the layman. However, it was a desire to exploit the richness of the marine ecosystem that motivated much of the Antarctic exploration in the eighteenth and nineteenth centuries (Walton and Bonner, 1985). Utilization of marine living resources continued into the twentieth century with first the whaling industry and more recent interest in the exploitation of fish, squid and the Antarctic krill.

The trophic structure of the Southern Ocean pelagic environment has often been represented as being comparatively simple, with the food-chain 'diatom-krill-baleen whale' representing the dominant path for energy transfer. On the one hand, this obviously neglects the complex interactions between other components, including the large number of other animal species which compete with or depend on the Antarctic krill (*Euphausia superba*). On the other hand, the very simple food-chain does symbolise some important properties of the trophic structure of the Southern Ocean pelagic ecosystem. In particular, it shows that energy flow may follow a relatively short path in which transfers occur between organisms dramatically different in size (Billen, Lancelot and Mathot, 1988). The key role of Antarctic krill in the pelagic ecosystem has been demonstrated by the effects of the decline of baleen whales as a result of the whaling industry. This anthropogenic perturbation of the ecosystem is thought to have left a significant krill surplus no longer consumed by the whales. This surplus has been taken up by increases in the biomass of several other species of krill predators (Laws, 1985).

THE PHYSICAL ENVIRONMENT

Large-scale features

As noted above, the Southern Ocean is a unique area of the World Ocean. The northern boundary is an oceanographic feature rather than a coastline, so that the Southern Ocean has a major role in interconnection between the Southern Hemisphere oceans. The movement of surface waters around the Antarctic continent is dominated by the zonal circulation of the Antarctic Circumpolar Current (West Wind Drift), and the more complex circulation close to the continent. The latter comprises the Antarctic Coastal Current (East Wind Drift) and two major gyre systems in the Weddell and Ross Seas. Pickard and Emery (1982), Foster (1984) and Gordon (1988) provide a thorough summary at this 'basin-scale'.

Several features of this circulation and its forcing mechanisms are of great biological significance. The Antarctic Circumpolar Current (ACC) is driven by strong westerly winds (Colton and Chase, 1983) and water motion reaches to the sea-bed (Nowlin and Klinck, 1986). The high rate of transport of this current – of the order of 125 Sv (Sverdrup = 10^6 m^3 s^{-1}) (see summary by Gordon, 1988) – is attributed to its large cross-sectional area rather than its velocity (Foster, 1984). Velocity is not uniform across the current (Baker and others, 1977; Georgi, 1978; Nowlin and Klinck, 1986) and two major streams with geostrophic current velocities of 25-45 cm s^{-1} account for more than half of the transport but about one quarter of the cross-sectional area. Since flow extends throughout the water-column, the ACC interacts with the sea-bed. This is of particular importance in relatively shallow parts of the ocean such as the Macquarie Ridge and Kerguelen Plateau. However, the critical region for topographic effects on the ACC is the Drake Passage and Scotia Ridge, which together with the outflow from the Weddell Sea Gyre (Carmack and Foster, 1975) deflect flow first to the north and then returning to the east as the ACC leaves the Scotia Sea. This area is one of high mesoscale variability, with the positions of fronts altering over distances of up to 100 km within 10 days (Legeckis, 1977) and significant eddy generation (Bryden, 1983). It now appears that eddy generation and other mesoscale variability are likely to have significant influence on biological distributions in parts of the Southern Ocean (e.g. Priddle and others, 1988).

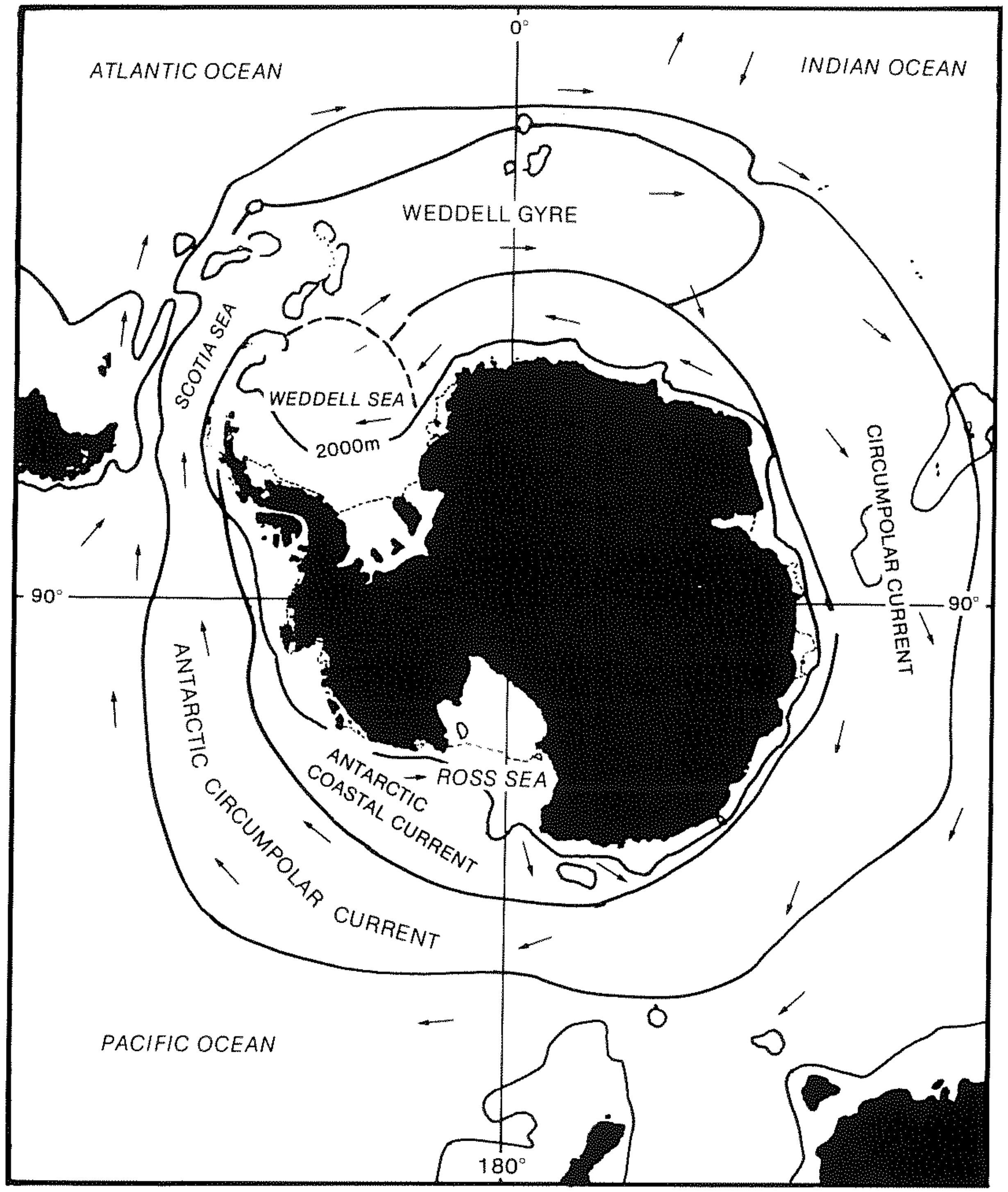


Fig. 5.1 Circulation pattern in the Southern Ocean.

Closer to the Antarctic continent, the western zonal flow of the Antarctic Coastal Current (East Wind Drift) is interrupted by both coastline and bathymetry. The largest single feature in this system is the Weddell Sea Gyre, which flows clockwise (cyclonic) to the east of the Antarctic Peninsula. This is a significant area in a global context, for much of the World Ocean's Bottom Water is formed in the Weddell Sea. The continental shelf around the coast of Antarctica and its off-lying islands is unusually deep (200 m or more) because of the depression of the land mass by the overburden of the inland ice-sheet which may reach several kilometres in thickness.

The interaction between sea-ice and the water column

Sea-ice dominates the environment of surface waters in the Southern Ocean, covering over half of the area south of the Subantarctic Front in winter (Squire, this volume). Much of this is relatively thin, seasonal ice which melts in summer, leaving only about 10% of the ocean area permanently covered. This seasonal variation in ice-cover results in significant modification of the physical conditions of the surface waters. Seasonal variation in incoming solar radiation is greatly accentuated through increased attenuation and albedo caused by ice in winter (Gosselin and others, 1986; Buckley and Trodahl, 1987; Sakshaug, this volume). The transfer of momentum from the air to the sea is greatly reduced by ice-cover (Squire, this volume). Melting ice removes heat from surface water and introduces buoyant, fresh meltwater. This produces a distinct physical structure associated with the zone adjacent to the melting of the sea-ice (Sullivan and others, 1988).

Over the Southern Ocean as a whole, sea-ice plays an important role in determining the physical properties of the water column which play a key role in biological processes. The predominance of seasonal ice in the Southern Ocean heightens the importance of ice as a biological environmental variable (Horner, this volume; Squire, this volume). In addition to the provision of a habitat for organisms both within and attached to the undersurface of the ice, the water column density structure at the retreating ice-edge results in increased stability which apparently enhances phytoplankton production (Smith and others, 1988, Sullivan and others, 1988). The interaction between the ice-associated- and pelagic ecosystems is exemplified by the overwintering survival of krill in the Weddell Sea, where these pelagic animals appear to survive by 'grazing' on under-ice algae (Marschall, 1988).

The physical and chemical environment of the upper water column

The combination of the low amount of solar heating at high latitudes and the great impact of ice melting on the annual thermal budget of the Southern Ocean means that temperatures in the Antarctic Surface Water are low and vary little. With salinities no higher than 34.5, the freezing point of seawater is about −1.9°C. Water temperatures remain close to this value in southerly waters close to the Antarctic Continent, whilst increasing heat flux in more northerly waters results in surface temperatures as high as 5°C in summer.

There is generally very little thermal, and hence density, stratification even during summer. Where a thermocline is present, this is commonly at depths between 30 and 60 m. High wind stress associated with regular storms often destroys this density structure. This situation is exacerbated in winter when the water column is more homogeneous and weather worse. In the ice-free Southern Ocean during winter, mixing depth may exceed 300 m (Heywood and others, 1985). In contrast, there are some specific sites where stability is enhanced. The presence of a marked density front associated with the ice-edge has already been noted. This arises from salinity gradients caused by melt-water floating over more saline seawater. This 'linear' ecosystem tracks across half of the Southern Ocean each year and development of a phytoplankton bloom associated with this feature may account for half of the total annual photosynthetic production at a particular locality (Smith and others, 1988).

Sheltered neritic sites may also provide areas where vertical mixing is reduced or inhibited. Large scale patterns of phytoplankton distribution can be mapped by satellite images from the Coastal Zone Colour Scanner (CZCS), now no longer functioning. Although good images are scarce for Antarctic waters, those which are available often clearly indicate the initiation or persistence of phytoplankton blooms in bays and channels. A well-documented site is the Gerlache Strait at the southern end of Bransfield Strait. Here, the topography of the land surrounding this narrow channel shelters it from wind whilst volcanic sills which come to within 40 m of the surface act as baffles which isolate the lower euphotic zone from wind stress. The density structure of the upper water column can survive most storms and very high phytoplankton biomass develops in this stable area. Water advected in the main area of Bransfield Strait may then act as an inoculum for other phytoplankton blooms (Heywood and Priddle, 1987).

One of the most distinctive aspects of the Southern Ocean as an environment for phytoplankton is the general superfluity of the common inorganic nutrients (Jacques, 1983). Representative values are summarised in Priddle and others (1986 – Table 1) and given in more detail in some of the research papers cited here. Concentrations of inorganic nitrogen may be as high as 55 mmol m^{-3}, with the great majority being nitrate, whilst silicon concentrations in the Weddell Sea are often as high as 90 mmol m^{-3}. Where phytoplankton growth at a site is high, these nutrients are greatly depleted – indicating that the high nutrient concentrations in other areas of the Southern Ocean can be attributed to underutilization by phytoplankton. Reasons for this are discussed below.

MICROPLANKTON

There is a considerable body of taxonomic information on the larger microplankton, especially on plankton diatoms, but less for some other groups such as picophytoplankton, bacteria and protists. Similarly, literature on the ecology and physiology of Antarctic marine microplankton has also been biased towards large-celled species. Although this deficiency is being remedied, we are still some way from a comprehensive understanding of the microplanktonic system and how it interacts with its environment and consumers.

Phytoplankton

Species composition

As noted above, the majority of the data available on the phytoplankton refer to larger-celled species – the net phytoplankton – and of these diatoms are usually the dominant group. Net phytoplankton may represent in turn a highly variable proportion of photoautotroph biomass in the Southern Ocean (Bröckel, 1981, 1985). Samples from areas of high biomass often contain large numbers of diatoms, including colonial species, and this can result in $\leq 90\%$ of the particulate chlorophyll biomass being retained by a 20 μm pore-size filter (Mullins and Priddle, unpublished data). The chlorophyll content of the smallest size fraction appears to be more constant over time and space, so that this fraction becomes proportionately more important at low overall biomass (Bröckel, 1981, 1985; Mullins and Priddle unpublished). Gieskes and Elbrächter (1986) reported that the pigment composition of these small particles indicated that many were isolated chloroplasts resulting from the breakage of larger cells by turbulence shear in surface waters. This suggests that the ecological significance of

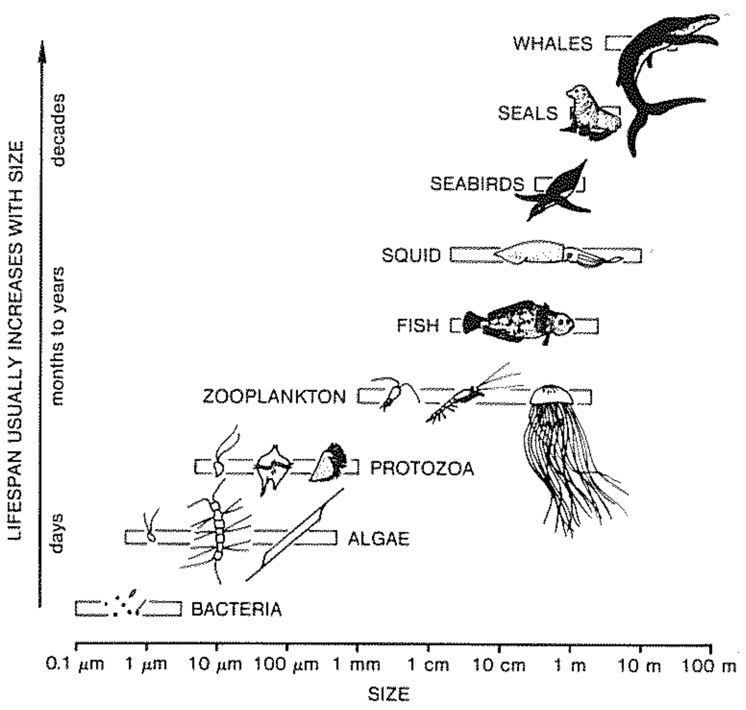


Fig. 5.2 Size ranges for components of the Southern Ocean pelagic ecosystem.

the chlorophyll biomass in the smallest size fraction is uncertain. The supposedly ubiquitous picocyanobacterium *Synechococcus* may be absent from much of the Southern Ocean. Marchant, Davidson and Wright (1987) and Stirling (unpublished data) found that this organism was effectively absent from samples of surface water taken at sea-temperatures < 4°C. Whether this feature applies comprehensively to the Southern Ocean is uncertain, but if it is so, then the microplankton in this area differs dramatically from most other areas of the World Ocean.

Where biomass is high, it is usually diatoms which dominate the net plankton and hence make the major contribution to overall biomass (El-Sayed, 1971; Heywood and Priddle, 1987). There are several characteristic taxa, some of which are endemic to Antarctic waters. Large-scale studies of the biogeography of diatom taxa in the Southern Ocean were first associated with expeditions, but some large-scale systematic surveys have been undertaken. Two major publications arose from the *Discovery* Investigations – Hendey (1937) provided an up-to-date compilation of taxonomy and distribution of the diatoms in the wide-ranging voyages of *Discovery* and *William Scoresby*, whilst Hart (1934, 1942) looked in more detail at biogeography and seasonal changes in the areas of the Bransfield Strait and Scotia Sea. Later voyages yielded information for other parts of the Southern Ocean, for instance the *Brategg* expedition in the Pacific Sector (Hasle, 1969) and the voyages of the *Ob* (Kozlova, 1964). Much of the information available up until the late 1960's has been summarised for selected species in the American Geographical Society's *Antarctic Map Folio Series* (Balech and others, 1968). Such a summary remains appropriate, as few modern expeditions provide the wide-ranging coverage of the earlier voyages but rather tend to concentrate on restricted areas. Several diatoms are shown to have circumpolar distributions – either in the more northerly waters of the Antarctic Circumpolar Current (e.g. *Rhizosolenia curvata* – see also Hart, 1937), or in the waters of the Antarctic Coastal Current and its gyres (e.g. *Actinocyclus actinochilus*). Many species have a more widespread distribution, such as the distinctive pennate diatom *Nitzschia kerguelensis*.

Diatom blooms commonly contain several species. Around South Georgia, for instance, these population maxima have comprised dense growth of *Thalassiosira scotia* and *Chaetoceros socialis* (Theriot and Fryxell, 1985), or *Eucampia antarctica* with *Odontella weissflogii*, *Rhizosolenia* and *Proboscia* spp., *Corethron* and *Thalassiothrix* (Priddle and Mullins, unpublished). A very dense bloom of diatoms near King George Island (South Shetland Islands) contained *Odontella weissflogii*, *Proboscia 'alata'*, *Chaetoceros curvisetum* and *Thalassiosira tumida* (Heywood and Priddle, 1987). Although not all diatom blooms in the Southern Ocean are dominated by centric genera as these were, the examples cited are quite typical and this predominance of colonial and chain-forming taxa appears to be typical.

The only non-diatom alga which commonly forms comparable biomass in the Southern Ocean is the colonial haptophyte *Phaeocystis poucheti* (Hariot) Lagerheim. This may occur at high local abundance in some coastal waters (Burkholder and Sieburth, 1961). *Phaeocystis* was the dominant phytoplankton species in a study in the eastern Weddell Sea in January (Nöthig, 1988) and the species occurs in association with the ice-edge in the Ross Sea (Palmisano and others, 1986). During a recent cruise in the open seas around South Georgia, this species was found in phytoplankton net-hauls made when the diatom bloom appeared to be declining and dissolved silica concentrations were unusually low (Priddle, unpublished data). The overall importance of *Phaeocystis* is uncertain, but its local impact may sometimes be great. Coccolithophorids, which form dense blooms in temperate oceans and are common in the Arctic, are thought to be rare or absent from Antarctic samples, but recent data suggest that they are more widespread and may dominate the nanoplanktonic community (Buma and others, 1989). Several other algal groups which may be abundant in net phytoplankton in other ocean areas are poorly represented. Dinoflagellates are well known from the Southern Ocean and exhibit a moderate degree of endemism within some genera (Balech, 1975). However no taxa, including photoautotrophs, reach abundances approaching those of the diatoms (Dodge and Priddle, 1987).

Production and ecology of the phytoplankton

The marked annual variation in solar radiation and ice-cover imposes a similarly strong seasonality on phytoplankton production (Whitaker, 1982; Clarke, Holmes and White , 1988). It is now understood that the average productivity over the entire Southern Ocean is similar to that of oligotrophic areas of the World Ocean (El-Sayed, 1984; Priddle and others, 1986). However, local maxima may be very high and utilise the full potential suggested by the typically high concentrations of inorganic nutrients in the Southern Ocean. The apparent paradox of high nutrients and low overall production has attracted attention from biologists (see reviews by Jacques, 1983; El-Sayed, 1984; Holm-Hansen, 1985; Priddle and others, 1986; Billen, Lancelot and Mathot, 1988). The occurrence of such high local production, and various shipboard experiments that indicate that under certain conditions phytoplankton can grow as fast as temperate communities and dramatically deplete the inorganic nutrient pool, make it most unlikely that growth is limited by availability of the common nutrients (Jacques, 1983; Priddle and others, 1986). Likewise, investigation of the effects of trace elements has usually indicated that these are not limiting (e.g. Hayes, Whitaker and Fogg, 1984). Work undertaken by Martin and co-workers (Martin and Fitzwater, 1988; Martin and Gordon, 1988) has implicated iron-deficiency as a limiting factor in Pacific Subarctic phytoplankton. Very recently, Martin, Gordon and Fitzwater (1990) have extended their observations to Antarctic waters. They equate high neritic phytoplankton growth in Gerlache Strait and low growth in Drake Passage to their respective high (7 μmol kg^{-1}) and low (0.16 μmol kg^{-1}) concentrations of Fe. Whether this will prove to be the overriding factor proposed by the authors remains to be tested.

Thus we can progress from the original paradox of Antarctic marine phytoplankton 'starving in the midst of plenty' to a more simple question – 'what prevents phytoplankton from utilizing dissolved nutrients in the Southern Ocean euphotic zone'. Three environmental factors may play a part in this sub-optimal performance. First, the energetic vertical mixing in the Southern Ocean water column may carry algal cells beneath critical depth and will expose cells to a highly variable irradiance environment (Mortan-Bertrand, 1988, 1989). Many (if not most) of the areas where phytoplankton biomass (and implicitly production?) maxima occur have physical properties which reduce vertical mixing and may thus enhance photoautotrophic growth. Conspicuous examples include coastal embayments (e.g. Whitaker, 1982), strongly stratified water columns (Priddle and Heywood unpublished) and the special density structure associated with the ice-edge zone (El-Sayed and Taguchi, 1981; Smith and others, 1988; Sullivan and others, 1988). The influence of vertical mixing on phytoplankton production has been thoroughly discussed since the ideas of Sverdrup (1953) on critical depth defined the problems in terms of the balance between light energy input and metabolic losses. A simple shipboard experiment involves keeping a water sample in a constant irradiance regime (e.g. Holm-Hansen, 1985; Fenton, unpublished) and the rapid growth of phytoplankton and corresponding exhaustion of inorganic nutrients lends credence to the idea that vertical mixing may well be a critical influence on growth rate *in situ*. However there is no firm evidence that this is the only mechanism operating in Antarctic waters.

Uniformly low water temperature is at first sight an obvious factor which might be restricting phytoplankton growth. Neori and Holm-Hansen (1982) measured carbon uptake by Scotia Sea and Bransfield Strait phytoplankton under controlled conditions and found that peak rates of photosynthesis occurred at temperatures around 7°C and that these were approximately double the rate at ambient temperatures. Tilzer and others (1986) made a comprehensive investigation of the relationship between photosynthetic parameters and combinations of irradiance and temperature. They suggested that light-limited photosynthetic rate would be temperature dependent. However, the translation of these laboratory experiments to the water column is difficult. It seems impossible to ignore the high biomass and growth rates achieved at some sites although their water temperatures are as low as surrounding 'oligotrophic' areas.

Finally, loss processes may be important in determining the *net* production of phytoplankton. These losses are processes that remove algae from the euphotic zone and can be broadly divided into 'passive' sinking or 'active' grazing. As noted above, the dominant, bloom-forming diatoms are commonly colonial and would be expected to have high potential sinking rates (Jaworski, Wiseman and Reynolds, 1988). Documented sinking rates for Antarctic marine diatoms are typically 1-10 m day^{-1} for single cells (Whitaker, 1982; Jacques and Hoepffner, 1984; Dunbar, 1985; Johnson and Smith, 1985) whilst those for larger aggregates may be assumed to be at the lower end of the range for flocs and faecal pellets, that is 20-100 m day^{-1} (Lorenzen and Welschmeyer, 1983; Dunbar, 1985). Diatom colonies may aggregate to form floc particles several millimetres in diameter (Kranck and Milligan, 1988). However, biotic processes may be at least as important as abiotic in the removal of phytoplankton from the euphotic zone. There is a variety of grazers in the system, from phagotrophic protists to large zooplankton such as salps and Antarctic krill. Deployments of serial sampling sediment traps in Bransfield Strait have revealed relatively short-lived sedimentation events where most material leaving the euphotic zone was in the form of krill faeces (Wefer and others, 1988). This clearly indicates the significance of catastrophic grazing events on a local scale. On a larger scale, the removal of phytoplankton by krill was estimated to be approximately 3% of daily production by Miller and others (1985). Whether this, and the flux to other zooplankters, affects total primary production over large areas of the Southern Ocean is uncertain, even where its local impact is obvious.

The heterotrophic microplankton

Data on the heterotrophic microplankton are sparse. Investigations of planktonic bacteria in the Southern Ocean suggest that biomass is comparable to other areas of the World Ocean (Fuhrman and Azam, 1980; Hanson and others, 1983; Painting, Lucas and Stenton-Dozey, 1985; Mullins and Priddle, 1987). Activity and growth rates measured for these communities are often low, with turnover times for organic substrates of the order of weeks or months. Typical generation times for Antarctic surface water bacterioplankton are around ten days, based on the ^{3}H-thymidine uptake method of Furhman and Azam (1980). Billen, Lancelot and Mathot (1988) suggest that the apparent low turnover rates measured in the Southern Ocean reflect a long lag in the response of these bacteria to substrate availability, showing that there is a two–three month delay in the response of bacterial numbers to phytoplankton biomass increase. However, there is apparently contradictory evidence for mineralization of nitrogen at rates comparable to other, temperate oceans (Rönner, Sorensson and Holm-Hansen, 1983), and for bacterial breakdown of amino acids (Mullins unpublished), suggesting that baterial activity can proceed at rapid rates and may respond to local variation in phytoplankton production. Much of the paradox derives from the types of response which bacteria may make, and whether this is achieved principally by metabolic changes or alteration in growth rate (Mullins and Priddle, 1987).

There are few studies of the larger phagotrophic protists. Taxonomic studies have indicated a wide range of loricate and naked ciliates, radiolaria, foraminifera, flagellates, choanoflagelates (e.g. Hada, 1970; Balech, 1975; Tumantseva, 1982; Buck and Garrison, 1983; Garrison and Buck, 1989). A number of studies of protist community composition indicate heterotrophic ciliate abundances from 10^1 to 10^6 organisms per litre, and flagellates at 10^1 to 10^3 litre^{-1} (South Atlantic waters – Hentschel, 1932; Drake Passage – Bröckel, 1981; Weddell Sea – Buck and Garrison, 1983; Hewes and others, 1985; Garrison and Buck, 1989; Atlantic and Indian Ocean sectors – Hewes and others, 1985; Sushin and others, 1986; Prydz Bay – Marchant, 1985; Pacific sector – Tumanseva, 1982; Hewes and others, 1985; Mamaeva, 1986; Bransfield Strait – Tien and others, 1987). As with the bacteria, the abundances documented by these studies are typical of other oceanic areas. The study by Hewes and coworkers (1985) used fractionation to investigate the trophic role of phagotrophs in the Antarctic pelagic marine ecosystem. They found that micrograzers in the size range 10-200 µm were important algal grazers.

Interactions within the microbial plankton

The trophic role of heterotrophs in the pelagic ecosystem has been the subject of recent debate, with the increasing emphasis in marine microbiology on the 'microbial loop' as a significant route for carbon flux (Smetacek and Pollehne, 1986). In a specifically polar context, there has been some speculation that heterotrophic microbes might support overwintering zooplankton during the winter when phytoplankton production might be insufficient to sustain grazers.

The diatom-dominated phytoplankton bloom described briefly above appears closer to the 'classical' food chain than to the microbial loop. Large cells and colonies dominate the phytoplankton and these account for the great majority of the carbon in the microbial plankton. The apparent lack of coupling between bacterial populations and these large-celled phytoplankton is an incidental indication of the isolation of these diatoms from the microbial loop (Mullins and Priddle, 1987; Priddle and Mullins unpublished). Fluxes in the microplankton would appear to be dominated by the loss of large cells to zooplankton grazers and possibly by passive sedimentation from the euphotic zone. Interactions within the heterotrophic microplankton possibly derive their initial carbon input from the relatively small but constant background population of smaller photoautotrophs and this system may only be poorly coupled to the zooplankton and their predators. Recent evidence has indicated that the decline of the diatom bloom is accompanied by a resurgence of the heterotrophic community, indicating an increased importance of microplankton fluxes. A detailed study of the pelagic ecosystem in Bransfield Strait has been a core activity of the RACER programme. This has revealed the development of a community of small-celled microplankton, including ciliates, during the austral autumn (Tien and others, 1987). Billen, Lancelot and Mathot (1988) investigated the seasonal development of bacterioplankton populations in Prydz Bay. Although their data derive from various studies in various years, there is an apparent tendency for the peak bacterioplankton biomass to be delayed until well after the phytoplankton maximum – again suggesting the transition from 'classical' food chain to microbial interactions. Whether this behaviour indicates the predominance of heterotrophic processes throughout the polar winter is uncertain.

ZOOPLANKTON AND NEKTON

There is a variety of zooplankton and nekton taxa in the surface waters of the Southern Ocean. The most conspicuous species is often a euphausiid crustacean, the Antarctic Krill *Euphausia superba* Dana. However, it seems likely that other groups, especially copepods, dominate the zooplankton biomass overall in the Southern Ocean (Voronina, 1966; Hopkins, 1971). Much of the early work on zooplankton provided information on geographic and vertical distribution, and life-history. Large-scale studies such as the *Discovery* Investigations have documented the biogeographic pattern of zooplankton species. Some species, such as some copepods, may be endemic to particular zones of the Southern Ocean. Other species, such as some of the euphausiids, are widespread within the sub-Antarctic Front. A few zooplankton taxa have worldwide distributions, such as the common hyperiid amphipod *Themisto gaudichaudii*.

With the advent of modern sampling methods, more has been learnt about the role of these zooplankters in the pelagic ecosystem. Serial sampling nets and high-frequency acoustics have revealed the extreme patchiness of the distribution of some species. The most notable example is the Antarctic Krill, where swarms are formed which may contain hundreds of tonnes of animals at packing densities of 1000 individuals per cubic metre. This swarming gives rise to extreme spatial variation on scales from tens of metres to kilometres (Murphy and others, 1988). Similar heterogeneity is seen in the distribution of other euphausiids, such a *E. frigida*, and *Themisto*. Such patchiness must have important consequences for the way in which these zooplankton interact with each other and their environment.

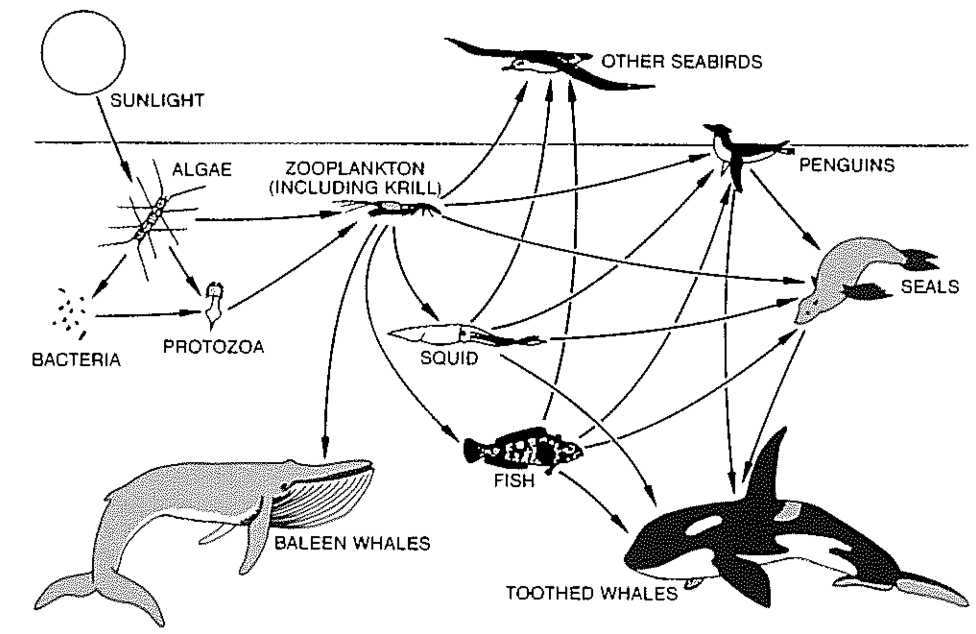


Fig. 5.3 Simplified food web for the Southern Ocean pelagic ecosystem.

There are, of course, both herbivores and carnivores in the zooplankton, with a wide range of sizes in both categories. Herbivores range from small copepods, such as *Calanus, Calanoides, Rhincalanus* and *Metridia*, to krill. Predatory copepods such as *Euchaeta antarctica* lie at the lower end of the predator size range, whilst large jellyfish lie at the other and a variety of arrow worms, amphipods and other invertebrates occupy the middle range.

Zooplankton grazers provide the route by which microplankton production enters the food web which sustains a wide range of secondary consumers. These grazing zooplankton are sampling mostly larger-celled organisms. Krill may retain particles as small as 2-3 µm although it seems likely that optimal feeding efficiency is attained for particles about 20-40 µm in size (Kils, 1982; Meyer and El-Sayed, 1983). Herbivorous copepods also feed within this size range. Salps are probably less selective feeders and may retain very small particles (Reinke, 1987; see also Deibel and Powell, 1987). Although selective feeding by some zooplankters may intuitively have the potential to influence particle size composition in the upper water column, this supposition is not borne out by field observations of species composition (see discussion in Priddle, Heywood and Theriot, 1986). Likewise it is hard to assess the impact of grazing by zooplankton on total microbial biomass. As noted above, the flux of material to zooplankton is probably of the order of 5% of total primary production (e.g. Miller and others, 1985). However, such broad estimates based on energy consumption conceal the local picture. Taking krill as an example, field studies and laboratory estimates of clearance rates (e.g. review by Morris, 1984) and measurements of faecal production (Clarke, Quetin and Ross, 1988) indicate a high food consumption rate which would easily exhaust phytoplankton at normal concentrations. The presence of dense swarms of krill, perhaps more than one million animals in 1000 m^3 of water, implies that the local impact of grazing will be catastrophic. How such patchy grazing impinges on the animals' food supply is uncertain. Recent studies of the variability in krill swarms showed that there was great variation both in gut fullness within each swarm and variation in mean gut fullness between swarms (Watkins and others, 1986; Priddle and others, 1990). Clearly, the variation within swarms reflects different feeding activity in individuals, whilst interswarm variation can be ascribed to differences in food availability to swarms. Thus a patchy grazer is interacting in a complex fashion with a patchy food supply (see also Murphy and others, 1988).

Life-histories differ amongst the herbivorous zooplankton. Most copepods pass through their life-cycle in one year, or two for some species, which involves a seasonal vertical migration (Atkinson and Peck, 1988; Marin, 1988; Atkinson, 1989). Following spawning in spring, the new generation grows within the euphotic zone as phytoplankton production reaches its summer peak. Older copepodids migrate to deeper water in the autumn. Atkinson (1989) notes some niche separation between two of the most abundant copepods around South Georgia, with consistent differences in time of spawning between *Calanoides acutus* and *Rhincalanus gigas*. During the summer, development for all species appears to be rapid.

Antarctic Krill are potentially very much more long-lived, with a suggested maximum life-span of the order of 6-7 years (Rosenberg, Beddington and Basson, 1986). This contrasts with earlier studies, based on simple interpretations of length-frequency data, which suggested that maximum age was 2-3 years. It now appears that size increase is very slow in older animals – Rosenberg and his co-workers fitted a modified von

Bertalanffy growth curve to length frequency data which allowed for winter stasis and hence the extended longevity estimates. Ross and Quetin (1986) provide a review of the energetics of breeding in *Euphausia superba*. They suggest that multiple spawning takes place through the period mid-December to end of February. This implies a very great diversion of energy to egg production, and these authors suggest that krill reproduction can only take place in areas of high phytoplankton biomass, perhaps to the extent that food availability is limiting reproductive success. The developmental sequence of krill takes about four months, with the eggs initially sinking and hatching at depths exceeding 500 m. As development proceeds, so the larvae migrate to shallower depths. The overwintering behaviour of adult krill may include feeding on under-ice algae (Marschall, 1988), although Morris and Priddle (1984) found that krill could feed at low concentrations of phytoplankton found in the open ocean around South Georgia during winter.

Krill and other zooplankton support a variety of secondary consumers. Again, these impinge on their prey populations at a variety of physical scales, and patchiness is a key property of both predator and prey. Krill provide the most extreme example of this, where they may be taken as individuals by small predators such as fish, whereas their largest predators, such as baleen whales, sample swarms.

PREDATORS

As already noted, the trophic structure of the Southern Ocean pelagic ecosystem is considerably more complex than the commonly represented food chain 'diatom to krill to baleen-whale'. There is a wide variety of animals consuming zooplankton and feeding at higher trophic levels. These predators include three groups of vertebrates – fish, birds and mammals – and an important invertebrate group – cephalopod molluscs. Some are permanent residents of the Southern Ocean whilst others migrate into the area during parts of their life cycle. Birds and seals breed on land or on the ice, so that their feeding ranges are necessarily proscribed at these times by the need to return to offspring at the breeding site. Although complete treatment of these predators is outside the scope of this book, their abundance and diversity provides a dramatic visualisation of the richness of the Southern Ocean pelagic ecosystem.

Cephalopods

Pelagic cephalopods, principally squid, are the least well known group of predators although they are obviously an important component of the Southern Ocean pelagic ecosystem. Because standard scientific sampling methods are very inefficient for catching these active animals, basic data on distribution and ecology are sketchy at best. However, several species are now the target of commercial fishery in waters adjacent to the Southern Ocean, for instance around the Falkland Islands. This and studies of material from squid predators has proved to be the most useful source of information on these animals.

Cephalopods differ from the other major groups of predators already mentioned in that they are short-lived and fast growing. Many species grow to maturity and then breed and die within a period of one year (Saville, 1987). This very rapid turnover is important both in their role within the Southern Ocean pelagic ecosystem, and in the assessment of potential fisheries yield. Clarke (1987) uses the Antarctic as a key 'case study' in a discussion of the estimation of cephalopod biomass based on consumption by predators. His estimate of a total annual consumption of cephalopods by mammals and birds of 35 Mtonne yr^{-1} might represent one third of the total cephalopod biomass in the Southern Ocean (Clarke, 1985).

Many of the cephalopod species in the Antarctic, as with the rest of the world's ocean areas, live at depth ranges in excess of the euphotic zone. However, it is clear that some are important predators in the surface waters and that their active habits, rapid growth rates and the schooling behaviour of some of these species will give rise to major predation pressure on zooplankton. Clarke (1987) points out that it is very possible that some squid species may migrate southwards across the Polar Frontal Zone in summer, thus representing a significant allochthonous input of biomass to the Southern Ocean.

Fish

The ichthyofauna of the Southern Ocean is dominated by a single order of perciform fishes, the Notothenioidii. This order, probably closely allied to the blennies, is endemic to the Antarctic and has radiated to fill most available niches within the Southern Ocean ecosystem. These fish are primarily demersal in habit, but a number of species have adapted to adult life in midwater but typically breed on the continental shelf. Various more typical mesopelagic groups, notably myctophids, migrate vertically into the surface layer.

The notothenioid fish show a number of unusual physiological characteristics. Most notable is the extreme reduction in the amount of haemoglobin in the blood. This reaches an extreme in the ice-fish (Channichthyidae) where haemoglobin is entirely lacking and fully-formed erythrocytes are absent. Low environmental temperature implies that oxygen carried in solution is sufficient for normal metabolism, although active species show various anatomical adaptations which maximise the transport of oxygen from the gills to the somatic tissue. Several species are associated with sea-ice and may encounter conditions where tissue freezing would be a risk. Possible 'antifreeze' compounds, mainly glycoproteins, have been identified in these species.

Being primarily demersal, the notothenioid fish lack a swim-bladder and are naturally more dense than seawater. Open-water species may achieve neutral buoyancy by reduction in the relative weight of skeletal material by reduced calcification. High tissue lipid content may also serve to reduce overall density (Kock, 1985).

Antarctic fish are generally considered to be slow-growing (Kock, 1985). They may however be important predators of zooplankton, especially krill, and are themselves significant dietary components for some birds and mammals. Several species have also been fished heavily. The notothenioid fish produce demersal eggs so return to shallow areas to breed (Burchett, 1983). This combined with their slow growth rates and time to reach maturity renders these species highly vulnerable to exploitation and already some stocks have been reduced drastically by fishing operations.

Birds

Seabirds form a conspicuous element of the Antarctic fauna, especially in summer when they migrate to islands and ice-free coastline to breed. Two orders are of major importance and they have distinct feeding ecologies. The Procellariiformes includes a variety of petrels and the albatrosses. These are mainly surface feeders, taking prey items ranging in size from copepods to large squid and carrion (depending on species). The depth ranges sampled may be only the upper tens of centimetres for small petrels such as prions (*Pachyptila* spp.), to one or two metres for albatrosses.

Penguins (Sphenisciformes) are highly specialised seabirds which are flightless and have become amphibious. They swim using the wings and achieve high speeds which allows them to capture fast-moving prey and avoid mammalian predators. Because of their diving ability, they sample a greater depth range than the surface-feeding petrels. Most of the Southern Ocean penguins (principally three representatives of the genus *Pygoscelis*) feed on krill and fish in the top 100 m of the water column. The larger Emperor Penguin (*Aptenodytes forsteri*) is particularly noteworthy. It feeds on squid and fish, diving to 300 m depth. It breeds at high latitudes where the short summer season has imposed a winter incubation period so that the chicks fledge in time for the most favourable time of the year. The related King Penguin (*A. patagonica*) is a similar bird but breeds at lower latitudes on subantarctic islands where such extreme breeding behaviour is unnecessary.

Outside the breeding season, most seabirds either disperse over a wide area of the ice-free lower latitude parts of the Southern Ocean or migrate even further north. In the breeding season however, they are limited in their foraging ranges by the need to return to their nests to feed young or relieve incubating partners. This range varies from species to species – for instance penguins may forage within a radius of tens of kilometres of their breeding site whereas albatrosses can travel up to 500 km. However, it is clear that the impact of these birds on their prey is highly localised but very important, especially around some islands in the Antarctic Circumpolar Current.

Seals

There are five species of true seals (Phocidae) and one eared seal (Otaridae) found in the Southern Ocean. Each has a unique ecology and all are well-adapted to their environment. Three species are intimately associated with the pack-ice. The Crabeater Seal (*Lobodon carcinophagus*) is the most abundant seal in the world and feeds on krill. This is accomplished with a distinctive dentition with multi-cusped teeth which act as a sieve. The Leopard Seal (*Hydrurga leptonyx*) shares the pack-ice habitat, although it is also found further north. It is a distinctive, sleek seal which also has multi-cusped teeth. These are more pointed than those of the crabeaters and Leopard Seals are active predators on penguins and other seals, although krill also forms a major component of the diet. The third seal of the pack-ice is the little-known Ross Seal (*Ommatophoca rossii*), which lives at higher latitudes and feeds mainly on squid and fish.

The Weddell Seal (*Leptonychotes weddelli*) occupies a different habitat. It is normally associated with fast-ice, where it breeds in late winter and maintains diving holes. It also feeds mainly on fish. These seals make prolonged dives, being capable of covering long distances between holes and sometimes ranging to depths of 300-400 m when feeding.

The two remaining species are found mainly on subantarctic islands where they breed on beaches. The Southern Elephant Seal (*Mirounga leonina*) is the largest phocid species, with bulls reaching lengths of over 4 m and weighing 4 tonne. It is a harem-breeding species with marked sexual dimorphism – with the largest females weighing less than one tonne. The Elephant Seal feeds at depth, primarily on squid.

The Antarctic Fur Seal (*Arctocephalus gazella*) is a typical eared-seal and is very much more agile than the phocid seals. It too is sexually dimorphic and breeding bulls maintain a harem. The fur seal feeds on krill, although fish are taken and may be a major dietary item for males. This seal was hunted almost to extinction for its pelt. Since the close of this industry the Antarctic Fur Seal has gradually and then explosively recovered its stocks (Payne, 1977) and is now expanding its range to the south. Such is the impact of these seals that there is now concern over the environmental damage done by them where population densities are particularly high.

Whales

The great baleen whales are often portrayed at the top of the Southern Ocean food web, feeding on the abundant Antarctic Krill. However, twentieth century whaling – first land-based and then pelagic – reduced the stocks of the baleen whales migrating into the Southern Ocean each summer until the industry was no longer worth prosecuting. Population levels of these whales were reduced to levels which some doubted allowed the survival of some species.

Five large species of baleen whales were probably the dominant consumers of Krill in the Southern Ocean (Laws, 1985). Three belong to the genus *Balaenoptera*, including the largest species, the Blue Whale *B. musculus*. The other species are Fin and Sei Whales (*B. physalus* and *B. borealis*), the Humpback Whale (*Megaptera novaeangliae*) and the Southern Right Whale (*Balaena australis*). The smallest baleen whale, the Minke (*Balaenoptera acutorostrata*), has not been exploited so heavily and remains more common. All of these baleen whales feed by engulfing large quantities of water (tens of cubic metres in the case of large animals) and then straining this through the baleen plates hanging from the upper jaw. The zooplankton in the water is retained and swallowed. The prey taken varies between species – Right and Sei Whales have finer baleen which may enable them to remove smaller animals such as copepods. However, krill are an important item in the diet of all baleen whales in the Southern Ocean and it is clear that the aggregation of these zooplankters in swarms makes them easy to capture (Murphy and others, 1988 –

see also Brodie, Sameoto and Sheldon, 1978).

The migration of the baleen whales into the Southern Ocean appears to follow the summer retreat of the sea-ice. These animals come into the high-latitude waters to feed – they breed further north in warmer water. Because they need to come to the surface to breathe, they cannot go into dense ice-cover. Maps of whaling catches appear to suggest that these whales exploited the high productivity of the marginal-ice zone (Mizroch and others, 1985).

There is a wide range of toothed whales in the Southern Ocean. The largest species, the Sperm Whale (*Physeter catodon*), is represented in the Antarctic only by a few males. These animals feed in deep water on squid. Smaller toothed whales and delphinids are found in the Southern Ocean. The most conspicuous is the Killer Whale (*Orcinus orca*) which is an active predator hunting in groups and taking fish, seals and penguins. Little is known of the biology and distribution of the other Antarctic toothed whales.

THE PAST, THE PRESENT AND THE FUTURE

It is a sad fact that commercial exploitation of the marine living resources of the Antarctic has already had a serious impact on the ecosystem over two centuries. In the last decades of this century, attention is focussing on lower levels of the trophic structure. The fishery for Antarctic Krill in the late 1980's has been the largest fishery for pelagic crustaceans in the world. At present, this appears to a relatively small uptake in comparison with the normal intake by predators, but even comparatively minor deficiencies in our knowledge of the biology of krill make the estimate of a future sustainable yield almost impossible to establish. Likewise, other species such as myctophid fish and some squid may become the subject of new fisheries.

However, the Antarctic seas may prove to have a greater importance to Mankind than merely as a source of protein. Appreciation of global changes induced by human activity has given a wider perspective to biological oceanography. At one level, we turn towards such a supposedly pristine environment as a barometer for global pollution (e.g. Cripps, 1989). More significantly, recent concern over the climate change associated with anthropogenic carbon dioxide emmissions and increases of other 'greenhouse' gases has focussed attention on the role of the oceans in the global fluxes of these gases. In the longer term, we may need to assess how the pelagic ecosystem of the Southern Ocean responds to climate change.

The history of the relationship between Mankind and the Southern Ocean contains a record of greed and ignorance alongside the great landmarks of exploration and discovery. With the perception of the importance of this region to us and to our planet, we should now hope for an informed and sensitive approach to this region of the planet.

ACKNOWLEDGEMENTS

I am pleased to thank my colleagues at the British Antarctic Survey for discussions of the various topics covered here, particularly Angus Atkinson, Ray Leakey, Eugene Murphy, Paul Rodhouse and Martin White.

CHAPTER 6

SOME ASPECTS OF THE LARGE-SCALE PHYSICAL OCEANOGRAPHY OF THE ARCTIC OCEAN INFLUENCING BIOLOGICAL DISTRIBUTIONS

Eddy C. Carmack and James H. Swift

The seas of the Arctic regions present a diverse set of regimes: some are broad shallow seas and some are deep basins; some regions are covered by ice year-round and some are never covered. Some of the water masses are among the freshest in the World Ocean, and others are among the saltiest. Some basins have relatively short residence times, while others have extremely long ones. Thus, there is no one "typical" Arctic water column displaying the full range of oceanographic conditions which one could expect to find. Arctic seas are linked, however, by common threads in their geography and climate that distinguish them from other parts of the ocean. In particular, Arctic seas are "mediterranean" in their configuration in that they are almost entirely surrounded by land. This means that exchanges with adjacent oceans are limited, and in most cases occurs through narrow and relatively shallow passages. The mediterranean nature of the Arctic Ocean also means that there are extensive boundary regions for interaction with basin interiors. These peripheral regions are unusually broad and shallow, comprising about 30% of the total surface area of the Arctic Ocean. It is over these regions that river inflow is introduced, where most of the seasonal fluctuation in ice cover occurs, and where physical and chemical interactions with the sea bed take place. A central theme that will appear time and time again in our discussion of water masses and circulation is the importance to the Arctic Ocean of its shelves and lateral boundaries.

The goal of this chapter is to present a short overview of the water masses and large-scale circulation of the Arctic Ocean between Fram and Bering Straits. We have taken the following approach: the physical setting (bathymetry, hydrology, and ice cover) of the Arctic Basin is described briefly in Section 2; strict definitions of the water masses and their spatial distribution are given in Section 3; and the current systems are covered in Section 4. In preparing this summary, we have placed an emphasis on the most recent studies of the region – the reader wishing a more detailed and historical review of the subject is referred to two articles by Carmack (1986, 1990). Regions marginal to the Arctic Ocean are not covered here; however, recent overviews are available for the Bering Sea (Coachman, 1986a), the Canadian Arctic Archipelago (Barry, unpublished), and the Greenland Sea (Hopkins, 1988).

GEOGRAPHICAL SETTING

Bathymetry

The Arctic mediterranean seas comprise the basins lying north of the Greenland-Scotland Ridge (Fig. 6.1). This system is about 17 x 10^6 km^2 in area and 17 x 10^6 km^3 in volume (Fig. 6.2). The two principal areas are the Arctic Ocean, and the Greenland, Iceland, and Norwegian Seas. They are connected by Fram Strait, the wide (600 km), deep (sill depth about 2600 m), passage between Greenland and Svalbard. The Arctic Ocean connects to the North Atlantic via Baffin Bay through the Canadian Arctic Archipelago (sill depth about 250 m) and to the Pacific through Bering Strait (sill depth about 50 m).

The Arctic Ocean is roughly divided into the Canadian and Eurasian Basins (maximum depths about 3800 m and 4200 m respectively) by the Lomonosov Ridge (sill depth about 1400 m). The Canadian Basin is further divided into the Canada and Makarov Basins by the Alpha-Mendeleyev Ridge; and the Eurasian Basin into the Nansen and Amundsen Basins by the Nansen-Gakkel Ridge. The continental shelf from Alaska to Greenland is relatively narrow, but from Svalbard eastward (the Barents, Kara, Laptev, East Siberian, and Chukchi Seas) the shelf is broad, typically from 600 to 800 km. A number of submarine canyons indent the shelf, the largest being the Svataya Anna and Voronin Canyons in the Kara Sea.

Ice cover

The average position of the ice boundary for summer and winter in the Arctic Ocean is shown in Fig. 6.2, together with the mean sea ice drift derived primarily from automatic data buoy reports (Polar Science Center, University of Washington, personal communication). Sea ice in the Arctic typically varies from about 7 x 10^6 km^2 in the boreal summer to 14 x 10^6 km^2 in the boreal winter (Walsh and Johnson, 1979). Ice forming in open water is typically about 2 m thick after the first year, and then tends towards a stable equilibrium thickness of about 3 m after a series of annual melt/thaw cycles. The extent of sea ice in the Arctic has been

Fig. 6.1 Bathymetry and geographical nomenclature for the Arctic Ocean. Continental shelves are shaded.

observed to vary interannually by about 5° of latitude at all locations where the ice advance is not bounded by land (Walsh and Johnson, 1979). At maximum winter extent this amounts to about a 30% variability for individual regions (see Johnson, 1980). While regional variations may be large, the total areal coverage at the time of minimum ice extent changes interannually by only about 2% (Carsey, 1982). Observations on sea ice drift, and the occurrence of areas of systematic coastal divergence and convergence, are described by Colony and Thorndike (1984, 1985). The optical properties of sea ice are discussed by Grenfell and Maykut (1977) and more detailed information of the fine-scale environment of sea ice is presented by Squire (this volume).

Hydrology

The upper layers of the Arctic Ocean are among the freshest in the world oceans, owing to the combined influence of river inflow, ice melt, an excess of precipitation over evaporation, and inflow of low salinity water through the Bering Strait.

Treshnikov (1985) lists the total annual streamflow from rivers entering the Arctic Ocean as about 3500 km^3 y^{-1}; a schematic illustration of the main inputs is shown in Fig. 6.3. An additional 1500 to 2000 km^3 yr^{-1} enters as a freshwater fraction in the Bering Strait inflow (see Coachman and others, 1975). The fresh water residence time (defined as stored volume divided by inflow rate) is estimated to be roughly 10 years for the whole Arctic Basin, with local values as low as 2 years applying to the southern Eurasian Basin (Aagaard and Coachman, 1975).

Significant annual and interannual variations occur in streamflow. The large Soviet rivers Yenisei and Lena exhibit on average about a forty-fold change between low flows in winter and peak flows in June and July, whilst the annual variation for the Mackenzie river is much less, about five-fold. Interannual variability is from 5 to 20% of the mean annual flow, depending on the individual rivers.

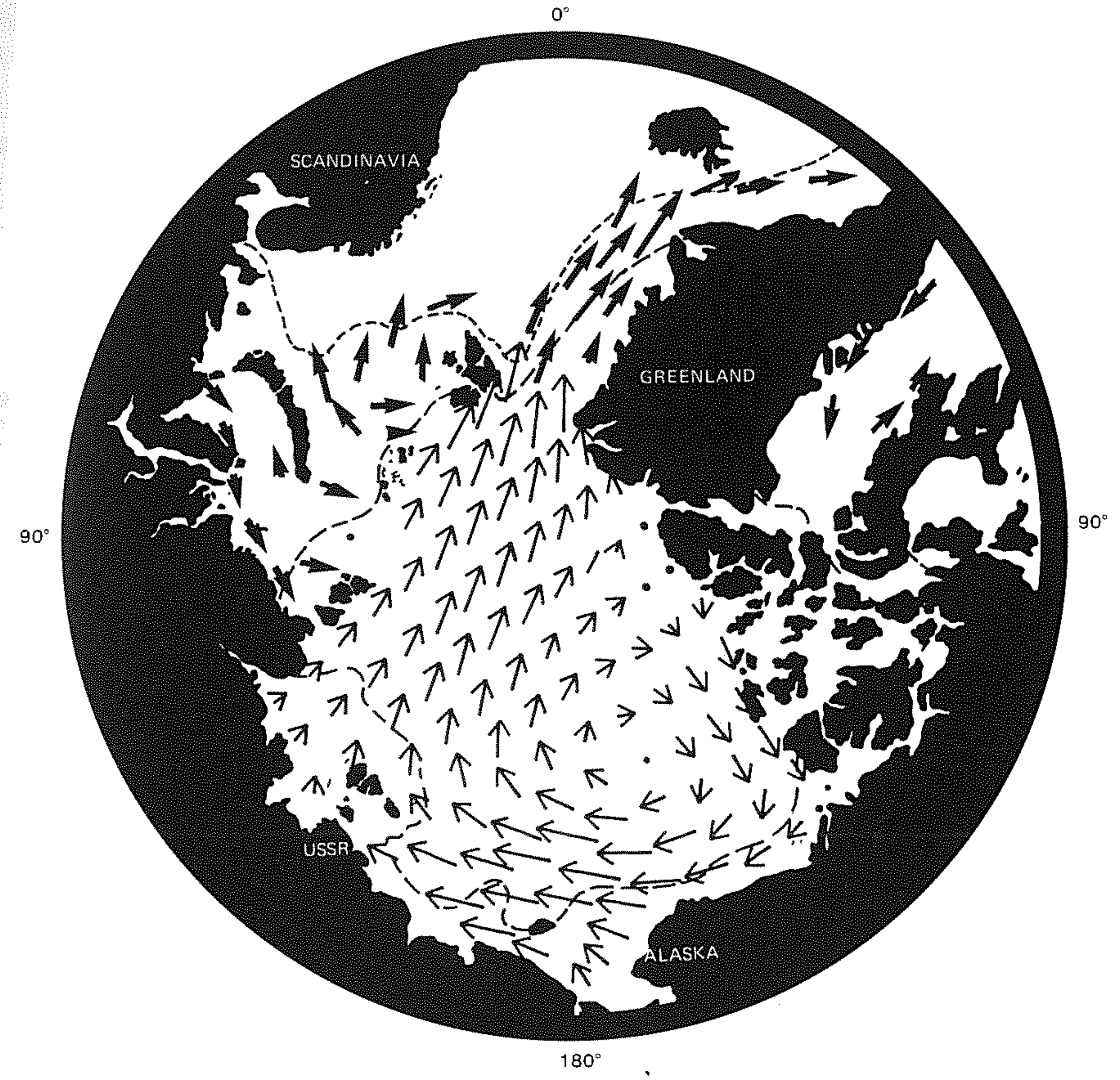


Fig. 6.2 Maximum (dotted lines) and minimum (dashed lines) ice extent in the Arctic Ocean; and mean sea ice drift (arrows), derived mainly from automatic data buoy tracks (from Polar Science Center, University of Washington, pers. comm.).

WATER MASS DESCRIPTION

Water mass definitions

The description of water masses of the Arctic mediterranean waters used below is based on the publications of Swift and Aagaard (1981) and Aagaard and others (1985b). While this classification system is based mainly on water mass distributions within the Greenland-Iceland-Norwegian Sea system, it can be applied to the Arctic Ocean with minor modifications, and has the advantage of maintaining a consistent description throughout the Arctic Mediterranean.

Three main layers make up the oceanic water column: a surface layer, including the Arctic pycnocline, which has densities less than $s_0 = 27.9$; an intermediate layer, derived initially from an influx of warm, salty water from the Atlantic and which has densities above $s_1 = 32.785$, and the deep water, formed by convection within the Arctic Mediterranean, which has densities below $s_2 = 37.457$ (here, s_0, s_1, and s_2 refer to potential densities relative to the 0, 1000, and 2000 dbar surfaces, respectively). The volumetric distribution of these layers within the various basins of the Arctic Mediterranean is shown in Fig. 6.4 (see Aagaard and others, 1985b).

Arctic Surface Layer. Three main classes of surface water are recognized. The first is Atlantic Water (AW) which is carried into the system as a branch of the Norwegian-Atlantic Current; it has temperatures above 3°C and salinities greater than 34.9. The second – Polar

Fig. 6.3 Map showing the freshwater inputs from major rivers into the Arctic Ocean. Mean annual discharges each river (m^3yr^{-1}) are shown in brackets. The areas of the segments are drawn proportional to the annual volume flow from each river, assuming a spreading depth of 1 metre (data from Treshnikov, 1985).

Water (PW) – is water that has been diluted by admixtures of fresh water and is generally cold, temperatures below 0°C, and fresh, salinities below 34.4. PW occupies the upper layers of the Arctic down to about 200 m depth, and makes up the surface outflow within the East Greenland Current and the Canadian Arctic Archipelago. The top 30-50 m of the PW is the seasonal mixed layer (Morison and Smith, 1981; Lemke and Manley, 1984; Lemke, 1987). In winter this layer tends to be vertically uniform in temperature and salinity. Ice melting in summer yields salt stratification; however, this water remains near freezing except in areas that become completely ice free. The lower part of PW is the main halocline, the layer with low temperatures ($T < -1°C$) and salinities between about 30.4 and 34.4.The third class of surface water is Arctic Surface Water (ASW) which is found mainly in the central gyres of the Greenland and Iceland Seas. It is warmer and more saline than PW, but cooler (0 to 3°C) and fresher than AW ($S = 34.4$ to 34.9). However, ASW is notably denser than either PW or AW, indicating that it is not a simple mixture between the two, but that modifications due to air-sea exchanges have occurred.

The Intermediate (Atlantic) Layer. From their examination of water mass transformations in the Greenland-Iceland-Norwegian Sea system, Swift and Aagaard (1981) identified three varieties of Arctic intermediate water, each with a different T/S signature. They noted that Arctic Surface Water usually lies above a temperature minimum at 75 to 150 m depth, a temperature maximum at 250 m, and a salinity maximum at about 400 m. To account for these features, the following distinction was made: Lower Arctic Intermediate Water (LAIW) lies immediately above deep water, includes the temperature and salinity maxima, and has both temperature and salinity decreasing with depth; Upper Arctic Intermediate Water (UAIW) lies between the temperature minimum and the temperature maximum, and has both temperature and salinity increasing with depth. Polar Intermediate Water (PIW) has somewhat lower salinities than the other two intermediate waters, but is largely distinguished by its association with overlying Polar Surface Water.

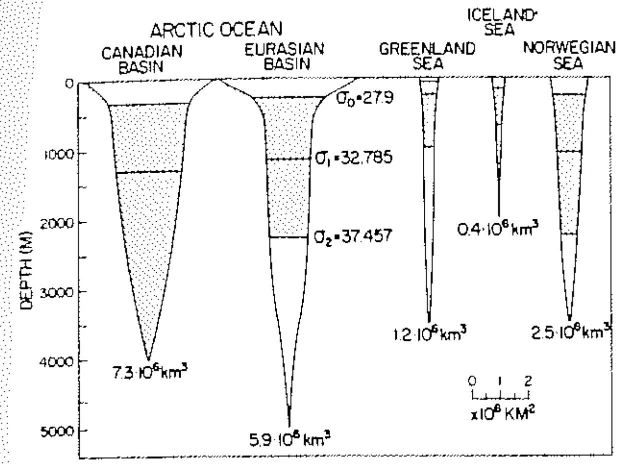


Fig. 6.4 Hypsometry of the Arctic Mediterranean, based primarily on GEBCO (General Bathymetric Chart of the Oceans): The horizontal coordinate is area of each depth. The total volume for each basin is given below the individual curves. The horizontal bars represent the mean depths within each basin of the isopycnals separating the surface, intermediate, and deep waters. (from Aagaard, and others, 1985b)

Relatively warm and saline water of Atlantic origin is carried into the Arctic through Fram Strait by the West Spitsbergen Current. Upon entering the Arctic Basin the initially high temperature and salinity of this water ($T > 3°C$, $S = 35$ in the Fram Strait) rapidly decrease as it is cooled by the atmosphere and by mixing with local waters. When the current encounters the sea ice margin northwest of Svalbard, melting further cools and dilutes this water until its T/S properties approximate those of water found within the Atlantic layer throughout the Arctic (Perkin and Lewis, 1984; Aagaard and others, 1987; Quadfasel and others, 1987). This water has the same general T/S properties as the Arctic Intermediate Water discussed by Swift and Aagaard (1981) and Aagaard and others (1981a); its core is identifiable over the entire basin at depths between 200 to 800 m by a temperature maximum and relatively high salinity.

Deep Waters. The lower portion of the water column is occupied by varieties of cold deep water ($T > 0°C$). Four basic varieties, each with distinctive T/S characteristics, are recognized at present. Greenland Sea Deep Water (GSDW) is the coldest (about −1.2°C) and freshest ($S <$ 34.90) variety, while Canada Basin Deep Water (CBDW) is the warmest (about −0.5°C) and most saline ($S > 34.95$). Intermediate in character are the Norwegian Sea Deep Water (NSDW; −0.9°C, 34.92) and Eurasian Basin Deep Water (EBDW; −0.7°C, 34.94). The general distribution of bottom salinities and possible spreading paths are discussed by Carmack (1990).

Arctic Shelf Waters. There seems to be no available synthesis on the distribution of Arctic shelf waters. However, a number of regional descriptions exist to give a collective view of shelfwater distributions. Starting with the Barents Sea and proceeding counterclockwise around the basin, the following references give useful descriptions of local water masses: the Barents Sea is discussed by Pfirman (1985); the Kara Sea by Hanzlik and Aagaard (1980); the Laptev and East Siberian Seas by Codispodi and Richards (1968, 1971); the Chukchi Sea by Coachman and others (1975); the Alaskan Beaufort shelf by Aagaard (1982); the Mackenzie Shelf by Macdonald and others (1987), and the Canadian Arctic Archipelago by Melling and others (1984). The shelf waters exhibit greater annual variability in salinity than surface waters in the open ocean, perhaps 2 to 4 on shelves as opposed to 0.5 offshore (Coachman and Aagaard, 1974). Owing to their proximity to river inflow, shelf waters are generally more dilute than their offshore counterparts during summer. However, due to brine-water release, and possibly the upwelling of saline water onto the shelf, shelf waters may then become more saline than offshore waters in winter (Aagaard and others, 1981; Melling and Lewis, 1982).

Summary classification

Water classes within the Arctic Mediterranean are defined as follows (Fig. 6.5):

Atlantic Water (AW) has temperatures above 3°C, and salinities above 34.9;

Arctic Surface Water (ASW) has temperatures above 2°C for salinities between 34.7 and 34.9, and temperatures above 0°C for salinities between 34.4 and 34.7;

Polar Water (PW) has salinities below 34.4;

Upper Arctic Intermediate Water (UAIW) has temperatures below 2°C and salinities between 34.7 and 34.9;

Lower Arctic Intermediate Water (LAIW) has temperatures from 3 to 0°C and salinities between 34.9 and 35.1;

Polar Intermediate Water (PIW) has temperatures below 0°C and salinities between 34.4 and 34.7;

Deep water has temperatures below about 0°C and salinities between 34.88 and 34.96.

Some additional points should be noted

The Arctic halocline, with typical salinities between 30.4 and 34.4, forms the high salinity end of the PW class.

The Arctic thermocline, with salinities above 34.4 and temperatures below 0°C, is contained within the PIW class.

The core of the Atlantic layer, with temperatures above 0°C, is contained in the UAIW class.

The deep waters of the Canadian Basin are more saline than those of the Eurasian Basin.

Water mass distributions

Owing to an inadequate number of high-quality oceanographic stations, it is difficult to give a detailed and coherent description of watermass distributions in the Arctic. However, the atlas of Gorschkov (1983) defines

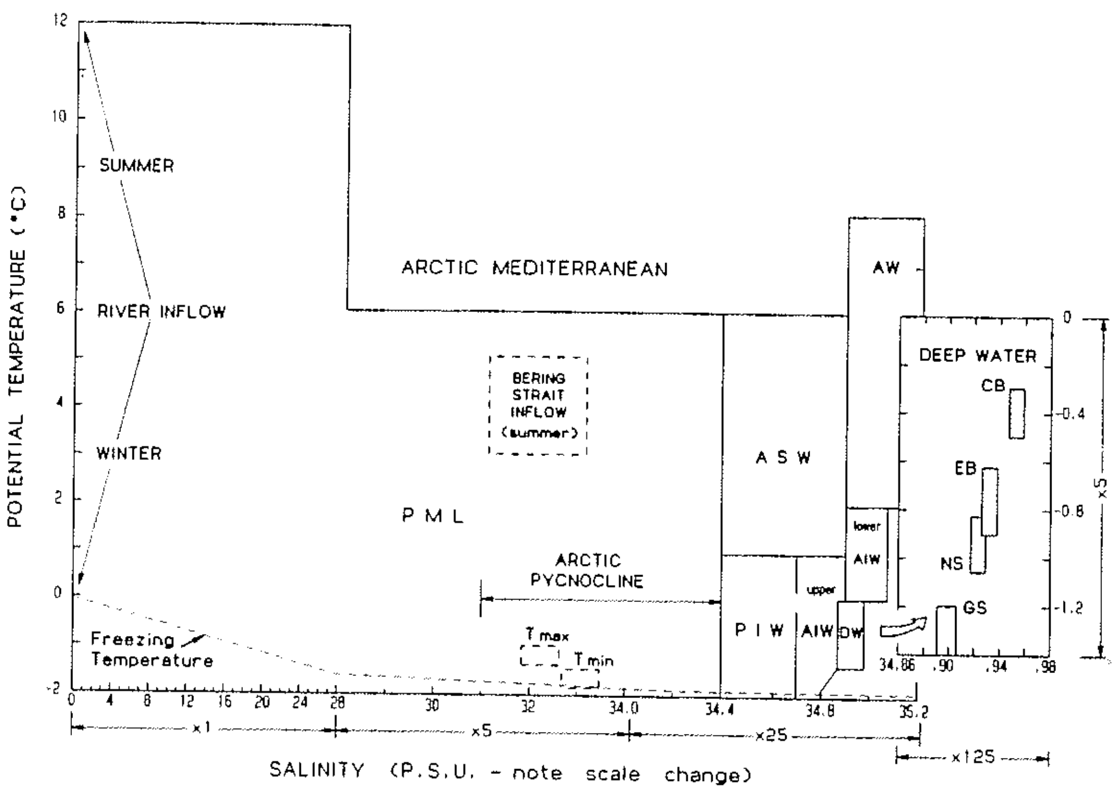


Fig. 6.5 Water Mass Definitions

twelve Arctic domains within which T/S curves are relatively similar (see Fig. 6.6). While the details of these different domains are beyond the scope of this chapter, two representative stations from the Eurasian and Canadian basins are shown in Fig. 6.7. It is important to note that the structure of PW varies across the basin. Surface salinities generally decrease from high values near Svalbard clockwise around the basin (see Gorschkov, 1983). In the Eurasian Basin salinity increases rapidly with depth, reaching 34.9 to 35.0 at about 200 m, while the temperature remains below −1.5°C to 150 m, and then begins to increase. In the Canadian Basin the halocline is deeper and the salinity increases more slowly with depth. The temperature of water in the Atlantic layer likewise decreases from high values (about 3°C) in the southern Eurasian Basin to a nearly constant value (about 0.5 °C) over most of the Canadian Basin. The deep water of the Eurasian Basin is colder and fresher than that of the Canadian Basin.

East of the Chukchi Sea in the Canadian Basin, T/S shows additional features: temperature minima near 31.6 and 33.1, and a maximum near 32.4. The temperature minimum near 31.6 is possibly a remnant of winter cooling. The maximum near 32.4 and the minimum near 33.1 possibly reflect the inflow of water from the Pacific through Bering Strait.

LARGE-SCALE CIRCULATION

Fig. 6.8 is a map of geopotential topography (0/1200 dbar) from Coachman and Aagaard (1974); added to this are the main current systems of Fram Strait and Bering Strait. The emphasis in this section will be to relate the major currents of the Arctic Ocean to water-mass distributions.

Exchange with adjacent seas

Transport through Fram Strait

Two main currents exchange water between the Arctic and the World Ocean through Fram Strait. The West Spitsbergen Current (WSC) is a northward moving extension of the Norwegian-Atlantic current that flows through Fram Strait off the west coast of Spitsbergen (Svalbard) carrying warm, relatively salty water into the Arctic Ocean. The East Greenland Current (EGC), which lies west of the East Greenland Polar Front, is the main current leaving the Arctic Ocean.

Transport calculations for the WSC range from 2 to 8 Sv, where 1 Sv = 10^6 m^3 s^{-1} (see Hopkins, 1988, for review). The most recent studies by Aagaard and others (1987), and Gascard and others (1988) support this range. However, three aspects of the WSC combine to make transport calculations difficult. The first is the large temporal variability of the WSC. Aagaard (1982) computed transports from current meter and hydrographic data and found variations between 0 and 9 Sv. Hanzlick (1983) noted the lack of significant lateral coherency between current meter moorings and argued that long-term variability was related to topographically-trapped waves. The second problem involves the recirculation confounding of water within Fram Strait. For example, using an inverse technique to insure mass conservation, Rudels (1987b) argued that while Atlantic Water is carried north by the WSC at a rate of 2 Sv, only half of this water enters the Arctic Ocean while the rest recirculates in the vicinity of the strait. The third concerns the dynamical complexity of the WSC. For example, Hanzlick (1983), Quadfasel and others (1987), and Aagaard and others (1987) all emphasise the banded structure of the WSC. Johannessen and others (1987b) noted the abundance of mesoscale eddies in the flow field. Gascard and others (1988) carried out an analysis of surface drifters and SOFAR floats, deployed at 100 to 200 m depth, and concluded that the WSC has a tendency to become unstable and generates frequent eddies that follow topographic contours. The continuation of the WSC into the Arctic is also complex, as the current appears to be split into two or more branches (Perkin and Lewis, 1984; Aagaard and others, 1987; Quadfasel and others, 1987).

Fig. 6.6 Domains over which water mass properties remain relatively uniform (from Gorschkov, 1983). Examples from domains 2 (Eurasian Basin) and 5 (Canadian Basin) are shown in Fig. 6.7.

The southward-flowing East Greenland Current (EGC) extends some 2500 km along the Greenland coast. In addition to transporting surface-, intermediate- and deep-water, the EGC exports sea ice from the Arctic, removing between 4000 and 5000 km³ of ice each year (Wadhams, 1983; Vinje and Finnekasa, 1986). There are two branches off the mainstream of the EGC: a relatively minor one at about 77°N, which strikes southeast along the Greenland Fracture Zone (see Quadfasel and others, 1987), and a larger one, the Jan Mayen Current, that branches eastward at about 73°N to form the southern margin of the Greenland Gyre. The water mass structure of the EGC has been described in detail by Aagaard and Coachman (1968a,b), Paquette and others (1985), Bourke and others (1987) and Foldvik and others (1988).

Transport calculations for the EGC have been made by several investigators (see Hopkins, 1988, for review): published estimates range from about 2 to 30 Sv. Most recently, Foldvik and others (1988) examined data from moored current meters and drifting buoys, and suggested a reasonable transport for the upper 700 m to be of the order of 3 Sv. In reconciling the wide range of these transport estimates, one must take into account the methods used, the spatial and temporal coverage of the data, and the specific domains and water masses included in the tabulation. Both Foldvik and others (1988), using moored current meter records, and Gascard and others (1988), using data from drift buoys and

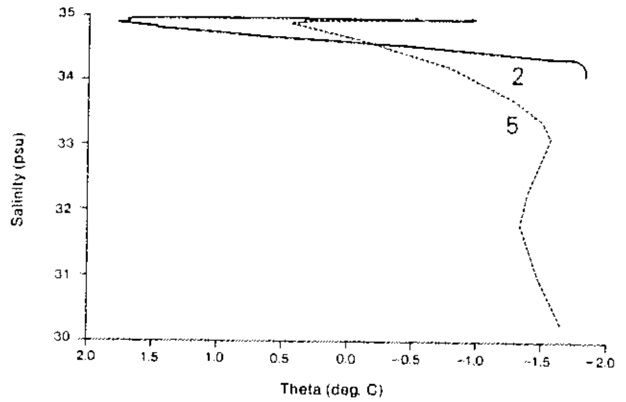


Fig. 6.7 Characteristic T/S curves for domains 2 and 5 within the Arctic Ocean.

SOFAR floats, conclude that the EGC is stable and not a source of mesoscale eddies.

Transport through the Canadian Arctic Archipelago

This region may be thought of as a broad continental shelf, dominated by the presence of islands, across which Arctic waters flow into Baffin Bay and on into the Atlantic. The deepest connection is through Nares Strait between Greenland and Ellesmere Island (about 250 m deep), while the western and eastern parts of the system are separated by sill depths less than 100 m. Several of the channels are sufficiently wide to permit geostrophically balanced counterflows (see Leblond, 1980). Owing to the large number of channels in this system the circulation is very complex. Rather, than viewing the through-flow as one continuous feature, it is better to consider the west to east passage of water as occurring through a series of linked basins, each with its own unique dynamic response and each interacting with its adjacent channels.

A major work on the residual flow through the Archipelago has been published by Fissel and others (1988). They estimated the total transport through the Archipelago to be about 1.7 Sv, which is in good agreement with the mass budget estimate of 2.1 Sv used by Aagaard and Greisman (1975). Mean flows ranged from about 0.2 to 20 cm s^{-1}, and were usually intensified near the shore. The strongest currents were found in the shallower central passages leading into Lancaster Sound, while the smallest currents were observed in the broad, deep, channels of the Western Archipelago.

Seasonal variability in volume transport remains largely unknown. Prinsenberg and Bennett (1987) suggested a five-fold increase in the transport through Barrow Strait during summer. Their estimates, however, were based on an empirical model calibrated from springtime measurements only, and Fissel and others (1988) question whether this approach is valid for summer, when strong baroclinicity develops. Fissel and others (1988) found no evidence of interannual variability in their data, but also admitted that longer time-series records would be required to settle this question.

Transport through Bering Strait

The generally northward flow through the shallow and narrow Bering Strait (about 50 m deep 85 km wide) connects the Pacific (Bering Sea) and Arctic (Chukchi Sea) Oceans. Flow through the strait is driven by a steric sea level slope of order 10^{-6} down toward the north due to the lower density of the Pacific relative to the Atlantic (Coachman and Aagaard, 1966). Wind effects on the transport are described by Aagaard and others (1985) and Coachman and Aagaard (1988). Westward intensification of the northward flow through Bering Strait and the occurrence of a western boundary current was pointed out by Kinder and others (1986). Model studies by Spaulding and others (1987) show that much of the transport variability comes from fluctuations in meridional wind stress. Further modelling studies by Overland and Roach (1987) suggest that the maximum flow through the strait is geostrophically limited, and that westward intensification of the flow results in the greatest transport coming from the Gulf of Anadyr.

Recent studies on the transport through Bering Strait (Coachman and Aagaard, 1981; Aagaard and others, 1985a, and Coachman and Aagaard, 1988) report the following:

> The long-term mean transport is about 0.8 Sv;
>
> There is an annual variation in transport of amplitude 0.6 Sv, with higher flows in summer than in winter when northerly winds reduce the transport;
>
> There is an interannual variability in transport that is tied to the meridional wind field.

Coachman and Aagaard (1981) note that the flow field in the southern Chukchi Sea immediately north of the Bering Strait divides into two regimes: a western part with broad, weak flows (less than 20 cm s^{-1}), and an eastern half with narrow, much stronger flows (almost 70 cm s^{-1}). However, while flow speeds differ, the transports within the two regimes are roughly equal. The water passing through the strait has high nutrient levels, and salinities between 31 and 33. This water probably ventilates the nutrient maximum layer of the Arctic halocline.

Arctic Ocean currents

Surface circulation

Two main current fields characterize surface flows in the Arctic Ocean. The first is the Trans-Polar Drift in which the surface waters of the Eurasian Basin move across the basin towards the North Pole, and then on towards Fram Strait. The second is the anti-cyclonic flow around the Beaufort Gyre in the Canadian Basin. Mean current speeds are slow in the central ocean, about 2 cm s^{-1}, but increase as water leaves the basin as part of the EGC.

The Beaufort Gyre was studied by Newton (1973) who found the total baroclinic transport of the gyre relative to the 500 dbar surface to be about 3 Sv, and that the gyre is intensified near the Alaskan shelf, presumably due to bottom topography. He noted that since the vertical density variation is contained above and within the pycnocline, the major portion of gyre transport (80%) occurs in the upper 300 m.

Boundary currents

There is evidence from at least two areas in the Arctic of shallow, subsurface boundary currents that flow in a direction opposite to the mean surface drift. The first is in the Nansen Basin along the continental slope between Svalbard and Franz Josef Land, and the second is along the continental slope in the southern Beaufort Sea. The presence of an undercurrent in the Nansen Basin is revealed by property distributions (Treshnikov, 1977; Aagaard and others, 1981b; Perkin and Lewis, 1984; Aagaard and others, 1987; Quadfasel and others, 1987). As the WSC passes through the Fram Strait and then subsides, it appears to bifurcate. North of 79°N, where the 200 m and deeper isobaths diverge, the current splits into two main cores. The western or offshore branch follows the western flank of the Yermak Plateau. North of 80°N a portion of this flow again splits off to contribute to the recirculation within the EGC. The eastern or inshore branch of the WSC follows the shelf break around Spitsbergen and into the Arctic Ocean. The first direct measurements of this flow were made by Aagaard (1988) who noted eastward flow that increased with depth to typical speeds of 20–30 cm s^{-1}.

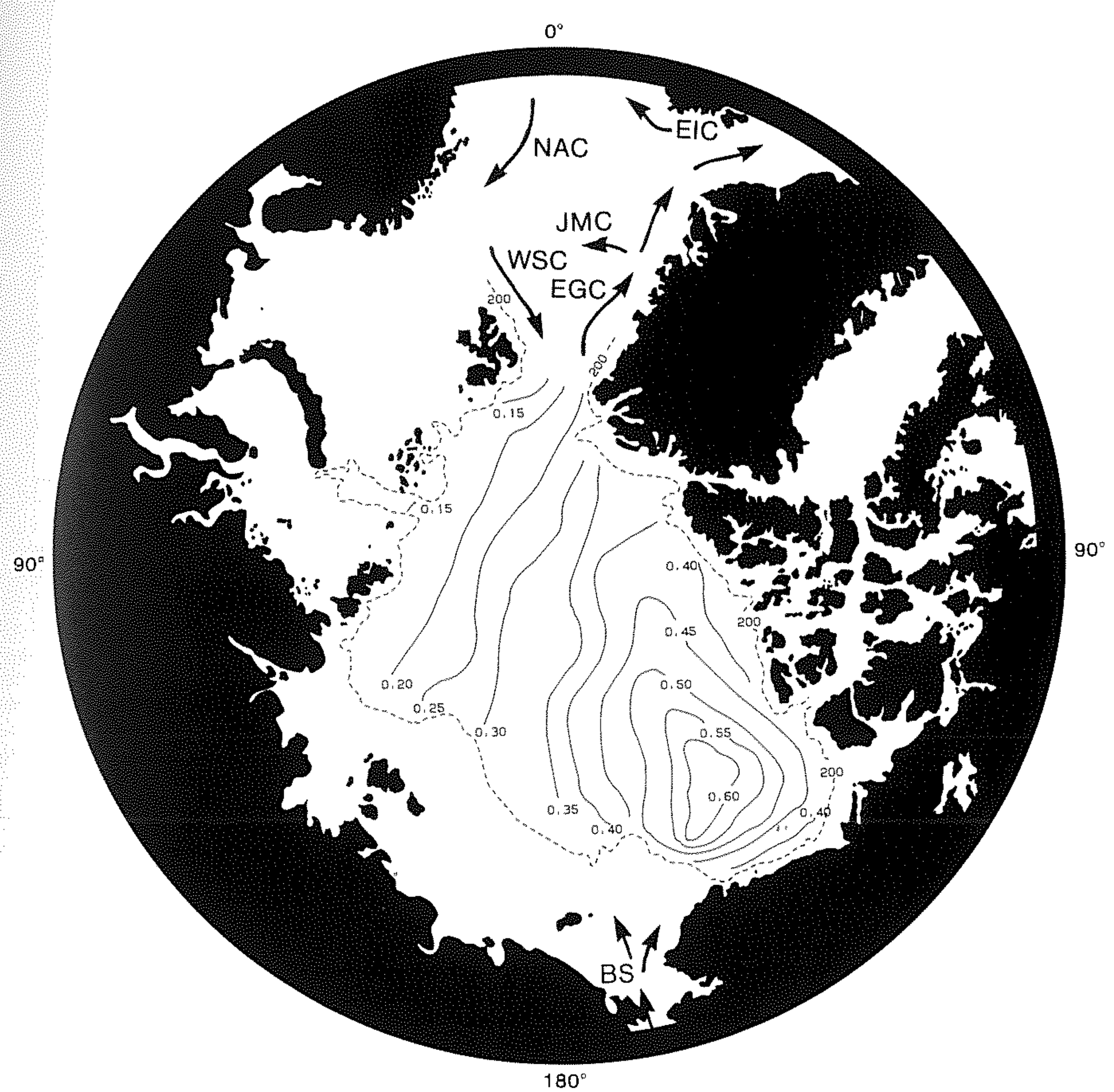


Fig. 6.8 Current systems of the Arctic Ocean and adjacent seas (from Coachman and Aagaard, 1974).

While the southern Beaufort Sea is generally thought of as an area of westward (clockwise) water- and ice-motion, the average subsurface motion above the continental slope is in the opposite direction; Aagaard (1984) called this flow the Beaufort Undercurrent. The presence of the undercurrent is indicated by a subsurface temperature maximum caused by the eastward flow of water originating in the Bering Sea (see Coachman and Barnes, 1961; Hufford, 1973; Mountain, 1974; Paquette and Bourke, 1974). Aagaard (1984) described the Beaufort Undercurrent as being a topographically steered eastward flow extending seaward of the 50 m isobath out to the base of the continental slope. Speeds are of order of 10 cm s^{-1} and increase with depth down to about 150 m. Transports are of order 1 Sv. The current is probably part of the large-scale circulation of the Canada Basin, and thus not locally driven.

A possible forcing mechanism for undercurrents in the Arctic has been discussed by Holloway (1987). He argues that the interaction of eddies with longshore

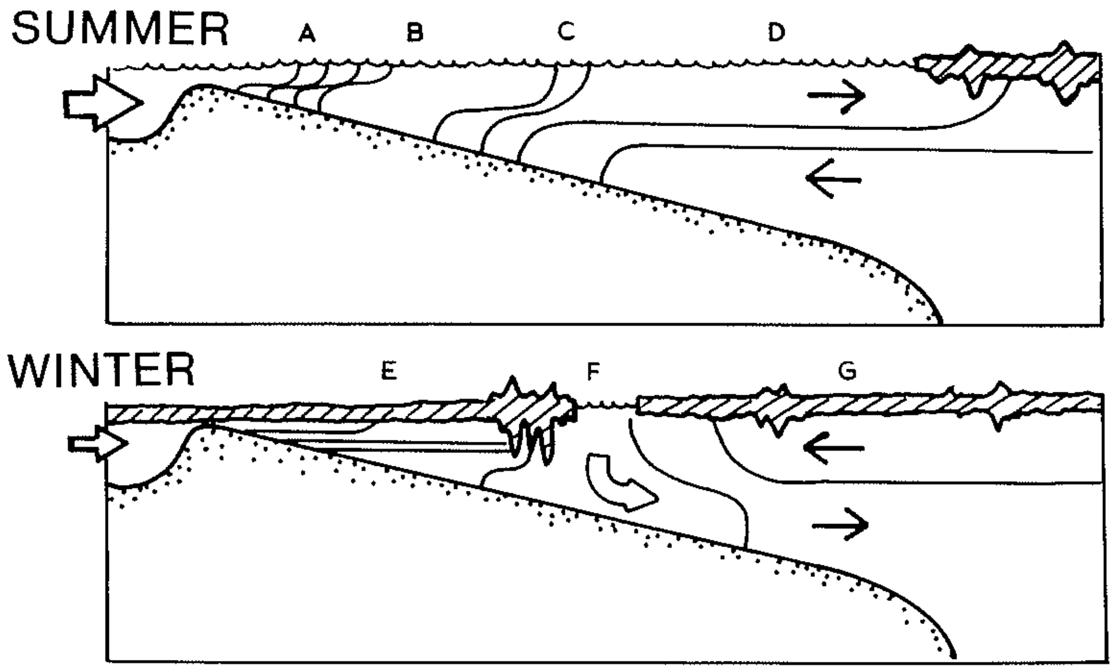


Fig. 6.9 Schematic of shelf/estuary systems during summer and winter.

variations in topography, together with coastally-trapped planetary wave propagation, results in a systematic forcing that acts on the mean flow. Applied to the Arctic, this mechanism predicts an eastward (cyclonic) flow following the basin margins which is of similar magnitude to the Beaufort Undercurrent.

Thermohaline circulation

Arctic shelf-estuary systems

The term shelf-estuary is here taken to mean the broad continental shelf regions whose circulation is influenced by river inflow. It is also over the shelves that much fresh-water is distilled by the annual cycle of freezing and melting. The melt water helps maintain the low salinity of the Arctic surface layer while the brine enrichment of shelf water by sea-ice formation helps ventilate subsurface layers. Hence, during summer shelves act as positive estuaries with a net outflow of low density water at the surface, while during winter they act as 'reverse estuaries' with a net outflow of high density water at depth (Fig. 6.9). Most studies relating to freshwater in the Arctic have focussed on budgets and basinwide effects (see Aagaard and Greisman, 1975; Ostlund, 1982; Anderson and others, 1983), which show that rivers influence strongly physical and chemical balances. However, budgets thus far have not taken into account the strong spatial and temporal variability in freshwater distribution that exists within the Arctic.

Halocline ventilation

Nansen (1906) was perhaps the first to note that because temperatures remain low within the halocline, its waters cannot be simple mixtures of Surface and Atlantic waters. Coachman and Barnes (1962) proposed that cold, saline waters draining through submarine canyons adjacent to the Eurasian Basin aided halocline formation. A similar process, involving the drainage of water from the Chukchi Sea through Barrow Canyon, was proposed by Garrison and Becker (1976). The hypothesis that the off-shelf drainage of brine-water derived from ice growth is largely responsible for halocline ventilation has been discussed by Aagaard and others (1981a), Melling and Lewis (1982), Killworth and Smith (1984), and Jones and Anderson (1986). As a means of identifying shelf regions that have potential for ventilation, Aagaard and others (1981a) calculated the amount of sea-ice formation required in winter to raise the shelf water salinity observed in summer to match that at the base of the halocline offshore. They suggest that the area from Svalbard to Severnaya Zemlya supplies the Eurasian Basin, while the Chukchi and northern Bering Seas, and possibly the region north of the Canadian Arctic Archipelago feed the Canadian Basin. Melling and Lewis (1982) also point to the Mackenzie Shelf as a source of halocline waters. They note that ice production in this region is increased by 60% over thermodynamic ice growth due to divergence of the ice cover, and also propose that the upwelling of saline water onto the shelf may augment the observed salinity increase.

More than one mechanism may be responsible for the halocline structure. Fig. 6.10 is a schematic of how the Arctic halocline may be maintained. In this picture the warm, salty Atlantic water enters the Arctic through Fram Strait via the West Spitsbergen Current. As it enters the Arctic Ocean this water is cooled by the atmosphere and by mixing with local waters. When the current meets the sea-ice margin northwest of Svalbard, ice melt and cooling generate a cold, dilute surface layer with T/S properties approximating those found above the Atlantic layer throughout the Arctic (see Quadfasel and others, 1987; Untersteiner, 1988; Moore and Wallace, 1988). This point of encounter is also a zone of maximum density at the surface. Prior to reaching this point surface cooling has increased the density of the surface layer; afterwards melting begins to decrease the surface density. As the flow continues eastward around the basin, contributions are first added from the Eurasian shelves, then from the Bering Sea inflow across the Chukchi Sea, and finally from the North American shelves. The net effect is a form of 'stacking-up' of layers, one upon the other, to form ultimately a thick and stable halocline.

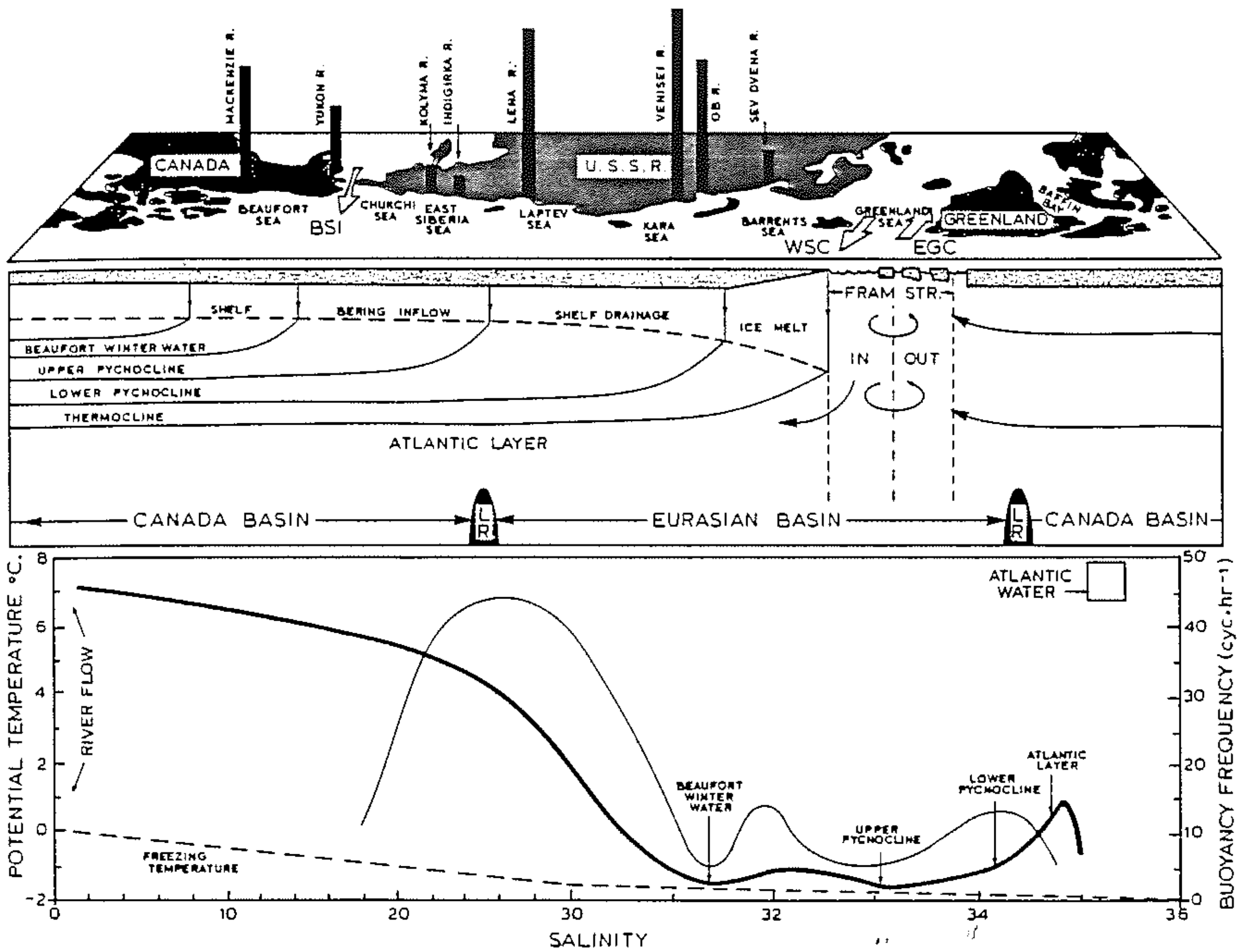


Fig. 6.10 Schematic drawing of the thermohaline circulation leading to the formation of the Arctic halocline.

Atlantic layer circulation

At present our knowledge of the circulation of the Atlantic layer in the interior of the Arctic Ocean is incomplete. It is fairly certain that upon entering the Arctic Ocean, water which represents a continuation of the WSC flows in a cyclonic direction along the continental margin of the Eurasian Basin (see Treshnikov, 1977). Within the Canadian Basin, however, it is uncertain even which direction water moves within the Atlantic layer. An anticyclonic flow is indicated by dynamic topography (Newton, 1973) and numerical modelling (Semtner, 1987), while the idea of cyclonic flow is supported by study of core properties (Timofeyev, 1960), current measurements near the continental margin (Aagaard, 1988), and an application of an inverse method to hydrographic data (Perkin, pers. comm.).

Deep water circulation

Killworth (1983) reviewed deep convection in the World Ocean. He organized his discussion around two types of convection: near-boundary sinking, and open-ocean sinking. The first of these involves the formation of a dense water mass on a continental shelf which subsequently reaches the ocean floor by descending a continental slope. The second occurs far from land, predominately within an oceanic gyre system. By far the greatest amount of attention to deep water formation in the Arctic Mediterranean has focussed on open-ocean convection in the Greenland Sea (Helland-Hansen and Nansen, 1909). However, a number of authors recently have discussed mechanisms for direct ventilation of the abyssal Arctic Ocean and a complex interbasin circulation. Aagaard (1981) called attention to the fact that deep water within the Canadian Basin has higher salinities than that within the Eurasian Basin, and questioned the classic ideas that all deep water within the Arctic Ocean derives from the Greenland Sea. Swift and others (1983) discussed contributions to the Arctic from both the Greenland and Barents Seas. The idea of direct ventilation of deep water in the Arctic by near-boundary processes was formalized by Aagaard and others (1985b); this hypothesis has gained some support from geochemical studies by Smethie and others (1988). Quadfasel and others (1988) have observed a dense plume descending a deep canyon which leads from Spitsbergen, crossing the Barents shelf into Fram Strait, and eventually entering the Arctic Ocean north of Spitsbergen.

A rough picture of the complex interbasin flow and recirculation of deep waters in the Arctic Mediterranean is emerging slowly. While the deepwater of the Arctic

Oceans comes partly from the Norwegian Sea, the deep water of the Norwegian Sea is itself derived partly from the Arctic Ocean. The deep outflows from the Arctic leave the western Fram Strait along the East Greenland continental slope at a depth where their density matches that of ambient water in the Greenland Sea, at depths of 1500 to 2000 m (Aagaard and others, 1985b). Mixing with the relatively new Greenland Sea waters, in about a 50-50 ratio, then results in water which forms the source of deep water for the Norwegian Sea (Swift and Koltermann, 1988). Eventually, the Norwegian Sea Deep Water flows back into the Arctic through the eastern Fram Strait, subsequently to be modified by shelf-derived waters in the Arctic Basin. Finally, some water from the Eurasian Basin crosses the Lomonosov Ridge in the Canadian Basin, where it too is modified by shelf sources, increasing its salinity to the highest values found in polar deep waters. This complicated scenario is supported by the distribution of non-conservative tracers. Dissolved oxygen is highest and nutrients are lowest in the young Greenland Sea waters. The deep waters of the Canadian Basin are the most isolated, due to the Lomonosov Ridge, and thus have the lowest oxygen values and highest nutrients. The Eurasian Basin oxygen concentrations are higher than those of the Norwegian Sea because they are modified by shelf-derived components, giving oxygen values not much lower than those in the deep Greenland Sea.

CONCLUDING REMARKS

In summary, there are many exciting things to learn about the large-scale physical oceanography of the Arctic Ocean, especially with regard to the interdisciplinary connections with biology and climate. Some of the more straightforward ties include the transport of nutrients and organisms by current systems, the establishment of ambient light climate by turbidity and sea-ice fields, the influence of strong stratification on particle settling, the seasonal cycles of circulation and mixing due to freshwater inflow and surface forcing, the material exchanges at the ice-water interface, and the transfer mechanisms operating at marginal ice zones and major frontal systems. The relationship between Arctic biology and climate is also important, including the influence of polar biota on the world CO_2 balance, and the question of whether possible alternate circulation patterns might result in a large-scale shift in nutrient availability. It is especially important to understand the mechanisms by which freshwater from river inflow and ice melt is disposed within the basin, for it is the distribution of salinity, specifically the thickness and horizontal extent of polar haloclines, which prevents deep convection and the local flux of both nutrients (from the nutrient maxima layer) and heat (from the Atlantic layer) to the surface.

How bright is the future? In writing up the scientific results of his 1893-1896 expedition, Nansen (1906) lamented the many advances in instrument design and theory that had occurred since his return, and wished for the opportunity to repeat this work. Given this chance he believed, "The North Polar Basin could thus in some ways become the best known region of the Ocean." Almost a hundred years has passed, and the singular feature of Arctic oceanography remains the dearth of good data and theory. The Canadian Basin, for example, likely will be the last major ocean basin for which a high-quality oceanographic transect becomes available. This lack of adequate data for interpretative purposes severely restrains physical modelling efforts, as well as our understanding of biological processes. It is difficult to see how reliable predictions about future climatic conditions can be extrapolated from our current store of data on the Arctic Ocean and its ice cover.

CHAPTER 7

ARCTIC PLANKTONIC ECOSYSTEMS

Egil Sakshaug

About 15 × 10^6 km^2 of the Arctic Ocean is covered by ice. About half of this area is seasonally ice-free (Parkinson and others, 1987). In addition, the Norwegian Sea and the southernmost part of the Barents and Bering Seas stay permanently open. The annual primary production in Arctic seas ranges from 5 to 290 g C m^{-2}. The higher estimates represent pelagic production in open or seasonally ice-filled waters; by comparison ice biota represent less than 3% of the total primary production (Subba Rao and Platt, 1984). Much of the seasonally ice-covered area belongs to wide shelf seas. The Barents Sea, for instance, is about 150-400 m (average 230 m) deep except at a few banks; the northern and eastern parts of the Bering Sea range from less than 50 m up to 200 m depth. In some places, particularly in the Bering Sea, the productive zone, which is usually 30-50 m deep in summer, may reach close to the bottom.

The Arctic Ocean represents different water masses. Waters north of Scandinavia and European USSR (the Barents Sea and eastwards) are primarily of northeast Atlantic origin, while the Bering Sea corresponds to Pacific waters. The deep Polar Basin is characterized by Atlantic waters, but the impact of the Bering Strait influx (which may be approximately one third of the volume of the Atlantic influx – Treshnikov and Baranov, 1977) is significant in the upper layers, particularly in the western part of the Arctic (Codispoti, 1983).

ENVIRONMENTAL CONTROL OF PRIMARY PRODUCTION

The variation in standing stock of primary producers is, as elsewhere, a function of the difference between the growth rate and the loss rates (mainly sinking and grazing). The growth rate is determined mainly by temperature, nutrient supply and the light regime. The low temperature in Arctic waters may set a limit for the growth rate, typically 0.6-1 doublings day^{-1} at prevailing temperatures (about -1.8 to 6°C). Because the temperature range is less than 8°C, temperature-dependent variation of the growth rate is restricted. Neither can temperature be regarded as a "stress" factor for algae which are adapted to a cold environment. Because the primary production is related both to the growth rate and the widely variable magnitude of the algal standing stock, it follows that primary production may to a large extent follow variations in the latter.

In the dark season, starting in autumn, ice may form, and vertical mixing is generally enhanced. This ensures that "new" nutrients are brought to the surface layers from below the euphotic zone. At the same time consumption of nutrients by algae is at a minimum because irradiance is insufficient for growth, so that nutrient concentrations will be at a maximum. This will, however, depend on the origin of the water. Winter waters of Atlantic origin are relatively low in nutrients compared to Pacific waters (Table 7.1). The molar nitrate/phosphate ratio for winter nutrients is, however, about the same in both waters. The molar silicate/nitrate is, in contrast, considerably higher in Pacific winter waters than in Atlantic winter waters (Table 7.1). The winter silicate/nitrate ratio in the northeast Atlantic may be the lowest observed maximum ratio in the world's oceans. The impact of the much higher silicate concentration in Pacific than in Atlantic waters can be traced through a large part of the Canadian Arctic (Codispoti, 1979). Generally diatoms from the Northeast Atlantic have a silicate content at saturation which is lower than that of diatoms from Antarctic waters (Sakshaug and Holm-Hansen, 1984). Ammonia and urea are regenerated by biological activity and concentrations are generally too low to support the large biomass of phytoplankton blooms.

Table 7.1. Typical winter values of nitrate, phosphate and silicate (μmol dm^{-3}) as well as the molar nitrate/phosphate and silicate/nitrate ratios in Arctic waters of Atlantic and Pacific origin. Data compiled by Sakshaug (1989).

	Atlantic	*Pacific*
nitrate	9–14	25–30
phosphate	0.5–0.6	1.5–2.0
silicate	4–5	35
nitrate/phosphate	18–23	15–17
silicate/nitrate	0.35–0.45	1.1–1.4

The growth season starts with a bloom which is triggered by the vernal increase in incident irradiance and daylength. In the weeks around the vernal equinox, darkness is quickly replaced by long days or even continuous daylight (Fig. 7.1a,b). The "baseline" atmospheric light regime on a clear day can be predicted from latitude and date. Beyond 60° latitude, scalar photon fluxes of more than 1500 μmol photons m^{-2} s^{-1} are unlikely at 0.5 m depth (Hegseth and Sakshaug, 1983). The light regime actually experienced by phytoplankton is, however, strongly modified by the presence or absence of ice, and by vertical mixing in the upper waters. In addition, cloudiness and fog (common in the Arctic summer) will modify the light regime. Finally, self-shading by the algae themselves may modify the light regime considerably when blooms become dense.

Ice under average conditions, with some snow, may let through only 0.3-1% of the surface light. Removal of snow may improve transmittance by more than a factor of ten (Meguro and others, 1966; Bunt and Lee, 1970; Sullivan and others, 1983). As a rule planktonic algae under the ice consume too little nutrient to reduce the

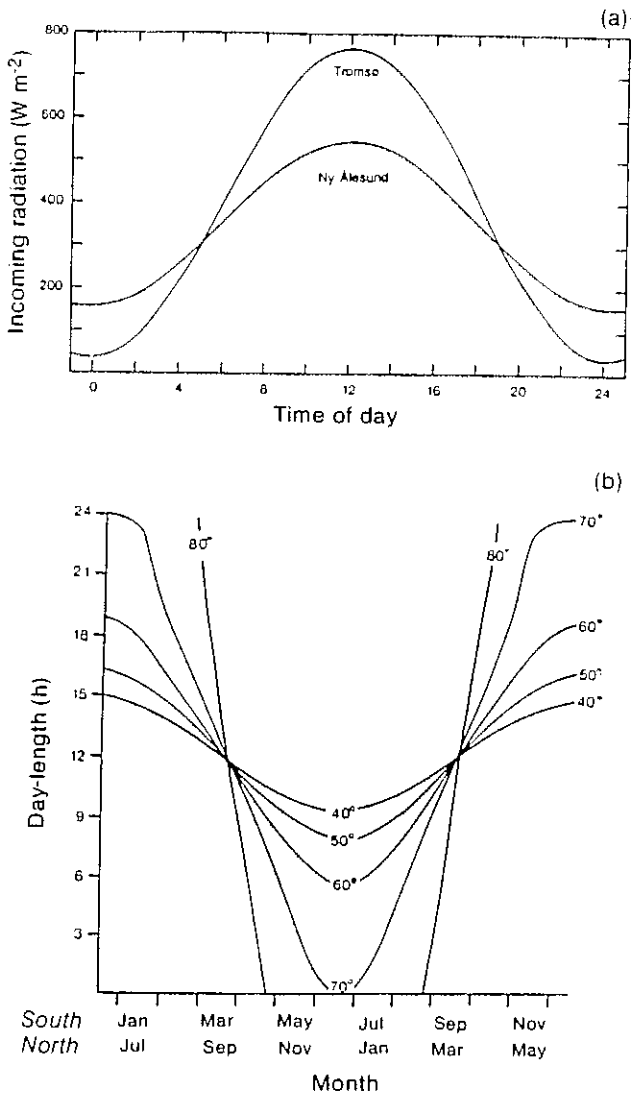


Fig. 7.1. (a) Diurnal variation in global radiation on clear midsummer days at Tromsø, Norway (70°N), and (b), seasonal variation in daylength at various latitudes. From Sakshaug (1989) based on data from Spinnangr (1968) and Holm-Hansen and others (1977).

winter concentrations significantly, except possibly in their immediate vicinity.

Vertical mixing in winter and spring may vary between 100 m and 300 m depth (Blindheim, 1989). This forces the algae to spend a considerable time in unfavourable light regimes. The formation of stable upper layers or a shallow pycnocline is therefore necessary to ensure a light regime favourable for phytoplankton growth. According to Sverdrup's (1953) model, a bloom results when the integrated gross photosynthesis is greater than the integrated respiration in the mixed layer (the concept of critical depth). This model appears realistic for the initial phase of the bloom, when losses due to sinking and grazing are presumably small. In the general case, however, all losses as well as the photo-adaptational response of the algae should be included – as in present-day extensions of this model (Slagstad, 1982). Blooms have not been reported in layers which are mixed to a depth of more than 40–50 m, even if Sverdrup's model may predict blooms in waters mixed to a far greater depth in summer (Sakshaug, 1989). This presumably reflects the importance of losses of algal biomass other than respiration, such as grazing and sinking.

In permanently ice-free oceanic areas such as the Norwegian Sea, the formation of a shallow pycnocline is temperature-dependent, and it may not form until May-June (Blindheim, 1989). This implies a correspondingly late bloom. In seasonally ice-covered areas, melting of ice creates a marked pycnocline at 20-40 m depth (the melt-water is almost fresh). Nutrient-rich waters then become exposed to surface light when the ice disappears. Under such conditions a spring bloom will develop rapidly. The melting may begin as early as April-May in the southernmost fringes of ice-covered areas (Loeng, 1989). Thus ice-edge blooms may potentially begin earlier than blooms in permanently open waters.

One may imagine an ice-edge bloom which follows the retreating ice-edge northwards while scavenging the newly exposed winter nutrients (the "ice-edge effect", Fig. 7.2). Accordingly a bloom should occur later in higher latitudes. Waters may stay ice-free for some 3-7 months in the outer fringes of the seasonally ice-covered area and exhibit a bloom in May or June (Braarud, 1935; Digby, 1953; Bursa, 1961; Hsiao and others, 1977; Saito and Taniguchi, 1978; Iverson and others, 1979; Loeng, 1989), whereas areas as far north as Dumbell Bay at Ellesmere Island (82°N) may become ice-free as late as August and for only 3-4 weeks, so that the "spring" bloom is still developing when refreezing sets in (Apollonio, 1980).

The concept of an ice-edge effect was first suggested by Gran (1931) on the basis of Antarctic data. This has been verified by later investigations (Alexander, 1980; Rey and Loeng, 1985; Smith and Nelson, 1985; Niebauer and Alexander, 1989). When the ice-edge is well-defined, the ice-edge bloom zone may extend for some 20-50 km seawards of the ice-edge (Rey and Loeng, 1985). Often, however, the ice-edge is far from well-defined, because local winds and currents cause the ice to drift and may confuse the picture (Buckley and others, 1979). Furthermore, blooms cannot be expected off edges of ice which drift on waters already depleted of nutrients; this is frequently the case late in the growth season.

As a rule, winter nutrients are completely depleted during the development of the spring bloom in Arctic waters; this is usually true even in nutrient-rich Pacific waters (Iverson and others, 1979; Walsh, 1983). Peak levels of biomass may range between 8 and 15 μg dm^{-3} chlorophyll *a* in waters of Atlantic origin (Rey and Loeng, 1985) and up to 40 μg dm^{-3} in the Bering Sea (Iverson and others, 1979). Assuming a chl/C ratio of about 0.02 for spring phytoplankton (Sakshaug, 1989), those peak biomasses should correspond to about 0.4-1 and 2 mg dm^{-3} of carbon, respectively. The annual primary productions of the Barents and Bering Seas are about 60-80 and 200 g C m^{-2}, respectively, of which more than 60% may be produced during the short period of the spring bloom (McRoy and Goering, 1974; Rey and Loeng, 1985).

In the early phase of the bloom the growth rate of the phytoplankton is determined by the light regime and the temperature. After the bloom peaks, when winter nutrients become depleted, further growth depends on the immediate nutrient supply. In Arctic waters this will be insufficient to sustain growth by the already large standing stock at rates determined by ambient temperature and irradiance/daylength. This is due to inadequate supply of "new" nutrients from below, through the pycnocline. Nutrient limitation sets in, and the "excess" algal biomass will sink or become grazed by zooplankton. As a rule, an appreciable amount of the algae will always sink out of the euphotic zone as the end of the bloom approaches: 50 to 70% is likely (Walsh and others, 1989). Thus a large fraction of the winter nutrients, derived from deep water and converted to biomass in surface waters during the bloom, will be returned to the deeper strata.

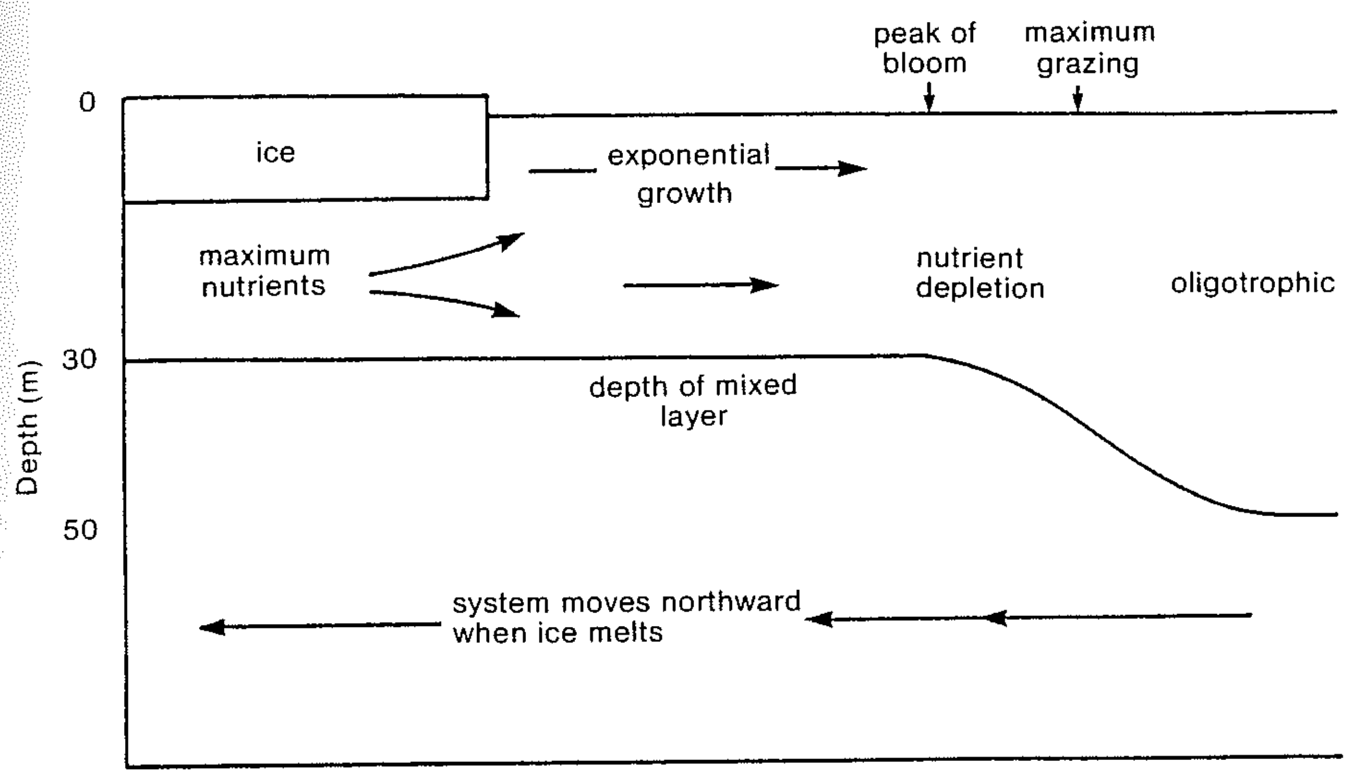


Fig. 7.2. Schematic illustration of the ice-edge effect (Sakshaug, 1989).

The efficiency of transfer of algal biomass to zooplankton is variable because high efficiency requires that maximum grazing pressure coincides with the phytoplankton bloom both geographically and in time. Most zooplankton drift with the currents and are exposed to variations in phytoplankton biomass as they happen. It is therefore important to graze intensively while a bloom lasts. Viewed in the extreme, zooplankton may have only one short, albeit rich, meal per year. It is therefore typical for high-latitude zooplankton to have large stores of lipids that serve as an energy reserve for the rest of the year (Clarke, 1983). In principle, if a bloom is short and hectic due to extreme stability and a shallow pycnocline, less may be grazed than during a bloom which has been prolonged by mixing and a deeper pycnocline. This seems to happen in the case of the copepod *Calanus finmarchicus* in the Atlantic waters south of the oceanic polar front in the Barents Sea. In years in which the Atlantic waters are relatively cold, the former seems to take place, and in warmer years the latter is more likely (Skjoldal and others, 1987). In the Arctic waters north of the oceanic polar front *C. glacialis* is predominant. This species has a two-year life cycle in contrast to the one-year cycle of *C. finmarchicus*. It is possible that the occurrence of two simultaneous generations represents an adaptation which may maximize the grazing pressure during the very restricted bloom period in this area (Tande and others, 1985; Skjoldal and others, 1987). Finally, year to year differences in the magnitude of the overwintering stock of zooplankton may be important in causing large interannual variability in the utilization of the spring bloom (Skjoldal and others, 1987).

Larger organisms which can perform horizontal migrations over some distance have an advantage over other smaller zooplankton in that they can follow the retreating ice-edge and the ice-edge bloom. Krill is a good example, but is of considerably less importance in the Arctic than in the Antarctic seas. In the Barents Sea, capelin (*Mallotus villosus*) is the key food source for higher animals. Capelin track the ice-edge bloom, but because they are carnivores they are usually separated from the ice-edge by some distance, due to the time delay between primary and secondary production (Skjoldal and others, 1987).

After the bloom has ended, nutrient concentrations stay close to the lower limit of detection, and in many areas the pycnocline formed during the melting of ice will persist until freezing begins. The algal community as a whole remains nutrient-limited, and standing stocks are small: in terms of chlorophyll, usually less than 0.5 μg dm^{-3}. Nutrient supply is largely regenerative within the euphotic zone, as reflected by the preponderance of ammonia uptake over nitrate uptake (Harrison, Platt and Irwin, 1982). The system is thus in principle similar to the oligotrophic systems of the central parts of warm oceans. Close to the pycnocline a maximum layer of chlorophyll is usually evident and may exhibit chlorophyll concentrations up to 15-20 μg dm^{-3}. The standing stock remains large in real biomass (carbon) terms. It presumably grows slowly and one limiting factor will be the restricted supply of "new" nutrients through the pycnocline.

Secondary large blooms have not been recorded in Arctic areas. However, minor biomass peaks, which are scattered geographically and in time, are likely, as a consequence of local wind-driven upwelling (Mork, 1981). Furthermore, alternating periods of calm and stormy weather may cause periods of deep mixing or upwelling (supply of "new" nutrients) to alternate with periods of stability (favourable light-regime for growth). This would represent a growth-enhancing feature of the post-bloom period (Riley, 1963; Legendre, Ingram and Simard, 1982). This effect may be likely in the low-pressure belt which normally crosses the oceans from 45-55°N on the west side to 55-75°N on the east side. Additionally, shallow bank areas may exhibit an enhanced production because they tend to disrupt the pycnocline and thus introduce "new" nutrients to the surface layers.

ALGAL RESPONSES

The optimum temperatures for growth or photosynthesis by Arctic planktonic algae are generally higher than those to which the algae are normally exposed. Some species recorded in the Arctic may even grow at temperatures of 15-20°C (Smayda, 1969; Durbin, 1974). There is no clear evidence that typical Arctic species grow faster at low temperatures than would temperate species. One cannot therefore speak of particular adaptations which counteract the effect of low temperature on the growth rate. However, far too little is known about the response of individual species.

Arctic phytoplankton species seem to tolerate variations in the light regime well, and this may include the particularly harsh combination of strong, sometimes continuous light and near-freezing temperatures over long days. This contrasts with many temperate species which tolerate such temperatures only when irradiance is low or days are short (Sakshaug, 1989). Phytoplankton may grow at a wide range of light regimes without appreciable variation in the growth rate (Sakshaug and Holm-Hansen 1986). Diatom species from the Barents Sea grown at -1°C have, for example, revealed an almost flat response for the growth rate at irradiances from 50 to 500 μmol photons m^{-2} s^{-1} at all daylengths when the cultures had time to adapt to each irradiance (Gilstad and Sakshaug, 1990). The growth rate increased, however, notably with daylength, but the increment was small from 19 to 24 h of light.

The flexibility of Arctic phytoplankton in coping with variation in the light regime rests on the plasticity of the photoadaptational mechanisms of the phytoplankton. In essence, photoadaptation serves to minimize the impact of light regime fluctuations on the growth rate. Among the photoadaptational parameters may be mentioned those that determine the function for quantum yield (carbon produced per unit irradiance), respiration, the chlorophyll/carbon ratio and the coefficient for absorption of irradiance of the algae (Ley and Mauzerall, 1982; Kiefer and Mitchell, 1983; Dubinsky, Falkowski and Wyman, 1986). The chlorophyll content of Arctic and subarctic diatoms may vary inversely with daylength and irradiance by a factor of more than six. Typically, enhanced chlorophyll contents are observed in early spring and late autumn and in the chlorophyll maximum layer near the pycnocline (Platt and others, 1982; Sakshaug and Andresen, 1986). When the algae are adapted to the ambient environment (steady state growth) and the irradiance is below inhibitory strengths, the gross growth rate of the algae (growth rate + respiration in the same units) may correspond to the product of daylength, irradiance of the algae, and quantum yield (Sakshaug, Kiefer and Andresen, 1989). Whereas the chlorophyll/carbon ratio is sensitive to light regime, nutrient deficiency and temperature, the quantum yield is sensitive only to irradiance. This growth model implies that is is necessary to treat the effect of daylength and irradiance separately, instead of modelling on total or average irradiance per day. This is important in polar regions where daylength variation is pronounced.

Phytoplankton have to cope with quickly fluctuating light, as caused, for instance, by changing cloud cover and by vertical transport in the water column. It is likely that phytoplankton become generally unadapted in such cases, because photoadaptation takes time, in the case of the chlorophyll/carbon ratio, a few hours to some days (Gallegos and others, 1983; Post and others, 1984). The chlorophyll/carbon ratio is often the same in the whole water column above the pycnocline, which indicates that the rate of mixing is much greater than the rate of adaptation (Sakshaug, 1989). The algal response in a quickly changing light regime can be illustrated by P vs I curves (Fig. 7.3). Such curves relate carbon uptake to irradiance during short-term incubations, ideally so short that photoadaptation is not given time to take place. The shape of the curve therefore reflects the photoadaptational status of the original sample. When carbon uptake is normalized to chlorophyll (assimilation number), the initial slope of the curve (α) for Arctic phytoplankton seems to be lower for shade-adapted than for sun-adapted algae. This may seem surprising, because a high slope indicates high photosynthetic efficiency in low light. When the higher chlorophyll/carbon ratio of shade-adapted algae is taken into account it appears, however, that the slope, and thus the photosynthetic efficiency normalized to carbon, becomes higher in shade-adapted algae (Fig. 7.3, right part). The curves then express the turnover rate for carbon in the cells, which again can be related to the growth rate. Total photosynthesis through the day, predicted by integrating the light regime in the mixed water column, seems to correspond well to that predicted on basis of P vs. I curves, unless photoinhibition is significant (Marra, 1978; Falkowski and Wirick, 1981; Gallegos and Platt, 1982). For translation of such data into growth rates it becomes necessary, however, to take the daylength and chlorophyll/carbon ratio into account, according to the growth model above. The latter is difficult to estimate in nature, because of interference in the measurement of carbon by non-algal matter.

It has been mentioned that ability to cope with strong light is important. Fig. 7.3 indicates that this may depend on the photoadaptational status of the phytoplankton. Generally, shade-adapted algae are more susceptible to strong light than sun-adapted algae. It is, however, also likely that specific differences are important. The carotenoid pigments diato- and diadinoxanthin may protect cells against strong light. The cellular content of such pigments differs notably from one species to another (Sakshaug, Demers and Yentsch, 1987). These pigments may respond to changes in the light regime in a matter of minutes and to fluctuations due to shifting cloud cover and vertical mixing (Welschmeyer and Hoeppfner, 1986). It is also possible that asymmetric photoadaptation may minimize inhibition by strong light. It has been shown (Gallegos and others, 1983; Post and others, 1984) that adaptation to strong light proceeds faster than adaptation to low light. For a water column in which the phytoplankton is transported cyclically up and down by mixing, one may imagine that the photoadaptational status of the algae after a time will correspond rather to the strong light near the surface than the average light regime of the column. Comparison of natural populations and laboratory cultures of the same species indicates that this may be so (Hegseth and Sakshaug, 1983; Sakshaug and Andresen 1986). This implies lowered susceptibility to photoinhibition (Fig. 7.3) as well as a lowered chlorophyll/carbon ratio. This mechanism may also imply lowered efficiency at low light, e.g. deep in the water column – at least in terms of carbon turnover (Fig. 7.3, right part). Photoinhibition also increases with the duration of exposure to strong light. In summary, one may thus expect that the impact of photoinhibition is smallest in waters which "turn around" quickly, and that waters mixed slowly to a large depth represent the most disadvantageous environment.

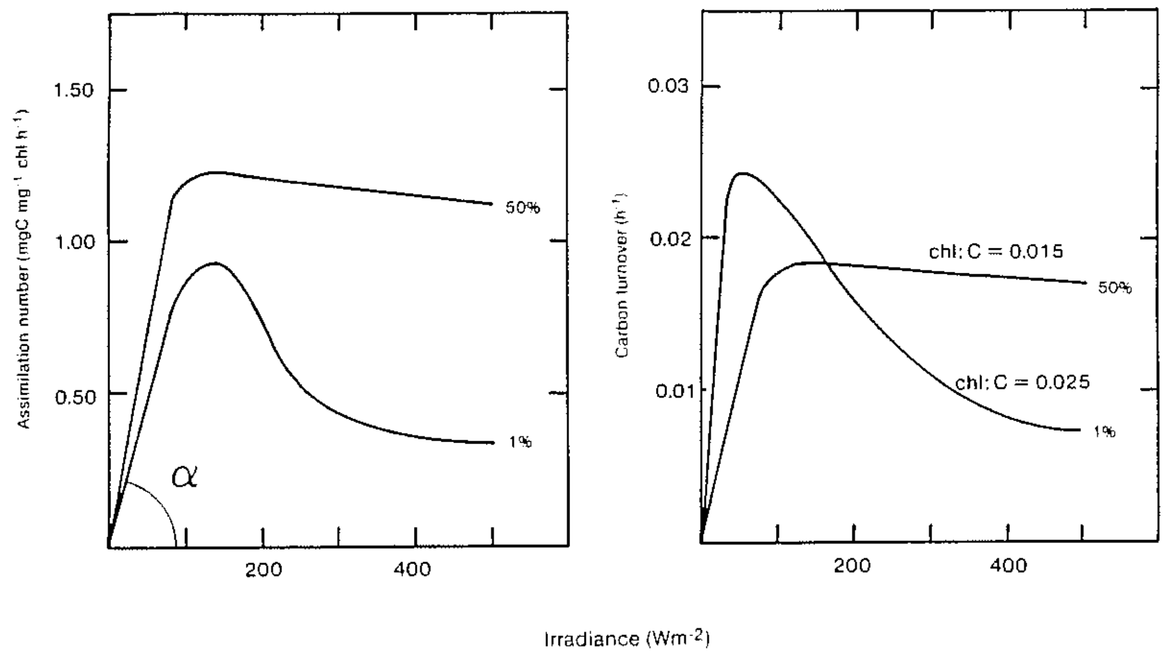
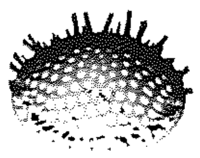


Fig. 7.3. Short-term response of carbon-uptake on varying irradiances (P vs I curves) for summer phytoplankton in Baffin Bay. One community was sampled from the mixed upper layer (50% light depth) and the other from the chlorophyll maximum near the pycnocline (1% light depth). When carbon uptake is normalized to chlorophyll (left graph), the initial slope of the curve may be somewhat smaller for the shade-adapted population (1%) than for the sun-adapted one (50%). When normalized to carbon (right graph), α is much larger for the shade-adapted community because of its higher chlorophyll to carbon ratio. The sun-adapted community has a higher maximum uptake rate and is also less susceptible to inhibition of carbon uptake in strong light. Redrawn from Platt and others (1982).

The latter may be more relevant in Antarctic than in Arctic waters.

The algal growth rate is a function of the difference between gross photosynthesis and respiration. All these parameters depend on temperature when the light regime is at optimum and nutrients are present in excess relative to algal needs. Investigations of natural communities of Antarctic phytoplankton (Tilzer and Dubinsky, 1987) indicate that even if gross photosynthesis decreases with temperature, respiration decreases more. In fact, respiration was only 2% of gross photosynthesis at -2°C in contrast to 17% at 8°C. Low temperature is thus no threat to survival, rather the contrary. Besides, shade adaptation also implies lowered respiration rates (Kiefer and Mitchell, 1983). As a consequence, gradual adaptation towards shade in the autumn and low temperature may in principle result in cells which may be characterized as physiologically resting cells and which may survive extended periods of darkness. Studies of both cultures as well as natural populations of the diatom *Skeletonema costatum* seem to support this idea (Falkowski and Owens, 1980; Sakshaug and Andresen, 1986). Thus survival strategies do not necessarily have to be based on particular resting cells such as resting spores and cysts.



CHAPTER 8

ARCTIC PLANKTON DIATOMS:

DOMINANT SPECIES, BIOGEOGRAPHY

Grethe R. Hasle

The composition of marine phytoplankton is characteristically variable. Variation occurs in space influenced by the distance from the coast, by latitude and by ocean circulation, and occurs in time, during the year and from one year to the other. Together, these form a mosaic of interwoven factors. The Arctic marine environment is no exception in this respect; the variation may even be especially accentuated due to the complicated topography and current systems. Another factor to be kept in mind when describing the species composition of the Arctic plankton is that species having the ice as their normal habitat may be present in the plankton as well. These complications imposed by nature itself are further increased by the varying methods for sampling and analysis employed in Arctic diatom research since its start in the middle of the 19th century. Updating of Arctic diatom taxonomy by the use of current methods, started but far from completed, also adds to the confusion.

The reservations made so far, imply that the literature can be used only for a fairly superficial overview of the distribution of Arctic planktonic diatoms. Some areas may be represented by a few net-hauls collected over a shorter or longer period of time, whereas water samples collected monthly during one or more years may have been studied from other areas. The many new nomenclatural combinations made from the 1960's and onwards introducing a great number of synonyms further complicate the use of the literature. On the other hand, the literature is extensive and no attempt will be made here to summarize it in full as many of the investigations provide little or no new information.

The list of diatoms recorded in marine Arctic plankton presented here (Table 8.1) is far from complete. It can be used, however, as a guideline to those species that are restricted to the Arctic or that form the bulk of Arctic diatom populations. Note that examples in the text are referred to by the names used in the original papers. To avoid confusion the reader is referred to Table 8.1 for synonyms. Examples from unpublished observations based on material collected by fine-meshed nets (10-30 μm) during the Norwegian Programme for Marine Arctic Ecology (Pro Mare) in the Barents Sea are used to illustrate the variation of the species composition with space and time. We are grateful to the collector, Dr Svein Kristiansen, who placed the samples at our disposal.

COMPOSITION OF THE MARINE DIATOM PLANKTON

The pioneer studies of Arctic diatoms were based, with a few exceptions, on collections of diatom ooze, bottom sediments, dust on ice-floes and left-overs from zoological gatherings (see Grøntved and Seidenfaden, 1938). Cleve (1873, p. 3) included in his investigation samples "taken on the surface of the sea between Europe and Greenland as well as from Davis Strait". Of the 144 diatom species he listed, ten were mentioned especially as "floating on the surface of the sea", either in the North Atlantic, 60°25′N, or in the Davis Strait, 61°25′–63°30′N, and were referred to five centric and two pennate genera: *Chaetoceros, Coscinodiscus, Biddulphia, Rhizosolenia, Thalassiosira, Fragilaria* and *Thalassiothrix* (Table 8.2). Except for *Biddulphia* and with the addition of *Endictya* the same genera were represented in a gathering of "diatoms living on the surface" collected in the Bering Sea during the "Vega"-Expedition (Cleve, 1883, p. 490) with *Thalassiothrix longissima* "in great abundance".

Østrup (1895) distinguished clearly between diatoms in the plankton and diatoms collected on the ice and offshore along the coast of East Greenland. The 13 plankton samples he examined were collected between 60°58′N and 76°07′N and thus included areas at latitudes higher than those covered by Cleve (1873, 1883). Østrup commented on the heterogeneity of the plankton material compared to the ice samples and on the dominance of a few species. Some samples could be characterized as *Chaetoceros*- and *Rhizosolenia*-plankton, others as *Chaetoceros*-plankton or *Thalassiosira nordenskioeldii*-plankton, whereas samples characterized by the presence of aggregates up to 12-13 cm in diameter floating along the edge of or between the ice-flakes consisted of *Melosira* and aggregates floating on the surface of the sea were dominated by *Fragilaria oceanica*. Still another sample, also an aggregate, was similar to material from ice holes being dominated by *Nitzschia* spp. Østrup suggested that this kind of material living on the ice but also floating in the sea should be called "secondary plankton" in contrast to the *Melosira* aggregates, which according to Østrup belonged to the plankton but found a secondary habitat on the ice.

The first comprehensive study of the species composition of the Arctic phytoplankton was based on 50 samples collected in Baffin Bay and the northern part of the Davis Strait from the beginning of May to the middle of October (Cleve, 1896). Among the almost 40 taxa recorded, *Asteromphalus atlanticus, Chaetoceros groenlandicus, Eucampia groenlandica, Lauderia confervacea* and *Thalassiosira gravida* were new to science, and *Coscinodiscus* (*lacustris* var.) *hyperboreus, C. bioculatus* and *Fragilaria cylindrus* could have come from melting ice. Gran (1897), examining four plankton samples from Little Karajakfjord, West Greenland, found most of the same species as did Cleve (1896), with the addition of two new species *Lauderia fragilis* and *Navicula vanhoeffenii*.

Table 8.1. Diatoms present in Arctic marine plankton

Current name	*Synonyms*
Achnanthes taeniata Grun.**	
Actinocyclus sp.	
Asteromphalus robustus Castr.	*A. atlanticus* Cl.
Bacterosira fragilis (Gran) Gran*	*Lauderia fragilis*
Chaetoceros atlanticus Cl.	
" *borealis* Bail.	
" *debilis* Cl.	
" *decipiens* Cl.	
" *diadema* (Ehr.) Gran.	*C. groenlandicus* Cl. *C. subsecundus* (Grun.) Hust.
" *furcellatus* Bail.**	
mitra (Bail.) Cl.**	
" *septentrionalis* Østr.***	
" *socialis* Laud.	
Coscinodiscus centralis Ehr.	
" *oculus-iridis* Ehr.	
Detonula confervacea (Cl.) Gran.	*Lauderia confervacea*
Eucampia groenlandica Cl.*	*E. zodiacus* Ehr. pro parte
Leptocylindrus danicus Cl.	
Melosira arctica Dickie*	*M. nummuloides* var. *hyperborea* Grun. *M. hyperborea* Grun.
Navicula pelagica Cl.*	
Navicula vanhoeffenii Gran.*	
Neodenticula seminae (Simons. and Kan.) Ak. and Yan.	*Denticula seminae*
Nitzschia cylindrus (Grun.) Hasle**	*Fragilaria cylindrus* *Fragilariopsis cylindrus* (Grun.) Krieger
" *delicatissima* Cl.	
" *frigida* Grun.**	
" *grunowii* Hasle*	*Fragilaria oceanica* Cl. *Fragilariopsis oceanica* (Cl.) Hasle
" *laevissima* Grun.*	
" *pseudonana* (Hasle) Hasle	*Fragilariopsis pseudonana*
" *seriata* f. *obtusa* Hasle*	
Odontella aurita (Lyngb.) Agardh	*Biddulphia aurita* (Lyngb.) Bréb.
Pleurosigma stuxbergii Cl.*	
Porosira glacialis (Grun.) Jørg.*	*Podosira glacialis* (Grun.) Cl. *Lauderia glacialis* (Grun.) Gran
Proboscia alata (Bright.) Sundstr.	*Rhizosolenia alata*
Rhizosolenia hebetata f. *semispina* (Hensen) Gran	
" *setigera* Bright.	
" *styliformis* Bright.	
Skeletonema costatum (Grev.) Cl.	
Thalassiosira anguste-lineata (A. Schm.) Fryx. and Hasle	*Coscinodiscus anguste lineatus* *Coscinosira polychorda* (Gran) Gran *Thalassiosira polychorda* (Gran) Jørg.
" *antarctica* var. *borealis* Fryx., Douc. and Hub.*	
" *baltica* (Grun.) Ostenf.**	*Coscinodiscus polyacanthus* var. *baltica*
" *bioculata* (Grun.) Ostenf.*	*Coscinodiscus bioculatus*
" *bulbosa* Syverts.	
" *gravida* Cl.	
" *hyalina* (Grun.) Gran*	*Coscinodiscus hyalinus*
" *hyperborea* (Grun.) Hasle and Lange*	" *lacustris* var. *hyperboreus*
" *kushirensis* Takano	
" *nordenskioeldii* Cl.	
" *poroseriata* (Ramsfj.) Hasle	*Coscinosira poroseriata*
Thalassiothrix longissima Cl. and Grun.	*Synedra thalassiotrix* Cl.

* species known to have their main distribution in the Arctic
** species known to have their main distribution in the Arctic and the Baltic and/or other brackish waters.
*** soon to be transferred to *Gonioceros*

The investigations reported so far were based on material collected by fairly coarse nets, whereas water samples used in more recent studies of Arctic planktonic diatoms were concentrated by centrifugation or sedimentation. This change in methodology improved the reliability of the estimation of the size of the diatom populations and, more important in this context, gave a more reliable picture of the relative abundances of the various species. Small *Chaetoceros* species, mainly *C. socialis* and *C. furcellatus*, *Fragilaria nana* (= *Nitzschia pseudonana* + small specimens of *N. cylindrus*, see Hasle, 1965b, p. 22), *Nitzschia delicatissima*, *Leptocylindrus danicus*, *Thalassiosira antarctica/gravida*, and *T. bioculata* were emphasized as the predominant diatoms in North Norwegian fjords in the spring (Gaarder, 1938), along the coast of Jan Mayen Island in April (Smayda, 1958), off Bear Island (Ramsfjell, 1960), in waters northwest of Spitsbergen in September-October (Heimdal, 1983) and in the Beaufort Sea in July-September (Horner, 1984).

Table 8.2. Diatoms "floating on the surface of the sea" – Davis Strait and North Atlantic – Cleve (1873).

Centric species	*Pennate species*
Biddulphia aurita	*Fragilaria oceanica*
Chaetoceros atlanticus	*Synedra thalassiotrix*
" *decipiens*	
Coscinodiscus centralis	
" *oculus-iridis*	
Rhizosolenia alata	
" *styliformis*	
Thalassiosira nordenskioeldii	

Table 8.3. Barents Sea (74°58′N, 27°46′E) 16 April 1986 – dominating species in a net-haul collected during a bloom in the ice-edge zone – relative abundance indicated by +++, ++, +.

Centric species	*Pennate species*
Bacterosira fragilis +++	*Nitzschia cylindrus* +++
Thalassiosira hyalina +++	" *grunowii* ++
Porosira glacialis ++	*Navicula vanhoeffenii*
Thalassiosira bulbosa +	" *pelagica*
" *antarctica*	" sp.
" *bioculata*	*Pleurosigma* sp.

Table 8.4. Dominant diatom species in samples from Barents Sea, May-June and August 1984

Arctic water		
St. no.	676	732
Lat. N.	76°48′	76°20′
Long. E.	33°08′	44°00′
t°C	−0.555	−1.219
S	34.345	
Date	04.06	10.06
Net mesh	20 μm	10 μm
Diatoms:	*Nitzschia cylindrus* +++ *Navicula vanhoeffenii* ++ *Thalassiosira bulbosa* " *hyalina* *Nitzschia grunowii*	*Chaetoceros socialis* +++ *Nitzschia cylindrus* ++ " *grunowii*+ *Thalassiosira bulbosa* + " *antarctica* +
Polar front water		
St. no.	628	648
Lat. N.	75°15′	74°30′
Long. E.	18°00′	23°32′
t°C	1.4	1.969
S	34.790	34.641
Date	31.05	01.06
Net mesh	30 μm	30 μm
Diatoms:	*Chaetoceros socialis* +++ *Thalassiosira anguste-lineata*	*Coscinodiscus* spp. *Chaetoceros* spp.
Atlantic water		
St. no.	704	836
Lat. N.	74°30′	75°45′
Long. E.	22°44′	32°23′
t°C	4.375	6.733
S	35.018	34.984
Date	01.06	12.08
Net mesh	20 μm	35 μm
Diatoms:	*Actinocyclus* sp. +++ *Thalassiosira anguste-lineata* + *Nitzschia seriata* " *cylindrus* " *grunowii* *Thalassiosira hyalina* *Thalassiothrix longissima* *Coscinodiscus* spp.	*Thalassiothrix longissima* *Chaetoceros* spp.

VARIATION WITH DISTANCE FROM THE ICE-EDGE, WATER MASSES AND TIME

The examination of a net haul collected in the Barents Sea in mid-April close to the ice-edge showed a predominance of the centric diatoms *Thalassiosira hyalina* and *Bacterosira fragilis* and the pennate *Nitzschia cylindrus*, with the centric *Porosira glacialis* and the pennate *N. grunowii* in slightly smaller abundances. Other diatoms characteristic of this habitat were present in still smaller abundances (Table 8.3). Whereas *Thalassiosira* spp. and related species characterize Arctic waters close to the ice-edge early in the season, *Nitzschia cylindrus* may be the predominant diatom species somewhat later in the season (May-June) to be succeeded one week later in the same area by *Chaetoceros socialis* (with resting spores) (Table 8.4). One station located in Atlantic water in early June the same year was dominated by *Actinocyclus* spp. and *Thalassiosira anguste-lineata*. Two stations located in Polar Front Water seemed to occupy an intermediate position, one being dominated by *C. socialis* resting spores and *T. anguste-lineata* in small concentrations, and the second one having *Coscinodiscus* spp. and one or two larger *Chaetoceros* species as the only diatoms seen.

Previously Cleve (1873) commented on the variation in species composition with time and geographical area. *Thalassiosira nordenskioeldii* and *Chaetoceros decipiens* were found in the Davis Strait and between Europe and Greenland in June, and *Rhizosolenia styliformis* in the Atlantic. In August in the Davis Strait the net hauls contained mainly *Thalassiothrix longissima*. Gran (1897) found the plankton of the Karajakfjord, West Greenland to be poor in diatoms in October-April and those present in May to be mainly the same as those on the ice in April. Pennate diatoms in ribbon-shaped colonies (*F. oceanica*, *F. cylindrus*, *Achnanthes taeniata*, *N. vanhoeffenii*) were predominant and *Melosira hyperborea*, *T. nordenskioeldii* and *T. hyalina* less abundant. In July-August the plankton consisted mainly of *T. nordenskioeldii* and in September of *C. furcellatus*. The plankton of Baffin Bay and the northern Davis Strait showed much the same trend (Cleve, 1896) but with the north Atlantic forms *C. atlanticus* and *Thalassiothrix longissima* present in October. The latter is consistent with our observations in Atlantic water in the Barents Sea in August 1984 (Table 8.4).

A one-year study of the plankton in Ullsfjord, North Norway (69-71°N) showed a shift in the diatom species from *C. furcellatus*, *C. socialis*, *F. oceanica/cylindrus*, *B. fragilis* and *T. hyalina* in March-May to *C. compressus*, *C. debilis*, *Leptocylindrus danicus*, *Nitzschia "delicatissima"*, *Skeletonema costatum* and *T. nordenskioeldii* in July-August (Heimdal, 1974).

BIOGEOGRAPHY

Only eight of the 40 diatom species recorded by Cleve (1896) were mentioned as characteristic of polar sea plankton, viz. *Chaetoceros mitra*, *Coscinodiscus hyalinus*, *Fragilaria cylindrus*, *F. oceanica*, *Melosira* (*nummuloides* var.) *hyperborea*, *Nitzschia frigida*, *N. laevissima* and *Pleurosigma stuxbergii*, whereas 15 were recorded at that time from areas outside the Arctic. Some of the species with a wider distribution were recorded in great abundances in the Davis Strait and Baffin Bay, e.g. *Chaetoceros atlanticus* and *Thalassiosira nordenskioeldii*.

Motoda and Minoda (1974) listed the planktonic diatom species recorded in the Bering Sea. The list includes most of the diatoms mentioned in this chapter and in addition many more which most likely have a wider and more southerly distribution. The records of *Thalassiosira baltica* and *Denticula seminae* are noteworthy, the former being recorded under the name *Coscinodiscus polyacanthus* from sediments and ice in other Arctic areas (Østrup, 1895) and in the plankton of the Baltic Sea, and *D. seminae* being mainly restricted to the Pacific Ocean.

The eight species emphasized as the predominant diatoms in the investigations from 1930 to the 1980's in Arctic fjords and seas also exhibit a heterogeneous distribution pattern. *Chaetoceros socialis*, *Leptocylindrus danicus* and *Nitzschia pseudonana* are most probably cosmopolitan. *Chaetoceros furcellatus* and *Thalassiosira bioculata* are restricted to the Arctic. *Nitzschia cylindrus* is present in the plankton and the ice in the Arctic and the Antarctic. *Thalassiosira antarctica* var. *borealis* is distributed at least as far south as the Oslofjord whereas the biogeography of *Nitzschia delicatissima*, as recorded in the investigations referred to above, is questionable.

SUMMARY

Recently published and unpublished observations of Arctic diatoms are more or less consistent with the results of the pioneer investigations. The characteristic diatoms of the Arctic water masses are, as recorded by Cleve (1873, 1884, 1896) and Gran (1897): *T. hyalina*, *Nitzschia cylindrus*, *N. grunowii*, *N. frigida*, *Navicula vanhoeffenii*, *N. pelagica*, *Bacterosira fragilis* and *Pleurosigma* sp. Recent investigations have shown that other species are also characteristic of Arctic waters, e.g. *Thalassiosira antarctica* var. *borealis*, *T. bulbosa* and *Nitzschia seriata* f. *obtusa*.

CHAPTER 9

THE PALEONTOLOGICAL SIGNIFICANCE OF FOSSIL DIATOMS FROM THE HIGH-LATITUDE OCEANS*

Rainer Gersonde

*Alfred-Wegener-Institute contribution No. 154

Depositional patterns of Cenozoic diatomaceous sediments in the high-latitude oceans have been affected by major changes in oceanographic circulation related to plate tectonic movements (e.g. opening of deep water pathways) and global climatic changes (e.g. onset of glacial regimes). The stepwise cooling in the polar regions was enhanced during the Neogene, and this resulted in progressively greater thermal differentiation between the high- and low-latitude ocean areas, leading to the establishment of biogeographic diatom provinces characterised by endemic floras. During the Neogene, in particular, the areas of the Southern Ocean and the Subarctic Pacific became major sinks for diatomaceous silica. Consequently in these areas Neogene diatoms are prominent microfossils useful for biostratigraphic age assignments and reconstructions of past oceanographic and climatic conditions.

INTRODUCTION

Areas of high latitude oceans are the most important sinks for biogenic silica accumulation. In contrast to the equatorial regions of the Pacific Ocean where a large portion of the accumulated biogenic silica consists of radiolarian skeletons, the biosiliceous components in the sediments of the northern and southern high latitude oceans are dominated by diatom cell walls.

Southern Ocean

More than 75% of all oceanic silica accumulates in a 900-2000 km broad circum-Antarctic siliceous sediment belt (Lisitzin, 1971), where biogenic silica can contribute up to 70% of the total sediment (DeMaster, 1979). As in the past, the present-day geographic distribution of this siliceous belt is linked strongly to the cold water oceanographic conditions of the circum-Antarctic Ocean. The northern boundary of the belt coincides with the Polar Frontal Zone, while the southern boundary is related to the northern extent of the average spring sea-ice distribution (Burckle and others, 1982; Burckle and Cirilli, 1987).

The opening of the Drake Passage (between South America and the Antarctic Peninsula) during the Oligocene allowed the establishment of the deep circum-Antarctic circulation system somewhere near the Neogene/Paleogene boundary, approximately 24 Ma[1] ago (Barker and Burrell, 1977) and lead to a stepwise thermal isolation of Antarctica. In relation to the establishment of the circum-Antarctic circulation system, siliceous biogenic productivity increased considerably during the Neogene and Quaternary (Brewster, 1980). During this time the siliceous biogenic belt expanded northward, which was interpreted to reflect the migration of the Polar Frontal Zone (Tucholke and others, 1976). Investigations of deep sea drilling and gravity cores recently recovered from the Weddell Sea (Barker and others, 1988a,b; Gersonde, unpublished) show a stepwise increase of biosiliceous components in the Miocene, related to the progressive cooling of Antarctica. In the Weddell Sea area the biosiliceous accumulation rate was high during the early and early late Pliocene (ca 4.5 - 3 Ma), then decreased considerably during the time period from about 2 to 0.6 Ma and increased again during the last 0.6 Ma (Abelmann and others, 1990).

In contrast to the Neogene, Paleogene sediments rich in biosiliceous components have been recovered infrequently in the southern high-latitudes ocean. The Deep Sea Drilling Project (DSDP), the Ocean Drilling Program (ODP) and the MSSTS-drill hole (McMurdo Sound) recovered a number of diatom-bearing Oligocene to uppermost Eocene sediment sequences in the circum-Antarctic Ocean, and a peak in diatom preservation occurs near the late Eocene/early Oligocene transition. Only a few middle and lower Eocene and Paleogene diatomaceous deposits are known. This pattern may be linked to the global cooling event at the Eocene/Oligocene boundary ("terminal Eocene event": Wolfe, 1978). Kennett and Shackleton (1976) consider this event to represent the onset of large-scale freezing conditions and first significant formation of sea ice on the ocean around the Antarctic continent. Miller and others (1987), on the basis of oxygen isotope data, conclude that continental ice sheets existed on the Antarctic continent since about the Eocene/Oligocene boundary (about 36 Ma).

Although in the Southern Ocean the occurrence and distribution of diatomaceous sediments shows a close link to cold climate and cold surface water conditions during the Cenozoic, well preserved diatom assemblages are also known from the Cretaceous, a time interval characterized by a generally warm and equable climate. Diatomaceous sediments were encountered from the upper Cretaceous in the southern Pacific Ocean (Hajos, 1974) and Seymour Island (Antarctic Peninsula, Harwood, 1988), and the upper lower Cretaceous in the

---

[1] Ma (meganannum) refers to units of years x 10^6 measured back from the present (A.D.) 1950 by international agreement). It is a fixed chronology analogous to the calendars tied to historical events. The abbreviation m.y. (million years) is used to express simple duration in units of yr × 10^6 in any given past interval.

Weddell Sea (Gersonde and Harwood, 1990; Harwood and Gersonde, 1990). The upper lower Cretaceous (Albian/Aptian) deposit represents the best preserved diatom assemblages of all known occurrences of this age and provides a new insight into an early state of diatom evolution.

High latitude North Pacific and North Atlantic

In the high latitudes of the Northern Hemisphere significant deposition of biosiliceous sediments occurs in the North Pacific, the Bering Sea, and the Sea of Okhotsk (McCoy and Sancetta, 1985). In the latter two seas biogenic opal content makes up to 55% of the total surface sediment, as reported by Jousé and others (1971). Continuous substantial diatom accumulation since the middle Miocene was recovered during Leg 19 from the Bering Sea and the extreme North Pacific (Koizumi, 1973). In contrast, the North Atlantic (North European Sea) topmost Holocene sediments bear diatom assemblages which in general are not well preserved. A time transgressive-sediment layer rich in diatoms occurs within a time interval ranging from 4,500 and 11,000 y BP[2] and is related to the Subarctic Convergence and its northward transition (Stabel, 1986). Indeed, deep-sea drilling results (DSDP Leg 38 and ODP Leg 104) show that in general most of the Pleistocene sediments of the European North Sea are devoid in biosiliceous components. Diatoms may occur within Pliocene sequences, but are more important only within Miocene sediments (Schrader and others, 1976, Eldholm and others, 1987). An expanded 1150 m thick Neogene section drilled in Baffin Bay (OPD Leg 105, Site 645) recovered only rare horizons bearing diatoms dated to be Plio-Pleistocene in age (Srivastava and others, 1987).

The differences in modern biogenic silica accumulation between the North Pacific and the North Atlantic Ocean can be explained by differences in water mass circulation. According to Berger (1970, 1974) the waters of the modern Pacific Ocean are enriched in silica by a factor of four in comparison to the North Atlantic. This pattern is explained by a circulation model with a North Pacific marked by an "estuarine" circulation system where shallow water is exchanged for deep water rich in nutrients, enhancing biosiliceous productivity and preservation of biosiliceous components in the sediment record. The North Atlantic Ocean on the other hand is characterized by an "anti-estuarine" type of circulation, where deep water (North Atlantic Deep Water, NADW) flows outward and is exchanged with shallow water poor in nutrients flowing into the system, and thus is a circulation type which becomes depleted in nutrients. Consequently the presence or absence of NADW formation could influence the sedimentation and preservation pattern of biosiliceous components in the North Atlantic during the geological past. However, Eldholm and others (1987) interpret the disappearance of biogenic opal during the Pleistocene in the European North Sea simply as a drop in surface-water productivity related to a stepwise establishment of glacial environmental conditions, although they state that calcareous microfossils are deposited.

Paleogene sediments drilled during DSDP Leg 19 in the Subarctic Pacific (Sites 183 and 192) did not possess biosiliceous components (Koizumi, 1973). However, the deposition of Paleogene diatoms in this area is documented by findings from dredge samples recovered in the Bering Sea Navarine Basin (Baldauf and Barron, 1987) and from land sections on the Komandorsky Islands (Gladenkov, 1988). Oligocene and Eocene diatomaceous sequences were drilled during DSDP Leg 38 in the European North Sea (Schrader and others, 1976), while ODP Leg 104 did not retrieve biosiliceous sediments from the Paleogene of the Voering Plateau region (Eldholm and others, 1987).

Arctic Ocean

The history of biogenic silica deposition in the Arctic Ocean is documented only in a few sediment cores. One core (Cesar 6) from the flank of the Alpha Ridge contains a 165 cm thick section with well preserved diatom assemblages dated as late Cretaceous (late Campanian) by Barron (1985b). Cores containing biosiliceous components from two other sites situated on the Alpha Ridge were described by Kitchell and Clark (1982) and dated late Cretaceous (Campanian-Maastrichtian) and Paleogene (probably Early Paleocene) in age. Based on this recovery Kitchell and Clark (1982) suggested open-ocean polar upwelling in the Late Cretaceous-Paleogene Arctic Ocean and proposed three phases in the post-mid Cretaceous history of silica deposition in the Arctic Ocean. Further knowledge on Pleistocene opal deposition may be provided by the investigation of piston cores recovered during RV *Polarstern* cruise ARK IV/3 (Thiede, 1988) from the Barents Shelf and the Nansen Basin (Abelmann 1988, pers. comm.). As with other oceanic regions only deep-sea drilling can provide a broader knowledge on past sedimentation processes in the Arctic Basin, which was probably an important silica sink during the late Cretaceous and Paleogene time period. Indeed much financial and technological input is needed to access the Arctic Ocean because of its permanent sea ice cover.

BIOSTRATIGRAPHY

Diatom biostratigraphy is based on the ranges, thus on the presence or absence, of stratigraphic marker species during geological time. The stratigraphic occurrence of marker species has been used for the definition of biostratigraphic zones, which in most cases are named after a prominent diatom species which occurs within the zone. Recently the zonal concept has been substituted or supplemented by the use of datum levels defined as First Appearance Datum (FAD) and Last Appearance Datum (LAD) for diatom species. Some authors also use First or Last Abundant Appearance Datum (FAAD, LAAD): datum levels which may depend strongly on environmental change. However, the latter datum levels may lead to confusion because most of the authors using FAAD or LAAD do not define the term "abundant".

Much effort is devoted to the calibration of the biostratigraphic zones and datum levels to the paleomagnetic time scale, a worldwide synchronous stratigraphy based on the reversals in polarity of the earth's magnetic field. Such a correlation is especially important to tie the zonations and datum levels to an absolute time scale, and for the intercalibration of the different biostratigraphic zonations established for the northern and southern high-latitudes, and the low-latitude regions.

Southern Ocean

For the Southern High Latitude Ocean planktonic marine diatom zonations were first defined by Jousé and others (1963). In *Ob* Core 256 retrieved from the Indian sector of the Antarctic Ocean four diatom assemblage zones were described spanning the Pleistocene and the late Pliocene. Donahue (1970a) established in her Ph.D. thesis (cited by many authors but never published) a diatom zonation using piston cores from the western Bellingshausen Sea (Pacific sector). The four diatom zones of Pleistocene and late Pliocene age were also correlated to the paleomagnetic time scale. Similiar work was undertaken by Abbott (1974) on cores from the Indian and Pacific sector restricted to the latest Quaternary (last 1 Ma), and further biostratigraphic work on Quaternary sediment cores from the Bellingshausen Sea was carried out by Akiba (1982).

Stratigraphic refinement of the latest Quaternary was developed by Burckle and Cooke (1983) based on the abundance pattern of the diatom species *Eucampia balaustium* (= *E. antarctica*). This stratigraphy was related to the ice-rafting record, and by second order correlation, to the oxygen isotope record. However, Burckle and Abrams (1986) record that the abundance pattern of *E. balaustium* appears to be diachronous[3] across the Polar Front. Burckle and Burak (1988) show that relative abundance variations of *E. balaustium* and *Hemidiscus karstenii* determined in late Quaternary deep-sea cores from the subantarctic region of the Indian sector of the Southern Ocean are close proxies for the oxygen isotope record. Abundance curves of a "glacial" and a "interglacial" species group covering the last 700,000 years are reported by Gersonde and Treppke (in press) in a study from an area situated south of the Polar Front. The species groups are dominated by *E. balaustium* and *Nitzschia kerguelensis* respectively, and the abundance curve for the latter species group shows a close resemblance to the pattern of the oxygen isotope curve.

McCollum (1975) described the first detailed diatom biostratigraphic zonation for the Oligocene to the Pleistocene based on material gathered during Deep Sea Drilling Project (DSDP) Leg 28 in the Ross Sea area (Pacific sector). Thirteen zones were established, of which eight were redefined for the Pleistocene and the Pliocene time interval (last 5 Ma) and these were correlated with the paleomagnetic time scale based on additional piston core studies. However, the origin of the paleomagnetic data used was not identified. Schrader (1976) re-examined part of McCollum's material. He revised the Miocene and Oligocene zonation of McCollum (1975) based on a comprehensive study of DSDP Site 278 (Pacific sector) because he found significant differences in the ranges of key species.

Later, Weaver and Gombos (1981) summarized the developments of southern high-latitude diatom biostratigraphy and proposed a regionally applicable Neogene (last 24 Ma) diatom zonation using species easily recognized with a broad geographic distribution. Based on a revised and comparative study of the DSDP Sites 278 and 266 (Indian sector) and on a number of piston cores from the Pacific and Indian sector, Weaver and Gombos defined sixteen zones. The five youngest zones spanning the last 2.7 m.y. were taken from McCollum (1975), the six zones defined by McCollum (1975) or Schrader (1976) were redefined, and five new zones were established. All together the zonation contains thirty diatom datum levels. It allows a time resolution of approximately 0.5 m. yr within the time interval of the last 4 Ma, and of 0.5 to 4 m. y. within the time interval from 4 Ma to 23 Ma. The youngest stratigraphic datum is at about 195,000 y. BP (uppermost part of oxygen-isotope stage 7), defined by the LAAD of *Hemidiscus karstenii* (Burckle and others 1978). Weaver and Gombos (1981) correlated the late late Miocene to Pleistocene diatom zones (last 8 Ma) with the paleomagnetic time scale, but again the original paleomagnetic data taken from piston core studies were not shown.

Ciesielski (1983) revised the zonation of Weaver and Gombos (1981) on the basis of DSDP cores from the Southwest (Subantarctic) Atlantic and described five additional Neogene zones. The late middle Miocene to Pleistocene zones were correlated to the paleomagnetic time scale. Indeed reliable paleomagnetic data exist only for the Pliocene and Pleistocene (Salloway, 1983), while the correlation to the Miocene zones is weak because of the questionable paleomagnetic data interpretation of Ledbetter (1983).

Critical and still unresolved points of the Neogene diatom zonation established by Weaver and Gombos (1981) and Ciesielski (1983) are:

1) Age discrepancies of Pliocene and Pleistocene zonal boundaries between the zonations established by the different authors (compare Ciesielski, 1983, Fig. 5). It cannot be determined if these discrepancies are caused by diachronous occurrence of species, misidentifications, sample spacing, unrecognized unconformities or weak paleomagnetic data and interpretation.
2) Some biostratigraphic marker species show definite north-south diachronous occurrence, whereas others are regionally absent (Burckle and Abrams 1986).
3) The Miocene zones are not tied to the paleomagnetic time scale.
4) Most of the diatom zones are defined by the LAD of species, a definition which causes problems because reworking of older species into younger sediments by bottom water activity is common in the Southern Ocean basins.
5) Some zones are defined by the LAAD of species - a definition which is, however, not supported by quantitative measurements.
6) Several species used as biostratigraphic marker species are poorly described or documented, which leads to misidentifications and consequently wrong age assignments.
7) Some Miocene zones range up to 4 m.y. in duration and should be refined.

Recent deep-sea drilling in the Atlantic and Indian sector of the Southern Ocean (Ocean Drilling Program

---

[2] BP: before present, to define dates within the Late Pleistocene.

[3] diachronous: species ranges of varying age in different areas. Contrary of synchronous.

Legs 113, 114, 119 and 120) recovered a number of well-preserved, continuous Neogene sections rich in diatoms. The excellent sections recovered by ODP Leg 113 Sites 689 and 690 (Maud Rise, southeast Weddell Sea, Antarctic Ocean) were chosen by Gersonde and Burckle (1990) for the establishment of a revised Neogene Antarctic diatom zonation. Altogether sixteen diatom zones and a number of additional stratigraphic useful diatom datums, which cover a time interval between the late early Miocene and the Pleistocene, are described. Six zones established by previous authors are in part modified or renamed, and ten new zones are proposed. The zones are calibrated directly to the paleomagnetic time scale, which allows an absolute zonal age determination and thus permits comparison of Neogene Antarctic diatom events with events described from the low- and northern high-latitudes. The zonal boundaries of this stratigraphy are mostly defined by the FAD of diatom species. These studies show that the lower Miocene and the middle to lower upper Miocene diatom zonation of the southern high-latitude diatom biostratigraphy resembles in part that of the tropical Pacific and the middle- to high-latitude North Pacific, respectively. The diatom stratigraphy of Gersonde and Burckle (1990) is directly calibrated with revised radiolarian and silicoflagellate zonations for the southern high-latitudes (Gersonde and others, 1990). Additional taxonomic studies on Neogene stratigraphic marker species are carried out by Gersonde (1990a, b). Based on the materials recovered during ODP Legs 119 and 120 in the area of the Kerguelen Plateau and Prydz Bay (Indian sector) Baldauf and Barron (1991), and Harwood and Maruyama (1991), respectively, propose further improvements for the Southern Ocean Neogene diatom zonation. In these two papers, 21 and 28 Neogene diatom zones and more than 100 additional datum levels calibrated with the paleomagnetic time scale are described. Large efforts are also done for the description and documentation of new stratigraphic useful. By these recent efforts a Neogene southern high-latitude diatom stratigraphy is now accomplished having a standard, which prior existed only for the tropical and the middle- to high-latitude North Pacific (compare Koizumi and Burckle, 1984 and Barron, 1985a).

The knowledge on Paleogene diatom assemblages from the Southern Ocean is more restricted to the late Eocene and Oligocene time interval (40 - 24 Ma). Hajos (1976) decribed stratigraphic ranges of late Eocene and early Oligocene diatoms from cores drilled south of Tasmania. Similiar work was undertaken by Gombos (1976) on material from the Falkland Plateau (Southwest Atlantic). A detailed diatom zonation for the Paleogene sequences was established by Gombos and Ciesielski (1983) based on DSDP Sites 511 and 513A (Southwest Atlantic). Fenner (1984) revised this zonation because she found different ranges of some marker species than those described by Gombos and Ciesielski (1983). Fenner (1984) defined five diatom zones for a time interval covering the late Eocene and Oligocene. First Appearance Datums (FAD) were used for the definition of most zonal boundaries to avoid problems related to reworking. Middle Eocene and late Paleocene diatoms from DSDP Sites in the South Atlantic were described by Gombos (1976, 1983, 1984). Further progress in the refinement of Paleogene diatom zonations for the Southern Ocean was also possible based on the investigation of deep sea cores drilled during the recent ODP Legs in the Southern Ocean. Baldauf & Barron (1991), and Harwood and Maruyama (1991) propose zonations for the Oligocene that are calibrated with the paleomagnetic time scale. A revised Paleocene diatom stratigraphy is prepared by Fenner based on ODP Leg 114 and DSDP materials. For late Cretaceous sediments from the Southwest Pacific Ocean a diatom zonation including nine zones and twelve subzones was established by Hajos (1974).

High latitude North Pacific and North Atlantic

For the Northern High-Latitude Oceans different Cenozoic diatom zonations have been established for the Subarctic region of the Pacific and for the North Atlantic European North Sea (Norwegian and Greenland Sea). Schrader and Fenner (1976) established the first diatom zonation for the European North Sea, including twenty-eight zones based on DSDP cores. Twenty-one of these zones fall within the Neogene and Quaternary (last 24 Ma), and seven occur within the Oligocene and late Eocene. Based on the same DSDP cores Dzinoridze and others (1978) propose another Cenozoic diatom zonation. The same marker species are used for the Eocene in both papers, whereas different biostratigraphic species were chosen for the Oligocene, Neogene and Quaternary. A correlation of the Neogene and Paleogene zonations established by Schrader and Fenner (1976), and Dzinoritze and others (1978) to zonations established for the low latitudes was compiled by Baldauf (1984) and for the Southern Ocean by Fenner (1985). Similiarly Barron (1985a) correlated the Neogene European North Sea zonation of Schrader and Fenner (1976) to other Neogene zonations. The European North Sea zonation is not yet directly tied to the paleomagnetic time scale, but further progress in achieving this goal can be expected in the near future based on deep-sea cores from ODP Leg 104 in this area (Eldholm and others 1987).

Koizumi and Burckle (1984) summarized the biostratigraphic results for the Neogene Subarctic Pacific Ocean. Ten first-order and five second-order datum planes were defined for the time interval ranging the last 6.5 Ma, based on the results of Donahue (1970b), Koizumi (1973, 1975), Burckle and Opdyke (1977), and Ujiie and others (1977). While these datum planes are tied to the paleomagnetic stratigraphy, no calibrated datum planes exist for the time interval prior to 6.5 Ma from sediment sequences originating the Subarctic Pacific Ocean. Barron (1985a) proposed a Neogene middle- to high-latitude North Pacific diatom zonation based on the results of Koizumi (1973) and Barron (1980) from sediment cores recovered during DSDP Legs 19 and 57 in the Subarctic Pacific and off Japan. This stratigraphy comprises seven Miocene, and five Pliocene and Quaternary zones. Barron (1985a) also states that the stratigraphy established by Schrader and Fenner (1976) for Lower Miocene sequences of the Norwegian Sea may be applicable to the North Pacific. A refined diatom stratigraphy for the late Pleistocene Subarctic Pacific (last 0.7 Ma) was established by Sancetta and Silvestri (1984) using a maximum of *Actinocyclus ochotensis*, and abundance fluctuations of *Rhizosolenia hebetata* and *Denticulopsis seminae*. The latter species abundance fluctuations were found to be roughly in phase with the global isotope record during the time period spanning the last 450000 years.

PALEOOCEANOGRAPHY

Diatom paleoecological studies for the reconstruction of paleooceanographic and climatic conditions are based on the abundance and the species distribution of diatoms recorded in the sediments. Because depositional patterns of diatomaceous sediments are related to areas with high surface water productivity (Lisitzin, 1971), the occurrence and abundance patterns of fossil diatoms can be used as a proxy for productivity in the geological past. However it should be remembered that in general only 1-5% of the diatom frustules produced in the surface water euphotic zone are preserved in the sedimentary record (Calvert, 1974). The quantitative analysis of diatom associations on the species level is used for the reconstruction of changes in surface water temperature, surface salinity, productivity and sea-ice coverage. Such reconstruction can only be successful when the autecology of the investigated species is known and modern analogues can be used for comparison. Publications which provide information on geographical species distribution and autecology of marine planktonic diatoms from the circum-Antarctic Ocean were published by Hart (1942), Kozlova (1964), Hasle (1969, 1976), Fenner and others (1976) and Burckle and others (1987). Quantitative studies on diatoms related to Antarctic sea ice were accomplished by Clarke and others (1984) and Gersonde (1986a). A comprehensive overview of the study of sea ice microalgae is given by Horner (1985).

Statistical methods, such as the factor analysis-transfer function technique established by Imbrie and Kipp (1971), have been used successfully for the reconstruction of, especially, Pleistocene environments. This technique uses data from surface-sediment assemblages and an atlas of oceanic parameters as a predictive data base for the estimation of individual paleoenvironmental parameters. The evidence of this statistical approach for the reconstruction of environmental conditions using diatom assemblages is supported by a broad study of surface-sediment diatom assemblages recovered from the Pacific Ocean. Kozlova and Muchina (1967) demonstrate that the distribution of species in the surface sediment closely reflects their distribution in the plankton, with the exception of weakly silicified forms which are dissolved before incorporation in the sediment. A very close spatial-geographical correspondence is proved for the Subantarctic and the Subarctic region.

Southern Ocean

Early paleooceanographic studies on sediments from the circum-Antarctic Ocean concentrate on the description and delineation of diatom assemblages preserved in the surface sediments and on rough estimations of paleoenvironmental changes within the Quaternary time period. Jousé and others (1962) were the first to stress the importance of fossil diatoms for paleooceanographic studies in the Southern Ocean area. Based on 162 sediment surface samples recovered from the Indian sector of the Southern Ocean Jousé and coworkers delineated the distribution of diatom species and defined one Subantarctic and one Antarctic diatom assemblage geographically separated by the Polar Frontal Zone. The diatom assemblages recorded in the surface sediment have been compared to those produced in the euphotic zone. The latter were studied in detail by Kozlova (1962), and problems related to the bias in the composition of surface sediment diatom assemblages by dissolution are discussed. In a subsequent and more comprehensive paper Kozlova (1964) extended the study of Jousé and others (1962), covering an area which includes the eastern Atlantic, the Indian and most of the Pacific sector of the Southern Ocean, and thus compiled a valuable base of later paleoenvironmental studies based on diatoms. The data from the Pacific sector were taken from an unpublished study by Koroleva and Nagaeva. Abbott (1974) also investigated surface sediments from the Indian sector of the Southern Ocean. He described one Subantarctic, one Subtropical and, tentatively, one Antarctic diatom assemblage. He discussed the effects of Antarctic Bottom Water on the geographical distribution of diatom assemblages in surface sediments. In a downcore study Burckle (1972) used a ratio of holoplanktonic to meroplanktonic diatoms for the reconstruction of Holocene paleoclimates on a sediment core from the Scotia Sea (Atlantic sector of Southern Ocean). The ecology and paleoecology of the diatom, *Eucampia balaustium*, was discussed by Burckle (1984b). Based on the distribution pattern of *E. balaustium* in surface water and in the sediment record it is concluded that although this species is widely distributed in the Southern Ocean, it is most abundant in neritic environments. A "pseudoneritic" environment, provided by floating ice, may also provide a substrate for proliferation of this species.

Some of the early users of the factor-analysis method were Truesdale and Kellogg (1979). Four diatom assemblages were defined quantitatively from surface sediments of the Ross Sea area and were related to oceanographic and environmental parameters as a base for downcore paleoenvironmental studies. The conclusions of this paper were contested by Fillon (1979), with a reply by Kellogg and Truesdale (1979). A rather descriptive compilation of the microfossil distribution in modern Amundsen Sea sediments, also including diatoms, is given by Kellogg and Kellogg (1987). Leventer and Dunbar (1988) discuss the response of the paleooceanographic conditions in McMurdo Sound (Ross Sea) to the historical "Little Ice Age[4]", based on quantitative diatom studies. They conclude that coastal polynya formation was more persistent during the "Little Ice Age" and suggest that within the southwestern Ross Sea, the production of high salinity shelf water, and hence Antarctic Bottom Water, may have been greater at this time.

A quantitative study comparable to that of Truesdale and Kellogg was accomplished by Defelice and Wise (1981) on surface sediments from two North-South core transects situated between South Africa and the Antarctic Continent in the Atlantic sector of the Southern Ocean (*Islas Orcadas* Cruises 11 and 12). Five assem-

[4] "Little Ice Age": cooling period between ca. 1600 and 1875 A.D.

blages were defined by factor analysis, reflecting different environmental conditions such as: a high diversity assemblage associated with the nutrient-rich, cold waters south of the Polar Front; an assemblage found north of the Polar Front reflecting warmer Subantarctic surface water; and a low diversity environmentally stressed assemblage, reflecting unstable conditions along the Polar Front, the northern boundary of winter sea-ice and the Antarctic slope. Defelice and Wise (1981) discussed the problems related to the widespread dominance of *Nitzschia kerguelensis* when using the factor analysis technique and concluded that this species is probably r-selected. Downcore studies of Defelice and Wise (1981), which were based on the occurrence of silicoflagellates are restricted to the last 300000 years and were interpreted to reflect migrations of the Polar Front and fluctuations in surface water temperature. Pichon and others (1987) completed a factor-analysis-based surface sediment study on the entire Atlantic and the western Indian sector of the Southern Ocean, using diatom assemblages from 28 core tops. However the data base for the areas south of 60°S is rather weak. Before statistical treatment the original data matrix was modified: the relative abundance numbers were replaced by four ranked abundance classes defined arbitrarily for each species. This was done to avoid problems related to the widespread dominance of *Nitzschia kerguelensis* and *Thalassiosira lentiginosa* and to increase the weighting of less abundant species. One of the three resulting diatom assemblages was associated with Subantarctic and the other two with Antarctic waters. These areas are delineated by distinct oceanographic features: the Polar Front and the northern boundary of the summer sea-ice distribution. Based on the comparison between the distribution of the three assemblages with surface water oceanographic parameters a set of transfer functions was derived, that was successfully used for the reconstruction of summer surface water temperatures during the last 20,000 years in the Southern Ocean (Labracherie and others, 1989; Bard and others, 1990).

Burckle (1984a) made the first attempt for the reconstruction of the oceanographic conditions during the last glacial maximum (18,000 y. BP) in the Southern Ocean based on a quantitative diatom assemblage analysis and preservational data. Using the factor analysis-transfer function technique Burckle concluded that during the last glacial maximum the late spring/early summer sea ice cover was shifted slightly northwards; the Southern Ocean was ice-free during many summers; the gyre systems were intensified, and a Weddell Sea Polynya probably existed.

However, with regard to the establishment of paleo-oceanographic transfer functions derived from factor analysis of species abundances, Shemesh and others (1989) state that the effects of differential dissolution of diatom species on thanatocoenoses[5] have been widely ignored. They conclude that for this reason, such transfer functions must be interpreted with caution. Shemesh and others (1989) found, that increasing dissolution causes relative depletion in *Nitzschia kerguelensis*, enrichment in *Thalassiosira lentiginosa* and slight enrichment in *Eucampia antarctica* (= *E. balaustium*), reflecting relative susceptibility to dissolution of the three species that dominate Antarctic sediments.

Antarctic diatoms have also been used for the delineation of pathways of Antarctic Bottom Water (AABW), for the mapping of disconformities in the sedimentary record related to paleooceanographic events, and for the reconstruction of fluctuations in Antarctic continental ice volume. Burckle and Stanton (1975), Booth and Burckle (1976), Burckle (1981) and Jones and Johnson (1984) used displaced Antarctic diatoms recovered from sediments in the South Atlantic and the Western Pacific as tracers for the pathways of Antarctic Bottom Water both today and in the geological past. Jones and Johnson (1984) reconstructed late Pleistocene/Holocene fluctuations in AABW in the Vema Channel (South Atlantic) and reported less abundant displaced Antarctic diatoms during glacial maxima than during interglacials.

Diatom biostratigraphic results were used by Osborne and others (1983), and Ledbetter and Ciesielski (1986) for the evaluation of deep-sea disconformities in the Indian and Atlantic sector of the Southern Ocean, respectively. The hiatuses were taken to define periods of increased bottom-water activity and to indicate circulation patterns of the Antarctic Bottom Water (AABW) and the Circumpolar Deep Water (CDW) during the late Neogene in the Southern Ocean. Increased AABW and CDW activity was recorded within a time interval spanning 4.3 to 3.5 Ma and related to a cooling of the Southern Ocean and fringing ice-shelves. Decreased AABW and increased CDW activity at about 2.5 to 3.0 Ma were interpreted to be related to the formation of Northern Hemisphere ice sheets and the increase of AABW and CDW velocity during 2.0 and 1.5 Ma was related to an Antarctic cooling. However, Burckle and Abram's (1987) re-examination of some cores used in this study resulted in different age assignments than stated by Ledbetter and Ciesielski (1986) and the investigations of cores recovered from the studied area (e.g. the Maud Rise, Abelmann and others, 1990) resulted in other sediment distribution patterns than reported by Ledbetter and Ciesielski (1986). Abundance patterns of siliceous microfossils, species composition of the preserved assemblages and time-geographic occurrence of hiatuses were the base for the estimation of Plio-Pleistocene paleoproductivity, surface water temperature and bottom water activity in the Atlantic sector of the Southern Ocean by Abelmann and others (1990). The lower Pliocene environment was characterized by high biogenic production and warmer conditions. Widespread hiatuses in deep and shallow water depth, followed by a distinct change in facies and modifications of the species composition indicate significant changes in oceanographic circulation patterns during the late Pliocene. Within the time interval late Pliocene to early Pleistocene, the erosional activity of water masses is restricted to water depth above 4400 m and biogenic silica production decreases considerably. Abelmann and others (1990) proposed, that this pattern is related to an intensified flow of North Atlantic Deep Water into the Southern Ocean circulation system due to stronger production of this water mass after the onset of major glaciation on the northern hemisphere.

---

[5] thanatocoenosis: a set of fossils brought together after death by sedimentary processes.

Based on the recovery of late Neogene marine planktonic diatoms from the Sirius Formation (Transantarctic Mountains), Webb and others (1984) and Harwood (1985) concluded that open-marine conditions prevailed in the Wilkes and Pensacola Basins (East Antarctic continent) during the time intervals 6.6 to 4.2 Ma and 3.1 to 2.5 Ma. Thus it was suggested that parts of the Antarctic continent were deglaciated during late Neogene time periods. However, late Neogene oxygen isotope values do not indicate substantial differences in temperature and ice volumes when compared to the present-day conditions (Kennett and Hodell, 1986).

Since 1983 experiments with year-long mooring of time-series sediments traps combined with quantitative studies of the underlying surface sediments have provided information about alteration of biogenic particles during settlement through the water column. Alteration results from mechanical breakdown by feeders, from opal dissolution, and from mechanisms of vertical and horizontal transport in the Southern Ocean. Knowledge of these parameters is essential for the evaluation of siliceous microfossil assemblages recorded in the sediments and used as indicators of environmental conditions in the geological past. Sediment trap studies in the Bransfield Strait and the Weddell Sea (Gersonde, 1986b, in press, a,b; Gersonde and Wefer, 1987; Wefer and others, 1988, 1990; Fischer and others, 1989) illustrate that the particle flux in Antarctic waters occurs in short pulses when flux values as high as 2 g m^{-2} day^{-1} can be reached. In the Bransfield Strait more than 90% of the annual flux occurs in December and January, while maximum flux in the Weddell Sea occurred during February and March (Abelmann and Gersonde, 1991). Thus the paleoenvironmental signal incorporated into the sediments can only represent environmental conditions during this comparatively short time span of the year. The studies also indicate the importance of fecal pellets as carriers of biogenic opal through the water column. Maximum pellet flux rates in the Bransfield Strait were estimated to be 4-6 x 10^5 pellets m $^{-2}$ day $^{-1}$, produced by krill and copepods, but the bulk of pellet content consisted of fragmented diatom frustules which could not be identified to species level. Thus it was suggested that most of the intact valves recorded in the sediments have settled through the water column by means other than fecal pellets: incorporated or attached to aggregates (Gersonde and Wefer, 1987). Alteration of diatom cell walls occurs in the upper portion of the water column by mechanical breakdown by feeders, such as krill, which affected especially the large frustules of *Corethron criophilum*. Alteration by dissolution of silica is enhanced at the sediment-water interface and may exert a strong bias upon composition of diatom assemblages preserved in the sediments. In the Weddell Sea only a minor portion of diatom species originally produced in the euphotic zone is incorporated in the sediments. There the fossil assemblages dominated by the resistant species *Nitzschia kerguelensis* did not reflect environmental conditions such as sea-ice coverage which affected the studied site more than half of the entire year (Gersonde, in press, a). Similiar conclusions were also deduced by Leventer and Dunbar (1987) based on short-time sediment trap studies in McMurdo Sound, Ross Sea.

High latitude North Pacific and North Atlantic

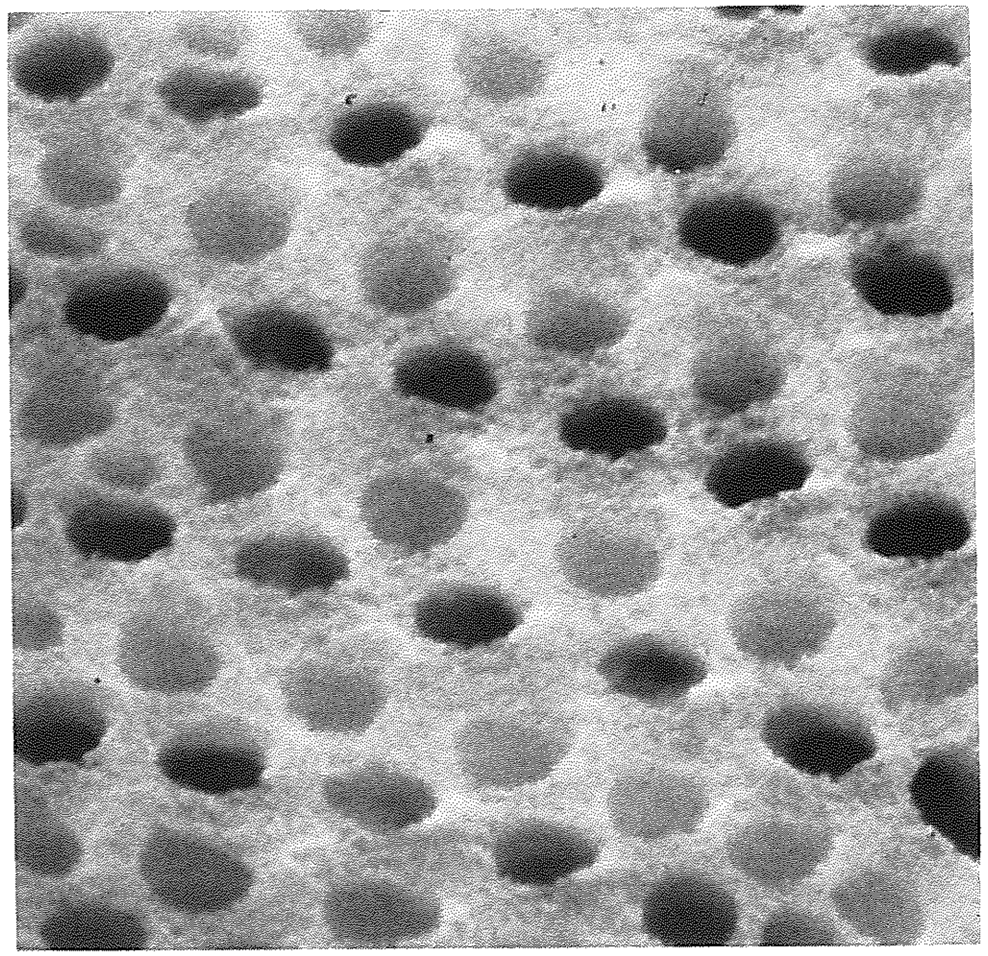
The first paleoenvironmental work on sediment cores from the North Pacific and Subarctic Pacific is that of Jousé (1960, 1962, 1967 and 1971). This work is based on the definition of cold-water and warm-water diatom assemblages and is restricted to the Pleistocene time period. Paleoenvironmental studies on North Pacific Pleistocene cores were also done by Donahue (1970b) and Koizumi (1973). Donahue (1970b) used a diatom temperature value index (Td values) for the evaluation of paleotemperatures. The Td value was established by Kanaya and Koizumi (1966) based on the relative proportion of "cold" and "warm" water species individuals in a given sample. Using the factor analysis-transfer function technique, Sancetta (1979) reconstructed winter and summer surface water temperature, and productivity at 18000 years BP, the last glacial maximum, in the North Pacific. Sancetta (1979) could also monitor the evolution of oceanographic parameters during the last 18000 years and showed that present conditions were established 8000 years BP. In a series of subsequent papers Sancetta (1981, 1983a) and Sancetta and Robinson (1983) elucidated the environmental and oceanographic history of the Subarctic Pacific and Bering Sea since the last glacial maximum (Wisconsin glaciation), based on downcore studies. Sancetta (1983b) described a new technique for the identification of the shelf-slope break based on diatom counts on material recovered in the Bering Sea.

Compared to the Subarctic Pacific, less diatom related paleoenvironmental work has been done in the area of the European North Sea because of the scarce occurrence of well preserved diatom assemblages in Pleistocene sediments. Sediment cores from the southeastern Norwegian Sea show a prominent diatom maximum in sediments dated to be late Weichselian (last glacial maximum) in age (Bjoerklund and others, 1979; Jansen and others,1983). Stabel (1986) related the time-transgressive diatom-rich sediment layer to the Subarctic Convergence and its northward transition. Only recently Schrader and Karpuz (1990) accomplished a quantitative study on diatom assemblages from surface sediments from two WE-sections across the Norwegian-Iceland Seas. Using the factor analysis-transfer function technique these data are related to physical and chemical surface water characteristics to create a basis for further paleoenvironmental downcore- studies. The distribution of diatoms in surface sediments of the Kane Basin (between Ellesmere Island and Greenland) was semi-quantitatively determined by Kravitz and others (1987), who found a positive relation between diatom abundance, and absence of sea ice and sediment ponding in deeper basins.

ACKNOWLEDGEMENT

Thanks are due to Julian Priddle (BAS), and Andrea Abelmann and Gaby Ott (AWI) for critical manuscript reading.

Taxonomy



CHAPTER 10

KEY TO DIATOM FAMILIES

INCLUDING ONLY THOSE FOUND IN POLAR WATERS
(IN PART AFTER SIMONSEN, 1979)

1a Valve structure towards a point ....**Centrales**
1b Valve structure towards a line ....**Pennales**

Centrales

1a Valves primarily with a marginal ring of processes and symmetry with no polarity ....**I. Coscinodiscineae**
1b Valves without a marginal ring of processes except for linking spines in some species; symmetry primarily with polarity 2
2a Valves primarily "unipolar"; pervalvar axis strongly developed ....**II. Rhizosoleniineae**
2b Valves primarily bipolar ....**III. Biddulphiineae**

Pennales

1a Valves without a raphe ....**IV. Araphidineae**
1b Valves with a raphe ....**V. Raphidineae**

I. Coscinodiscineae

1a Valves with strutted processes and at least one labiate process; spines or occluded processes may be present, areolae with foramina outside, cribra inside ....F. Thalassiosiraceae
1b Valves with labiate proceses or spines only, when areolae well developed foramina inside, cribra outside, pseudoloculi sometimes present 2
2a Valves often with strongly developed pervalvar axis, chain formation common, resting spores occur 3
2b Valves generally disc-shaped with less developed pervalvar axis, chain formation and resting spores unknown 4
3a Labiate processes and sometimes marginal linking spines present, usually heavily silicified ....F. Melosiraceae
3b Labiate processes absent, more or less prominent spines present ....F. Leptocylindraceae
4a Valves with homogeneous areolation all over the valve, valve surface homogeneously curved or flat, labiate process often scattered on valve face 5
4b Valve areolation not homogeneous or valve surface divided into sectors, labiate process only marginal 6
5a Valves without pseudonodulus, often labiate processes on valve face, marginal labiate processes may be of different sizes ....F. Coscinodiscaceae
5b Valves with pseudonodulus, labiate processes marginal and all of the same size, or if pseudonodulus is absent, then additional single central labiate process is present ....F. Hemidiscaceae
6a Valves with enlarged areolae, partly ray-shaped, reaching from a central area almost to the valve margin ....F. Asterolampraceae
6b Valves without enlarged areolae, valve surface often divided into sectors or with prominent marginal labiate processes ....F. Heliopeltaceae

II. Rhizosoleniineae

1 Valves with a single, usually eccentrically located labiate process ....F. Rhizosoleniaceae

III. Biddulphiineae

1a Valves with setae, linked in colonies, end valves of colonies with a low labiate process ....F. Chaetoceraceae
1b Valves without setae 2
2a Valves usually with elevations, some with linking spines, pseudocelli common, labiate processes in distinct pattern ....F. Biddulphiaceae
2b Valves may have elevations, pseudoocelli lacking, external tubes of labiate processes often long ....F. Eupodiscaceae

IV. Araphidineae

1 Valves lacking a raphe, possessing a central raphe sternum (axial area, labiate processes either at both apices or only at one, or subcentral) ....F. Diatomaceae

V. Raphidineae

1a Raphe not subtended by fibulae and not closed by a canal on the inside 2
1b Raphe subtended by fibulae or closed by a canal on inside 3
2a Both valves of a frustule with a raphe ....F. Naviculaceae
2b Only one valve of a frustule with a raphe ....F. Achnanthaceae
3a Frustules symmetrical on the apical axis, raphe traversing across the valve ....F. Auriculaceae
3b Frustules usually symmetrical on the apical axis, raphe eccentric to central but running from one end of the valve to another ....F. Bacillariaceae

GENERA WITH SPECIES COMMONLY FOUND IN EITHER POLAR REGION

- Family Thalassiosiraceae
  - *Bacterosira*
  - *Detonula*
  - *Porosira*
  - *Skeletonema*
  - *Thalassiosira*
- Family Melosiraceae
  - *Melosira*
  - *Paralia*
- Family Leptocylindraceae
  - *Corethron*
  - *Leptocylindrus*
- Family Coscinodiscaceae
  - *Coscinodiscus*
  - *Stellarima*
- Family Hemidiscaceae
  - *Actinocyclus*
  - *Azpeitia*
- Family Asterolampraceae
  - *Asteromphalus*
- Family Heliopeltaceae
  - *Actinoptychus*
- Family Rhizosoleniaceae
  - *Dactyliosolen*
  - *Rhizosolenia*
  - *Proboscia*
- Family Biddulphiaceae
  - *Eucampia*
- Family Chaetoceraceae
  - *Chaetoceros*
- Family Eupodiscaceae
  - *Odontella*
- Family Diatomaceae
  - *Fragilaria*
  - *Licmophora*
  - *Synedra*
  - *Thalassionema*
  - *Thalassiothrix*
  - *Trichotoxon*
- Family Achnanthaceae
  - *Achnanthes*
  - *Cocconeis*
- Family Naviculaceae
  - *Amphora*
  - *Banquisia*
  - *Berkeleya*
  - *Caloneis*
  - *Diploneis*
  - *Entomoneis* (= *Amphiprora*)
  - *Gyrosigma*
  - *Haslea*
  - *Manguinea*
  - *Membraneis*
  - *Navicula*
  - *Lyrella*
  - *Parlibellus*
  - *Pinnularia*
  - *Plagiotropis* (= *Tropidoneis*)
  - *Pleurosigma*
  - *Stenoneis*
  - *Trachyneis*
  - *Pseudogomphonema*
  - *Rhoikoneis*
  - *Stauroneis*
- Family Auriculaceae
  - *Auricula*
- Family Bacillariaceae
  - *Hantzschia*
  - *Nitzschia*
  - *Cylindrotheca*
  - *Bacillaria*

Note: Please refer to Round and others (1990) for a revised classification scheme

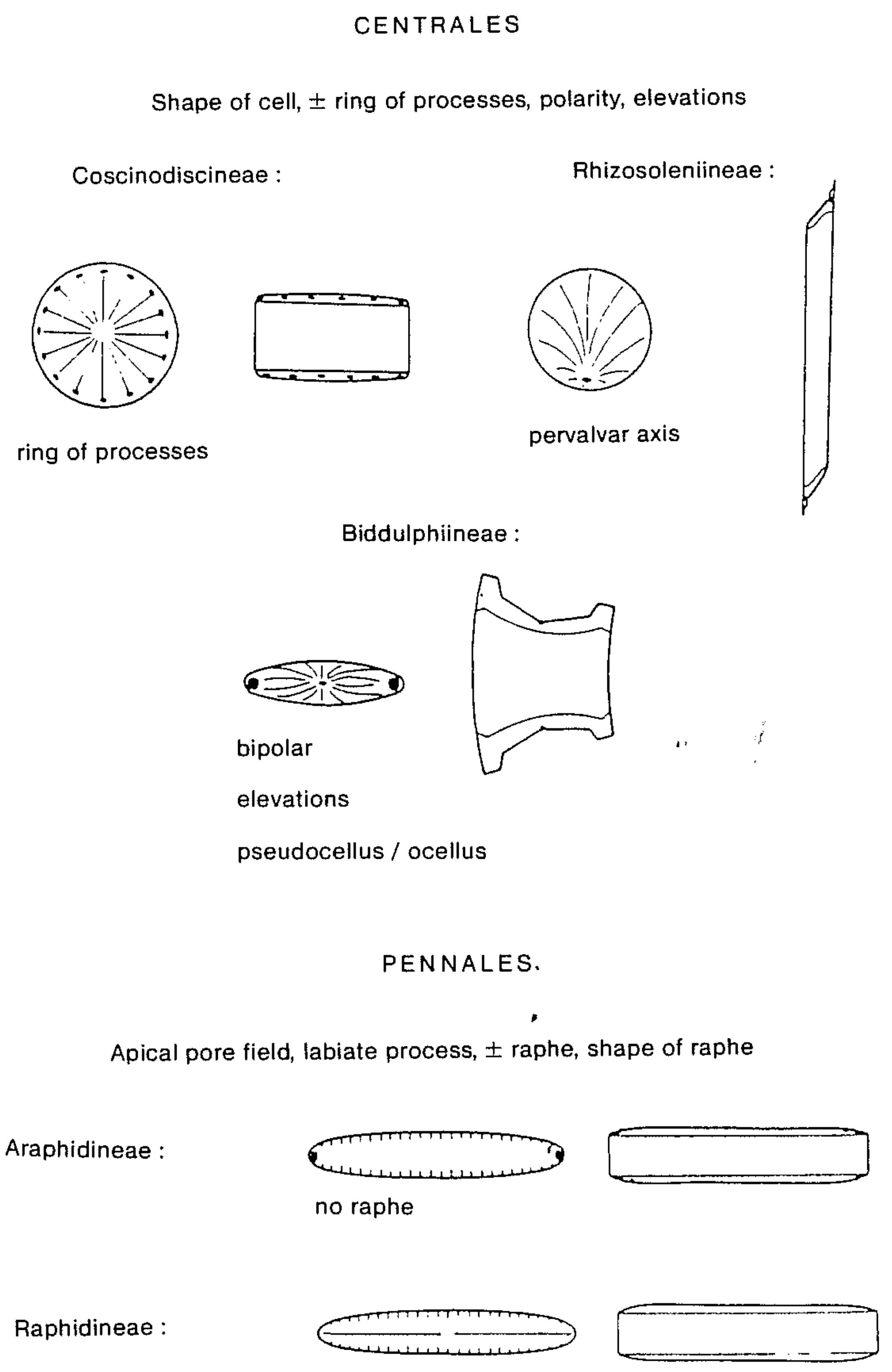


Plate 10.1 Line drawings to aid Key to Families. Drawn by E. E. Syvertsen.

GLOSSARY

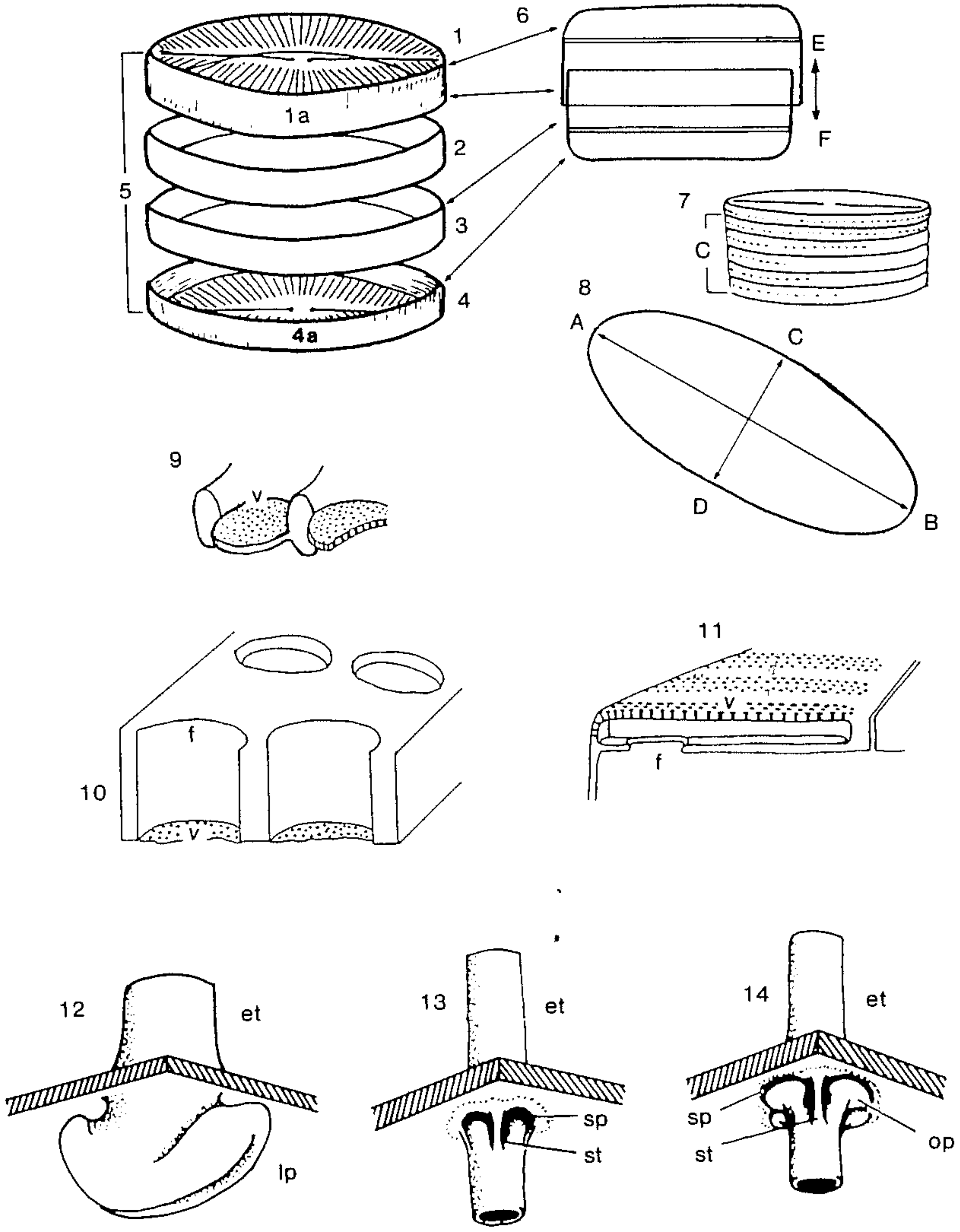


Plate 10.2. Line drawings of selected features of the frustule structure.

Figs 1-6 Components of the frustule

Fig. 1 Epivalve

Fig. 1a Mantle of epivalve

Fig. 2 Epicingulum

Fig. 3 Hypocingulum

Fig. 4 Hypovalve

Fig. 4a Mantle of hypovalve

Fig. 5 Complete frustule

Fig. 6 Complete frustule showing overlapping cingula, E-F, see Fig. 8

Fig. 7 Theca with cingulum composed of several girdle bands (copulae)

Fig. 8 Axes of the frustule, A-B = Apical axis, C-D = Transapical axis E–F of Fig. 6 = pervalvar axis

Figs 9–11 Types of areolae

Fig. 9 Punctate areolae with vela (v)

Fig. 10 Loculate areolae with foramen (f) and vela (v)

Fig. 11 Alveolate areola with foramen (f) and vela (v)

Figs 12–14 Some types of processes which penetrate the valve wall

Fig. 12 Labiate process (lp) with long external tube (et)

Fig. 13 Trifultate strutted process (st) with accompanying satellite pores (sp)

Fig. 14 Operculate strutted process (op)

Figs 1–8, 11 taken from Barber and Haworth (1981); Fig. 9 taken from Mann (1978); Figs 12–14 taken from Priddle and Fryxell (1985)

Plate 10.3. Line drawings of valve shapes

Fig. 1 Circular
Fig. 2 Elliptic
Fig. 3 Narrow elliptic
Fig. 4 Ovate
Fig. 5 Lanceolate, wide
Fig. 6 Lanceolate, narrow
Fig. 7 Lanceolate, fusiform
Fig. 8 Rhombic
Fig. 9 Rectangular
Fig. 10 Linear
Fig. 11 Clavate
Fig. 12 Linear with gibbous centre
Fig. 13 Triundulate
Fig. 14 Trapezoidal
Fig. 15 Trapezoidal
Fig. 16 Sigmoid
Fig. 17 Sigmoid lanceolate
Fig. 18 Sigmoid rhombic
Fig. 19 Sigmoid linear
Fig. 20 Panduriform
Fig. 21 Panduriform, gently constricted
Fig. 22 Reniform

Figs taken from Barber and Haworth (1981); Figs 14 and 15 valves in girdle view, all others in valve view.

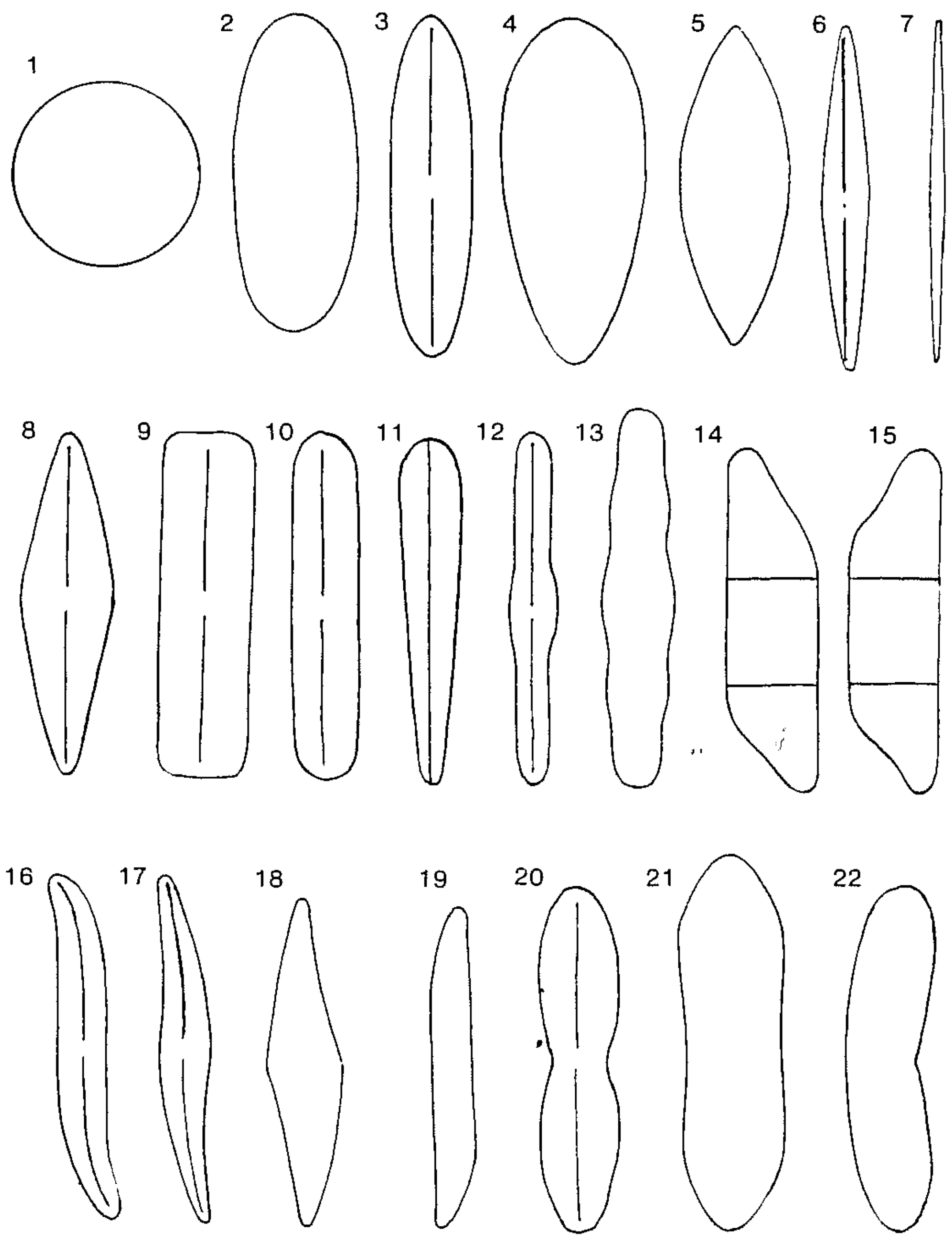


Plate 10.4. Line Drawings of Varying Valve Symmetries

Heteropolar – Ends of the valve differing in shape or size
Isopolar – Ends of the valve similar in shape or size
Isobilateral – Valve outline similar on either side of the apical axis
Dorsiventral – Valve outline dissimilar either side of the apical axis, the ventral side being narrower

Fig. 1 Spatulate
Fig. 2 Ovate
Fig. 3 Clavate
Fig. 4 Bilobate
Fig. 5 Clavate
Fig. 6 Hastate
Fig. 7 Clavate
Fig. 8 Semilanceolate
Fig. 9 Semilanceolate
Fig. 10 Semicircular
Fig. 11 Crescentic
Fig. 12 Arcuate
Fig. 13 Arcuate
Fig. 14 Auricular
Fig. 15 Reniform
Fig. 16 Sigmoid linear
Fig. 17 Sigmoid lanceolate
Fig. 18 Sigmoid rhombic
Fig. 19 Panduriform
Fig. 20 Panduriform
Fig. 21 Panduriform
Fig. 22 Elliptic
Fig. 23 Elliptic
Fig. 24 Elliptic
Fig. 25 Elliptic
Fig. 26 Subcircular
Fig. 27 Linear
Fig. 28 Linear
Fig. 29 Linear
Fig. 30 Rectangular
Fig. 31 Rectangular
Fig. 32 Acicular (Spindle)
Fig. 33 Fusiform
Fig. 34 Lanceolate
Fig. 35 Lanceolate
Fig. 36 Rhombic
Fig. 37 Rhombic
Fig. 38 Rhombic

Figs taken from Barber and Haworth (1981)

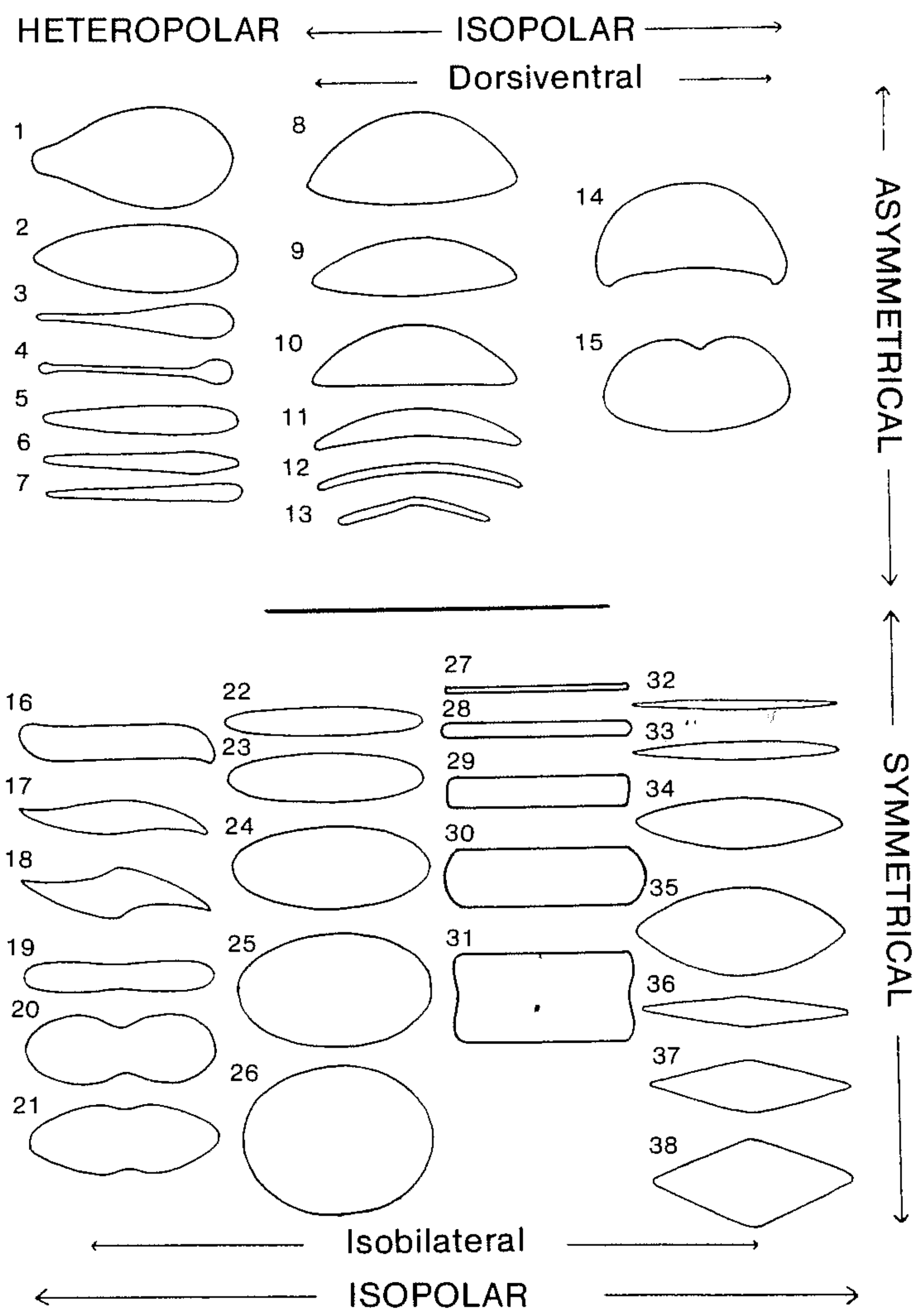


Plate 10.5. Line drawings of valve structure and areolae patterns as found in centric diatoms

Fig. 1 Areolae all of equal size

Fig. 2 Areolae increasing in size from valve centre

Fig. 3 Areolae increasing in size from valve centre then decreasing to margin

Fig. 4 Areolae decreasing in size from valve centre

Fig. 5 Areolae arranged in radiating striae

Fig. 6 Areolae arranged in radial and subradial striae

Fig. 7 Areolae arranged in short irregular striae

Fig. 8 Areolae arranged in curved sectors with the longest striae on the edge of the sector

Fig. 9 Areolae arranged in straight sectors with the longest striae in the middle of the sector

Fig. 10 Areolae arranged in linear striae

Fig. 11 Areolae arranged in eccentric striae

Fig. 12 Structure of a *Rhizosolenia* cell seen in ventral and lateral views

Fig. 13 Pseudonodulus (p) of the Hemidiscaceae

Figs 1–11 taken from Barber and Haworth (1981); Fig. 12 taken from Sundström (1985)

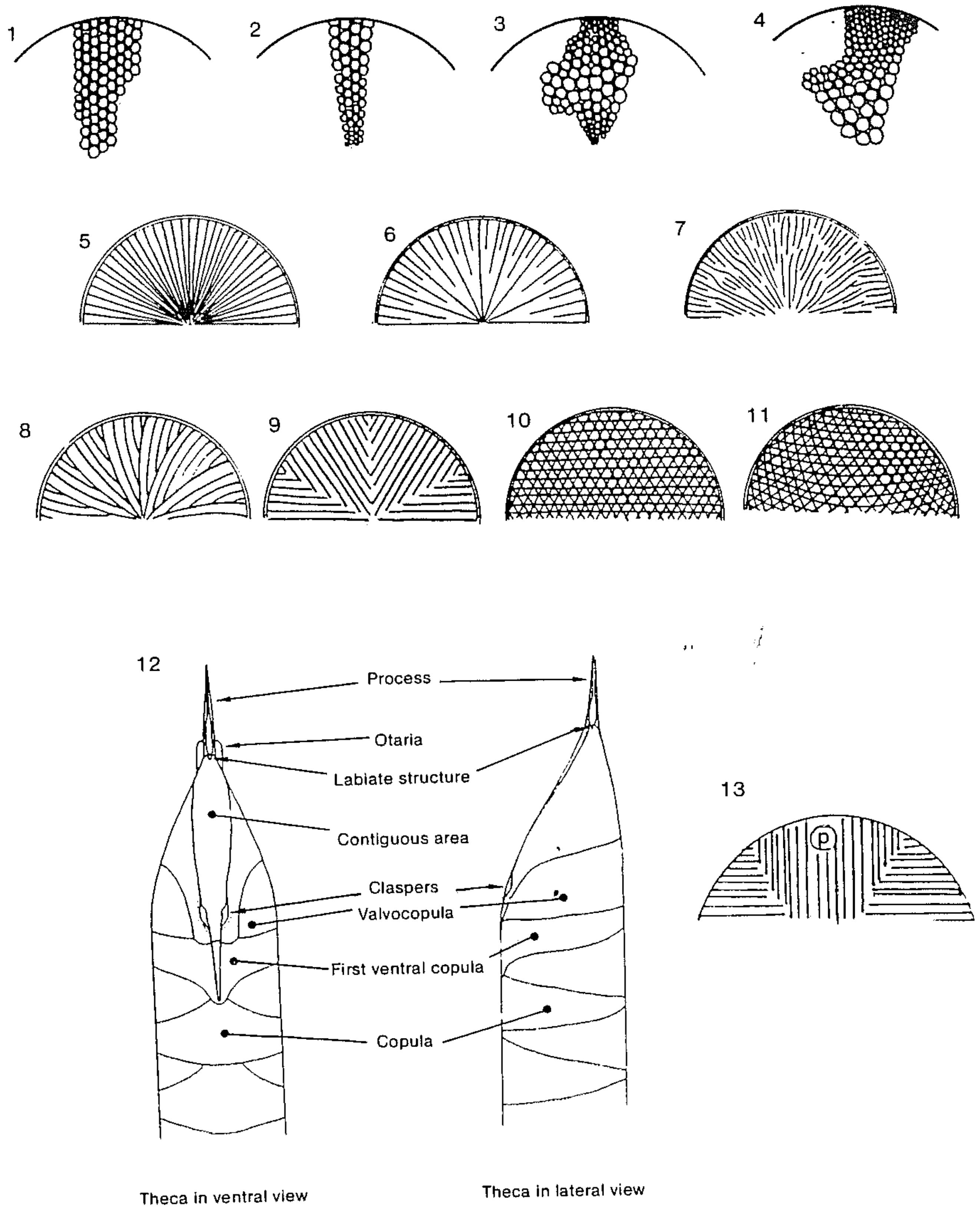


Plate 10.6. Line drawings of areolae patterns as found in pennate diatoms

Fig. 1 Striae parallel throughout

Fig. 2 Striae radiate throughout

Fig. 3 Striae radiate throughout but more closely spaced at the apices

Fig. 4 Striae radiate at the centre but convergent at the apices

Fig. 5 Striae curved around the central area

Fig. 6 Striae sigmoid around the central area

Fig. 7 Striae gently radiate to gently convergent

Fig. 8 Striae pattern different bilaterally

Fig. 9 Striae strongly radiate to strongly convergent

Fig. 10 Striae oblique throughout

Fig. 11 Striae radiate and sigmoid throughout

Fig. 12 Striae strongly radiate to convergent with abrupt changeover

Fig. 13 Striae lineate, not bounded at the edge

Fig. 14 Striae lineate and bounded at the edge

Fig. 15 Areolae equally spaced and separated

Fig. 16 Areolae closer spaced towards margin

Fig. 17 Areolae not clearly separated

Fig. 18 Areolae rectangular in shape

Fig. 19 Areolae bacilliform in shape

Fig. 20 Areolae alternately spaced in double rows

Fig. 21 Areolae in double or multiple rows in the stria

Fig. 22 Areolae hexagonal

Fig. 23 Areolae arranged in longitudinal and transverse striae

Fig. 24 Areolae arranged in decussate striae

Fig. 25 Areolae in curved quincunx striae

Fig. 26 Alveoli with wide internal opening (appears as wide band across striae)

Fig. 27 Alveoli with narrow internal opening

Fig. 28 Alveoli crossed by hyaline band

Fig. 29 Striae scabrous (areas where areolae are absent)

Fig. 30 Striae plain

Fig. 31 Alveoli with medium width internal opening

Fig. 32 Striae interrupted close to the valve margin

Fig. 33 Alveoli with internal opening close to valve margin

Fig. 34 Striae composed of fine areolae

Fig. 35 Striae composed of coarse areolae

Fig. 36 Striae forming undulate longitudinal rows

Fig. 37 Striae composed of fine areolae in irregular lines

Figs taken from Barber and Howarth (1981)

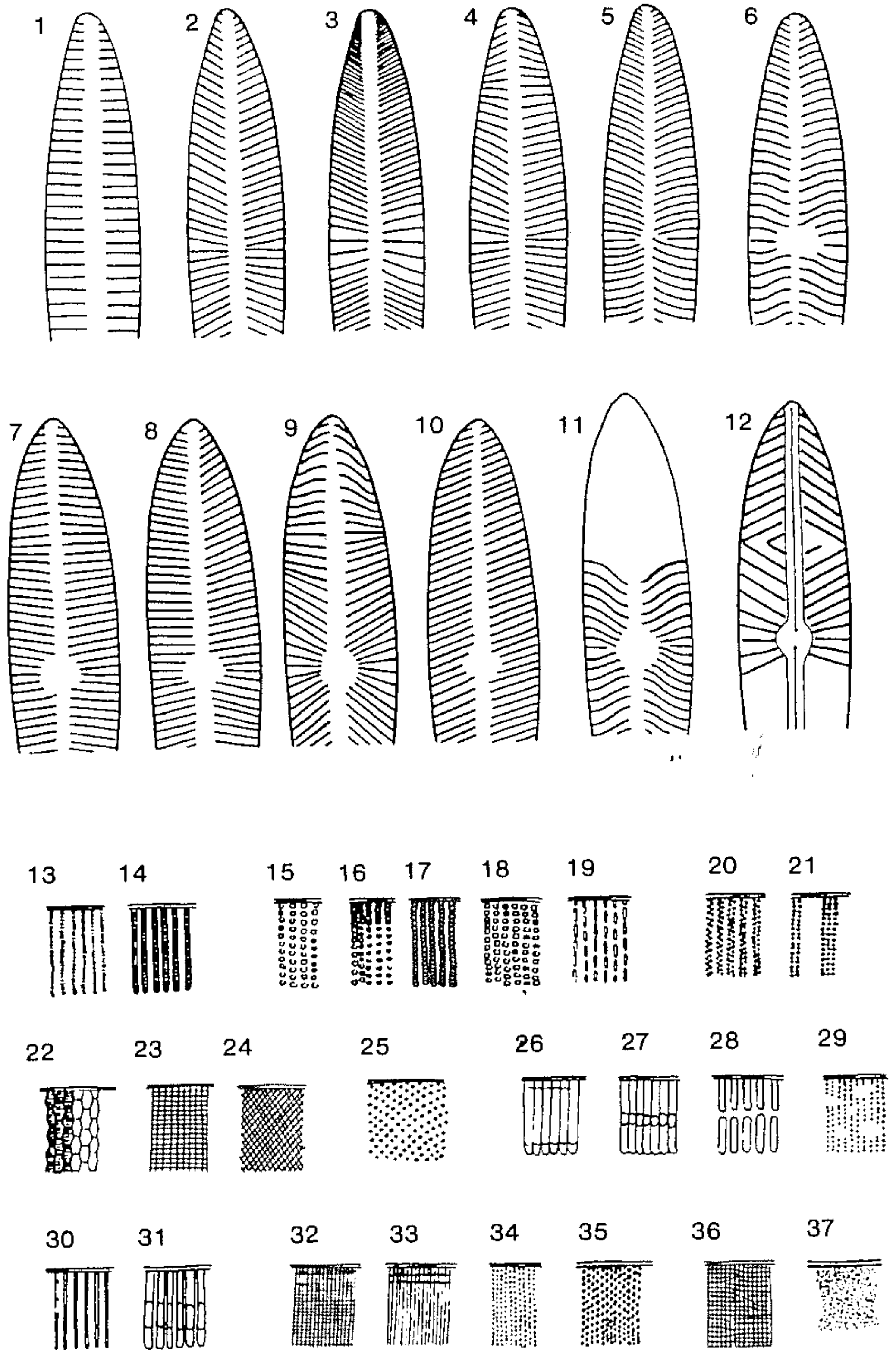


Plate 10.7. Line drawings of cell apices, margins, and other valve structures

Fig. 1 Apices broadly rounded, obtuse

Fig. 2 Apices cuneate

Fig. 3 Apices broadly rostrate

Fig. 4 Apices spatulate

Fig. 5 Apices capitate

Fig. 6 Apices subcapitate

Fig. 7 Apices apiculate and produced

Fig. 8 Apices apiculate

Fig. 9 Apices sigmoidly cuneate

Fig. 10 Apices capitate

Fig. 11 Apices narrowly rostrate

Fig. 12 Margin striate

Fig. 13 Margin punctate

Fig. 14 Margin areolate

Fig. 15 Valve with wide lyrate or lateral hyaline areas not extending to the margin

Fig. 16 Valve with narrow lyrate hyaline areas

Fig. 17 Valve with wide lyrate areas containing additional structure

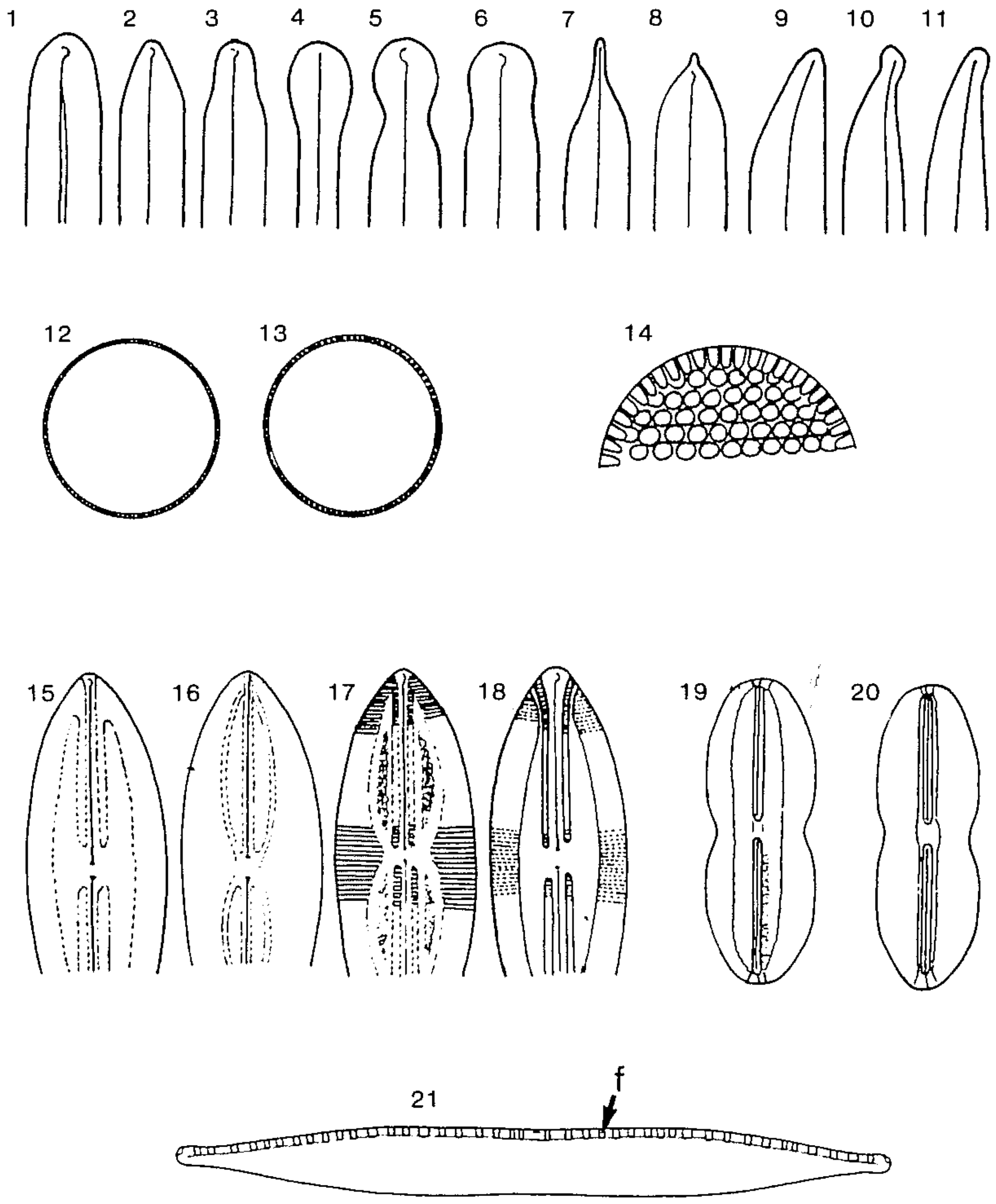
Fig. 18 Valve with lyrate areas extending to the margin

Fig. 19 Wide longitudinal canals of *Diploneis*

Fig. 20 Narrow longitudinal canals of *Diploneis*

Fig. 21 Canal raphe of *Nitzschia*, raphe subtended by fibulae (f)

Figs 1–20 taken from Barber and Haworth (1981); Fig. 21 taken from Mann (1978)



CHAPTER 11

FAMILY THALASSIOSIRACEAE

SECTION 1: Grethe R. Hasle and Erik E. Syvertsen

SECTION 2: Greta A. Fryxell and Jeffrey R. Johansen

SECTION 1

A key to genera of the family Thalassiosiraceae found in the Arctic and/or Antarctic:

1a Cells in colonies joined by thin threads from valve face 2
1b Cells in colonies joined by external parts of marginal processes 4
2a Adjacent cells abutting; many central processes in a cluster; pervalvar axis elongated .... *Bacterosira*
2b Cells separated by a shorter or longer distance; cells discoid 3
3a Threads from processes evenly distributed on the valve; no particular central or subcentral processes .... *Porosira*
3b Threads from processes arranged in a definite pattern .... *Thalassiosira*
4a Adjacent cells abutting; a single thread from a central process .... *Detonula*
4b Adjacent cells not abutting; no central thread .... *Skeletonema*

All genera have disc shaped chloroplasts in a varying number.

GENUS BACTEROSIRA Gran

B. fragilis Gran, the only species of this genus, is characterised by cylindrical, weakly silicified cells held close together in colonies, separated only by a lenticular-shaped central opening. The structures best seen in LM on cleaned valves in permanent mounts are the central cluster of strutted processes; the marginal ring of strutted processes, including one labiate process, may be more difficult to discern. Resting spores are distinctly different from the vegetative cells.

How to identify:
This species will usually be easier to identify as colonies in water mounts rather than as cleaned valves in permanent mounts where it may be confused with *Thalassiosira* spp.

Characters to look for in girdle view:
1. Abutting adjacent cells in colonies
2. Lenticular-shaped opening between cells in colonies

Characters to look for in valve view:
1. Central cluster of numerous processes
2. Valve structure of radial ribs rather than rows of areolae

GENUS DETONULA Schütt

This genus is represented in cold waters of the northern hemisphere by one species, *Detonula confervacea* (Cleve) Gran, which, in girdle view, is slightly similar to *B.fragilis* and *Leptocylindrus danicus* Cleve. *D.confervacea* usually has a shorter pervalvar axis than these diatoms. The resting spores differ from the vegetative cells by a usually shorter pervalvar axis, the simpler external structure of the strutted processes and a much more heavily silicified cell wall.

How to identify:
The species is readily identified as colonies in water mounts. Cleaned valves in permanent mounts may be confused with *Thalassiosira* spp.

Characters to look for in girdle view:
1. Adjacent cells in colonies abutting entirely
2. Marginal processes, best seen on the terminal valves of a colony

Characters to look for in valve view:
1. Shape of marginal processes (winged terminal part in vegetative cells)
2. Valve areolation (ribs more than areolae in vegetative cells, coarsely silicified areolae in resting spores)

GENUS SKELETONEMA Greville

This genus is poorly represented in polar waters, and when present, by the cosmopolitan *S.costatum* (Greville) Cleve. The species is occasionally so weakly silicified that the connecting siliceous external structures of the marginal processes are difficult to see.

How to identify:
The species is readily identified in water mounts as colonies as well as single cells. In permanent mounts of cleaned material the species will mostly be present as single terminal valves or as the sibling valves of neighbouring cells united by the external parts of their marginal strutted processes. If seen in valve view, *S.costatum* (especially the terminal valves, which have a near central labiate process) may be confused with *Detonula confervacea* or *Thalassiosira* spp.

Characters to look for:
1. The silicified external structures of the marginal processes linking cells to form colonies

Plate 11.1. Scale bars= 10μm

Figs 1, 2. *Bacterosira fragilis*, **Fig. 1.** Colony with resting spores, **Fig. 2.** Single valve.

Figs 3, 4 *Detonula confervacea*, **Fig. 3.** Colony with resting spores, **Fig. 4.** Single valve.

Figs 5–7. *Skeletonema costatum*, **Fig. 5.** Colony, **Fig. 6.** Terminal valve, **Fig. 7.** Valve of cells inside the colony.

Fig. 8. *Porosira* spp., girdle view.

Fig. 9. *P.glacialis*, valve view.

Fig. 10. *P. pseudodenticulata*, valve view.

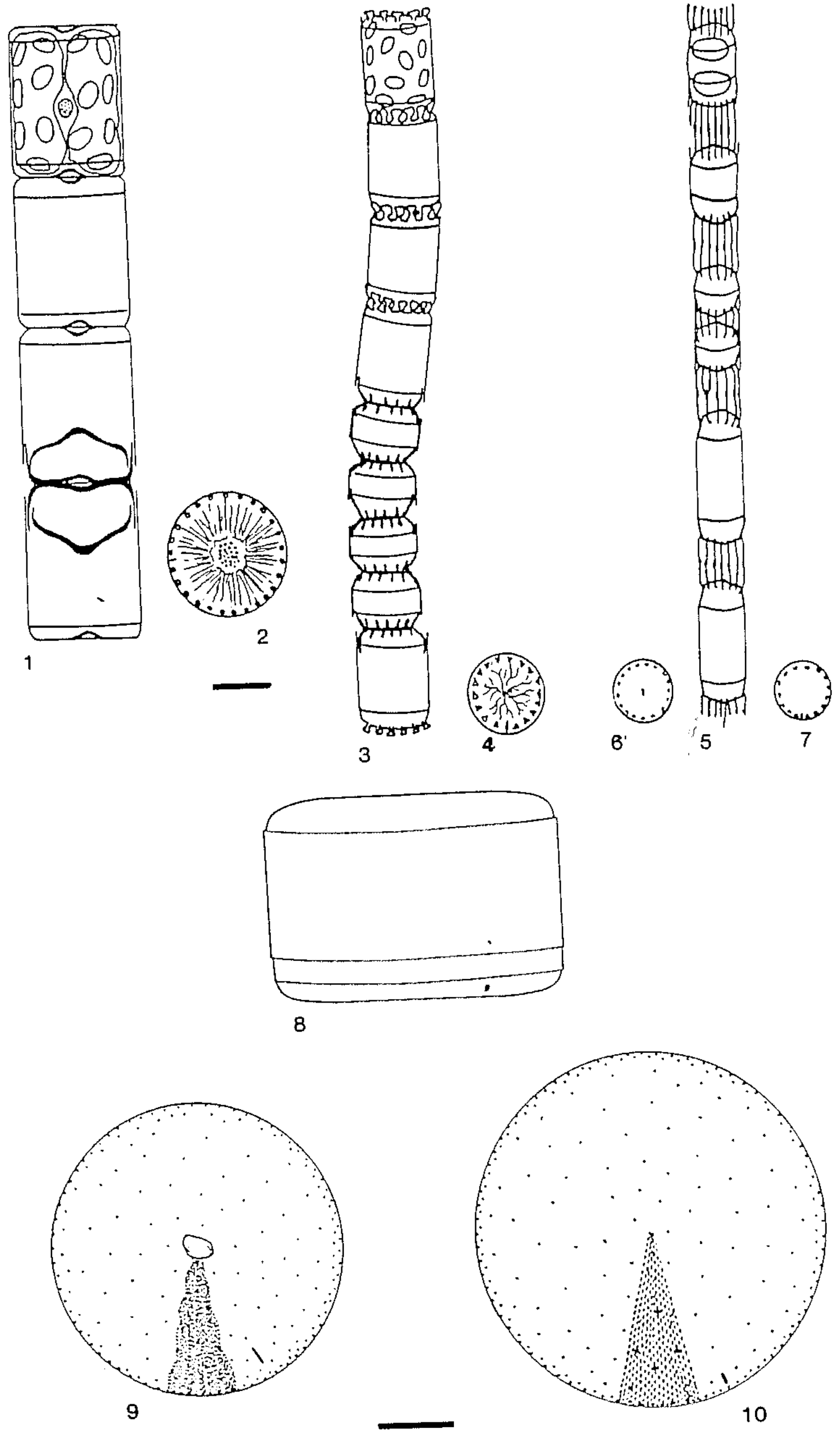


Table 11.1. Morphometric and distributional data on species in the Thalassiosiraceae

	Diameter in µm	*Pervalvar axis in µm*	*Areolae in 10 µm*	*Marginal processes in 10 µm*	*Distribution*
B.fragilis	18–24	diam.	30	5–9	Arctic
D.confervacea	6–20	15–30	30–40	10	Arctic
S.costatum	2–22	2–61	20–40?	6–8	Cosmopolitan
P.glacialis	36–64	30–40	25–26	—	Bipolar
P.pseudodenticulata	60–80	—	10–12	—	Antarctic

For further information on Thalassiosiraceae see Hasle (1973a) and for *Skeletonema costatum* see Hasle (1973b).

GENUS POROSIRA Jørgensen

Two species, *P.glacialis* (Grunow) Jørgensen and *P.pseudodenticulata* (Hustedt) Jousé, are represented in polar waters. The threads that unite the cells into colonies are very thin and do not preserve well, hence colonies will usually not be seen in preserved material. Single cells of both species may be easily confused with *Coscinodiscus* spp. or with single cells of *Thalassiosira* spp. in water mounts. The valve structure is usually obscured in cells filled with the numerous chloroplasts. In empty cells the unevenly distributed strutted processes scattered all over the valve are discernible as small spots and the single labiate process as an elongate structure in the marginal zone. None of the strutted processes has a definite central or subcentral position.

The valve areolation is resolved in permanent mounts of cleaned material as radiate, spiralling or wavy striae.

How to identify to species:
The areolation of *P.glacalis* is not resolvable in water mounts whereas that of *P.pseudodenticulata* is. The distinction between the two species is better revealed in cleaned valves mounted in a medium with a high refractive index. The weakly silicified *P.glacialis* has wavy striae of mainly rectangular areolae and an irregular annulus. The more coarsely silicified *P.pseudodenticulata* has regular hexagonal areolae in radiate and spiralling rows and no or an indistinct annulus.

Characters to look for:
1. The unevenly distributed valve processes
2. The areolation

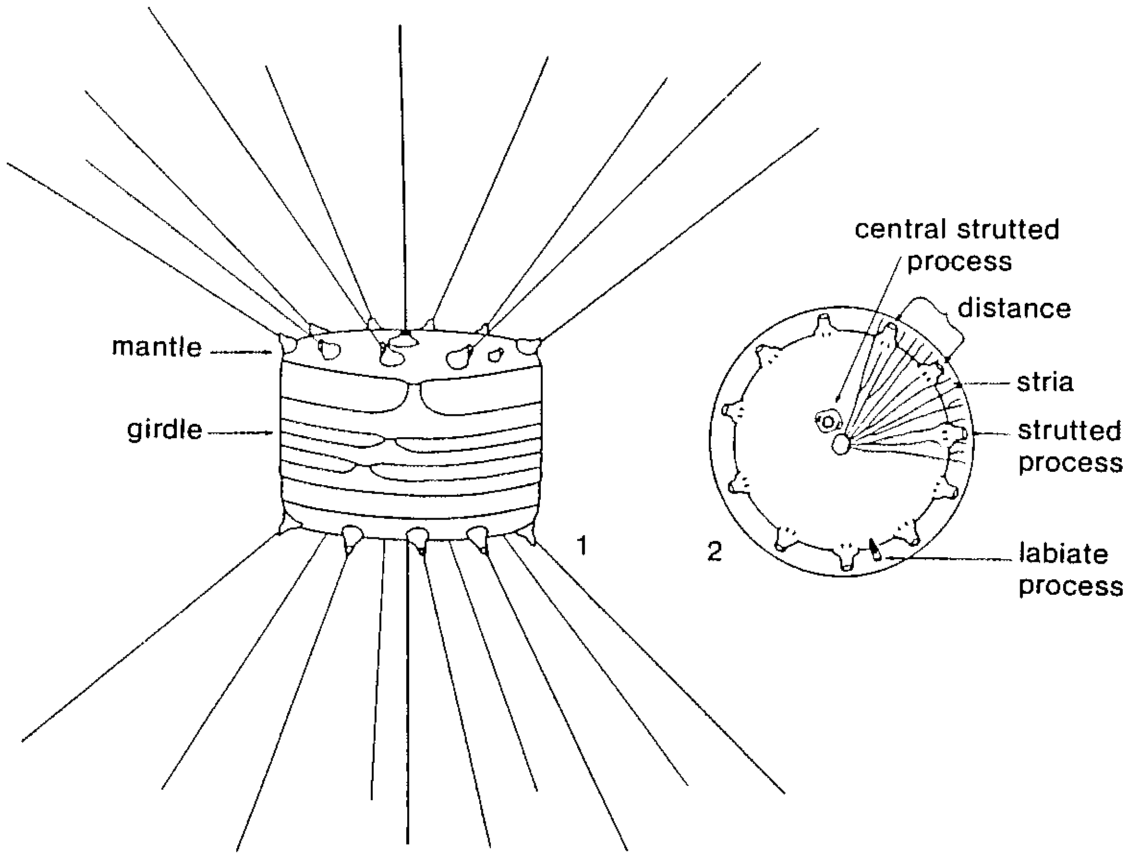


Plate 11.2 Line drawings of features of *Thalassiosira*

GENUS THALASSIOSIRA Cleve

The character distinguishing this, the type genus of the family Thalassiosiraceae, is colony formation by threads of a certain length extruded from strutted processes located in a definite pattern on the valve face. Resting spore formation is known for some of the species.

How to identify to species:
Some species may be identified from water mounts based on the shape of the cell in girdle view (the curvature of the valve face and the shape and height of the mantle), the thickness and length of the connecting threads, and the overall appearance of the colony. Positive identification usually has to rely on cleaned material in permanent mounts.

See Plate 11.2 and 11.3 for illustrations of the following features of *Thalassiosira*.

Characters to look for in girdle view:
1) Curvature/undulation of valve face
2) Shape and height of valve mantle
3) Connecting thread(s), length and thickness (indicating number of central processes)
4) Threads extruded from the margin of valve face and/or mantle (indicating location and number of marginal rings of processes)

Characters to look for in valve view:
1) Location and length (external/internal) of process tubes
2) Number and arrangement of central strutted processes
3) Number of marginal rings of strutted processes
4) Distance between marginal strutted processes (number in 10 µm)
5) Distance of marginal strutted processes from margin (number of areolae)

Table 11.2. Morphometric and distributional data on *Thalassiosira* in northern polar waters

Taxa	*Diameter in µm*	*Valve areolae in 10 µm*		*Marginal processes in 10 µm*	*Number of central processes*	*Number of labiate processes*	*Polar distribution*
		face	*mantle*				
T. bioculata (Grun.) Ostenf.	20–60	20		2	1	1	High Arctic
T. bulbosa Syvertsen	2–16	36–42		4.5	1	1	High Arctic
T. hyalina (Grun.) Gran	16–45	ca.13-24		5–9	2–15	1	High Arctic
T. antarctica var. *borealis* Fryx., Douc. & Hubb.	18–43	20–24		8	several	1	High Arctic to Subarctic
T. nordenskioeldii Cleve	10–50	14–18	14–18	3	1	1	Subarctic to Temperate
T. constricta Gaarder	12–28	40	60	3–5	3–12	1	Subarctic to Temperate
T. hispida Syvertsen	5–25	18	24–26	5	1	1	Subarctic to Temperate
T. gravida Cleve	17–62	20		5–10?	many	1	Subarctic to Temperate
T. poroseriata (Ramsfjell) Hasle	14–38	14–15		1–2	1–8	1	Subarctic to Temperate
T. kushirensis Takano	8–35	15–24		7–8	a few–30	1	Subarctic to Temperate
T. conferta Hasle	3.5–25	25–27		ca.3	1	1	Subarctic to Temperate
T. pacifica Gran	7–46	10–14	20	5	1	1	Subarctic to Temperate
T. anguste-lineata (A. Schmidt) Fryx. & Hasle	14–78	10–11	smaller	3–4	many	1	Subarctic to Temperate
T. angulata (Greg.) Hasle	12–39	8–18	14–24	3	1	1	Subarctic to Temperate
T. baltica (Grun.) Ostenf.	20–120	10–14	smaller	6–7	2–9	3–4	Arctic brackish
T. hyperborea (Grun.) Hasle & Lange	17–42	8–12		3–5	1–8	1	Arctic brackish

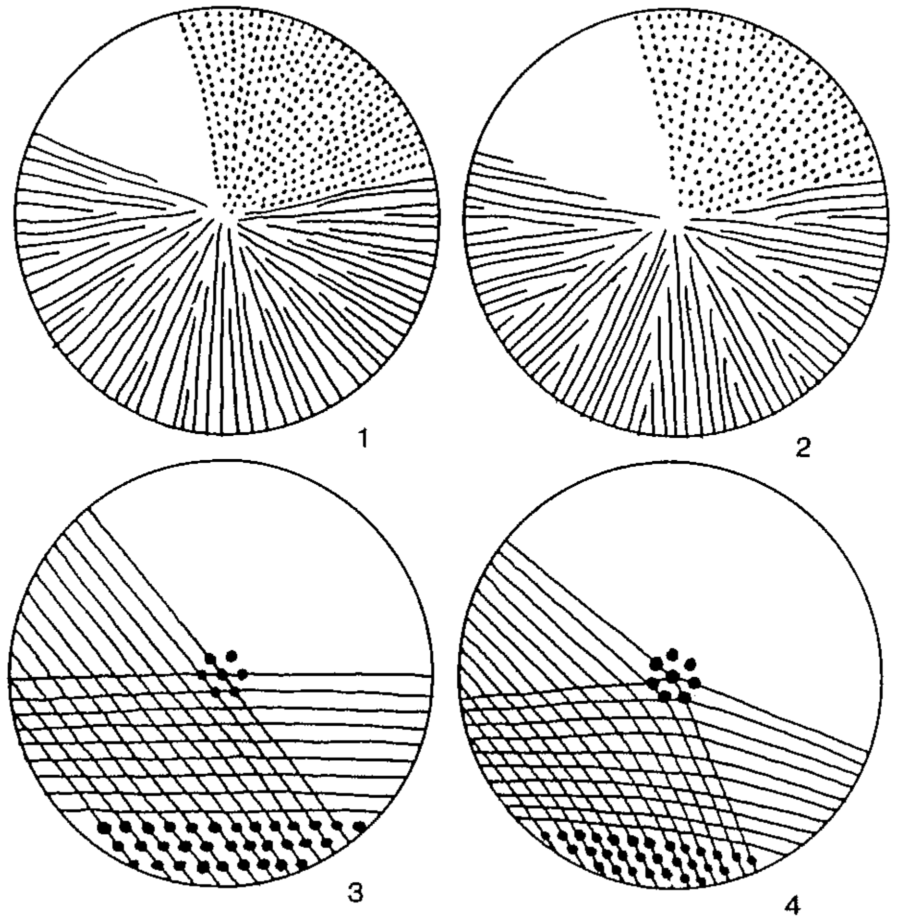


Plate 11.3. Stylized drawings of areolae patterns in *Thalassiosira*.

Fig. 1. Radial bifurcating array

Fig. 2. Fasciculated pattern. Note that areolae rows in each fascicle are parallel to the central row.

Fig. 3. Linear array. Six areolae surround the central areola; pattern of parallel rows of areolae is continuous across the face of the valve.

Fig. 4. Eccentric pattern. Seven areolae surround the central areola; pattern of adjacent, curved rows of areolae is continuous only from the margin to the central areola.

Figs taken from Johansen and Fryxell (1985)

6) Strutted processes on valve face
7) Number and location of labiate processes
8) Location of labiate process(es) in the marginal ring of strutted processes
9) Areolae array and size

THALASSIOSIRA

Key to species found in the Arctic

1a Valves flattened or curved 2
1b Valves tangentially undulated ....*T. hyperborea*
2a One central process 3
2b More than one central process 11
3a Processes with external tubes 4
3b Processes with long internal tubes 5
4a Bases of marginal strutted processes distinctively withdrawn from valve margin 6
4b Bases of marginal processes close to margin 7
5a Labiate process close to valve centre ....*T. bioculata*
5b Central strutted processes in distinct rows 8
6a External tubes of labiate and strutted processes of approximately same length 9
6b External tube of labiate process extremely short and located between two close-set strutted processes which are larger than the others ....*T. conferta*
7a Bases of strutted processes distinctly swollen, labiate process midway between two strutted processes ....*T. bulbosa*
7b Labiate process taking the place of a strutted process, ribs on valve margin ....*T. pacifica*
8a Central strutted processes in one row, marginal strutted processes wide apart, 8-10 μm between them ....*T. poroseriata*
8b Central strutted processes in one or two rows, marginal strutted processes closer together, 4-6 μm between them ....*T. trifulta*
9a Bases of marginal processes 2-4 areolae from margin 10
9b Bases of marginal processes 7-8 areolae from margin ....*T. nordenskioeldii*
10a Labiate process always close to one strutted process, strutted processes wide apart, 3 in 10 μm ....*T. angulata*
10b Labiate process usually midway between two strutted processes, strutted processes closer, 5 in 10 μm ....*T. hispida*
11a Central cluster of strutted processes 12
11b Subcentral ring of strutted processes 13
12a One marginal ring of strutted processes 14
12b More than one marginal ring of strutted processes 15
13a Ring of isolated strutted processes midway between valve centre and margin, marginal processes close-set, 7-8 in 10 μm ....*T. kushirensis*
13b Ring of groups of strutted processes midway between centre and margin, marginal processes widely space, 3-4 in 10μm ....*T. anguste-lineata*
14a Valves extremely weakly silicified, marginal processes widely spaced, 3-5 in 10 μm .....*T. constricta*
14b Valve areolae resolvable in LM, marginal processes closer, 5-9 in 10 μm ....*T. hyalina*
15a One marginal labiate process 16
15b More than one labiate process ....*T. baltica*
16a Weakly silicified valves, 2-3 marginal rings of strutted processes ....*T. antarctica* var. *borealis*
16b Scattered strutted processes on valve face ....*T. gravida*

Plate 11.4. Line drawings of species found in high Arctic waters: a = colonies in girdle view X500; b = valves with processes X1000. Scale bars = 10 μm.

Fig. 1 *Thalassiosira bioculata*

Fig. 2 *Thalassiosira bulbosa*

Fig. 3 *Thalassiosira hyalina*

Fig. 4 *Thalassiosira antarctica* var. *borealis*

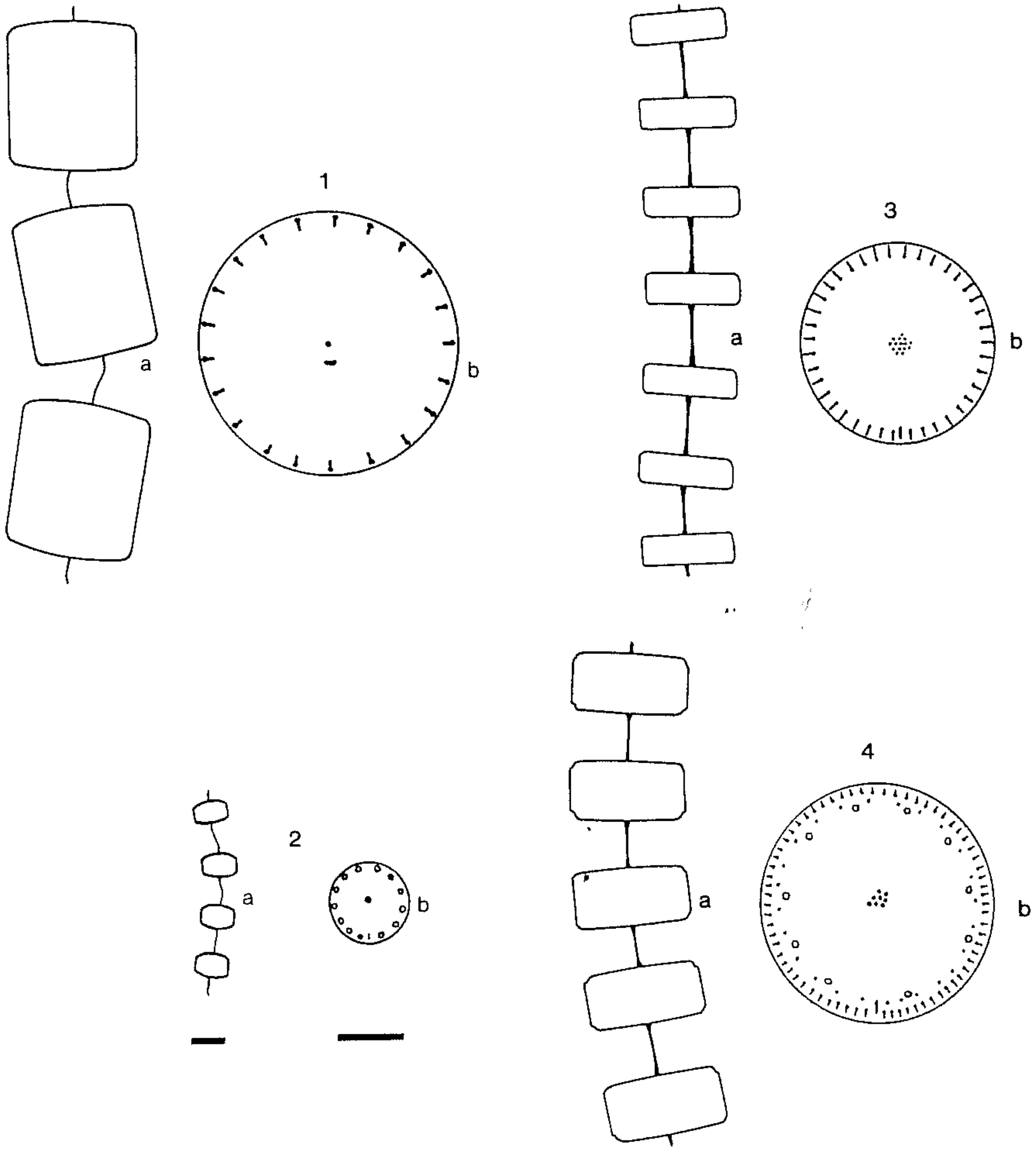


Plate 11.5. Line drawings of species found in Subarctic-Temperate waters: a = colonies in girdle view X500; b = valves with processes X1000. Scale bars = 10 μm.

Fig. 1 *Thalassiosira nordenskioeidii*

Fig. 2 *Thalassiosira constricta*

Fig. 3 *Thalassiosira poroseriata*

Fig. 4 *Thalassiosira gravida*

Fig. 5 *Thalassiosira kushirensis*

Fig. 6 *Thalassiosira conferta*

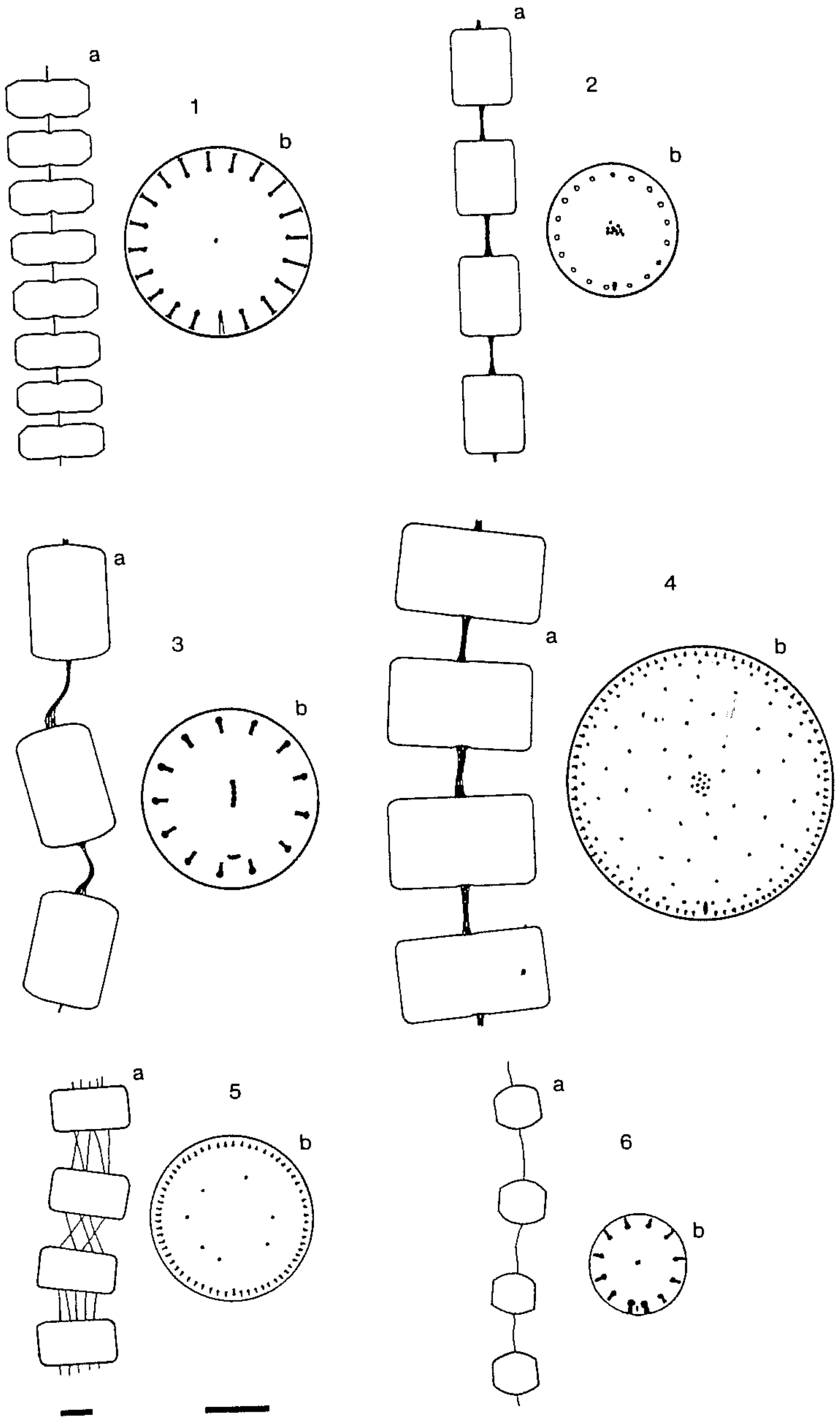


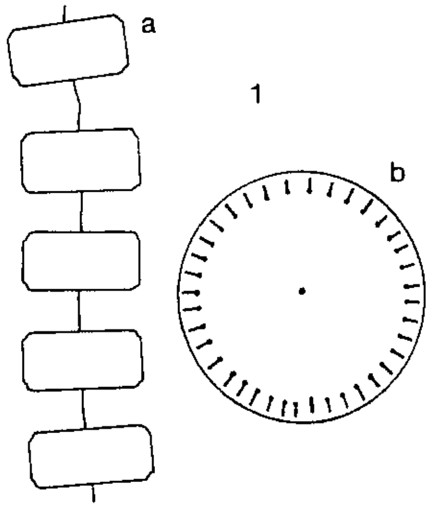
Plate 11.6. Line drawings of species found in Subarctic-Temperate waters: a = colonies in girdle view X500; b = valves with processes X1000. Scale bars = 10 μm.

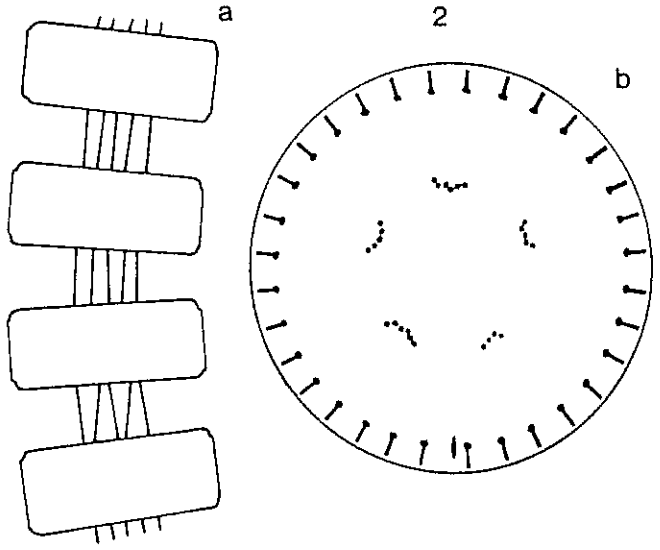
Fig. 1 *Thalassiosira pacifica*

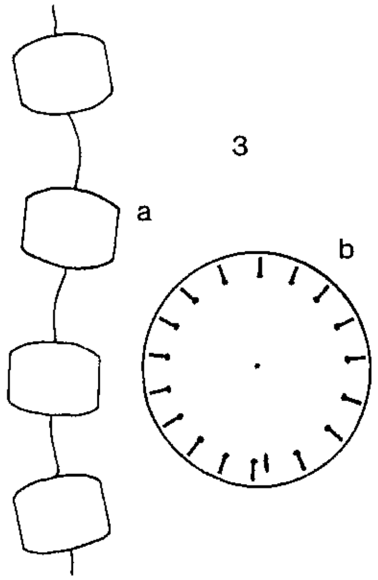
Fig. 2 *Thalassiosira anguste-lineata*

Fig. 3 *Thalassiosira angulata*

Fig. 4 *Thalassiosira hispida*







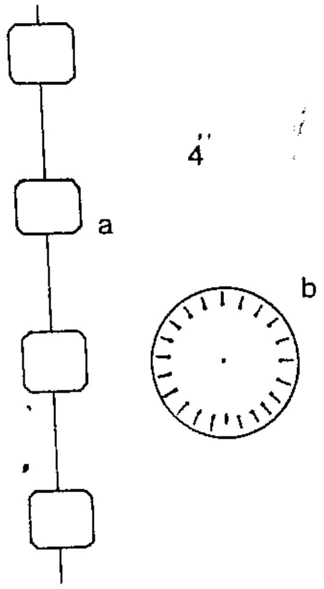
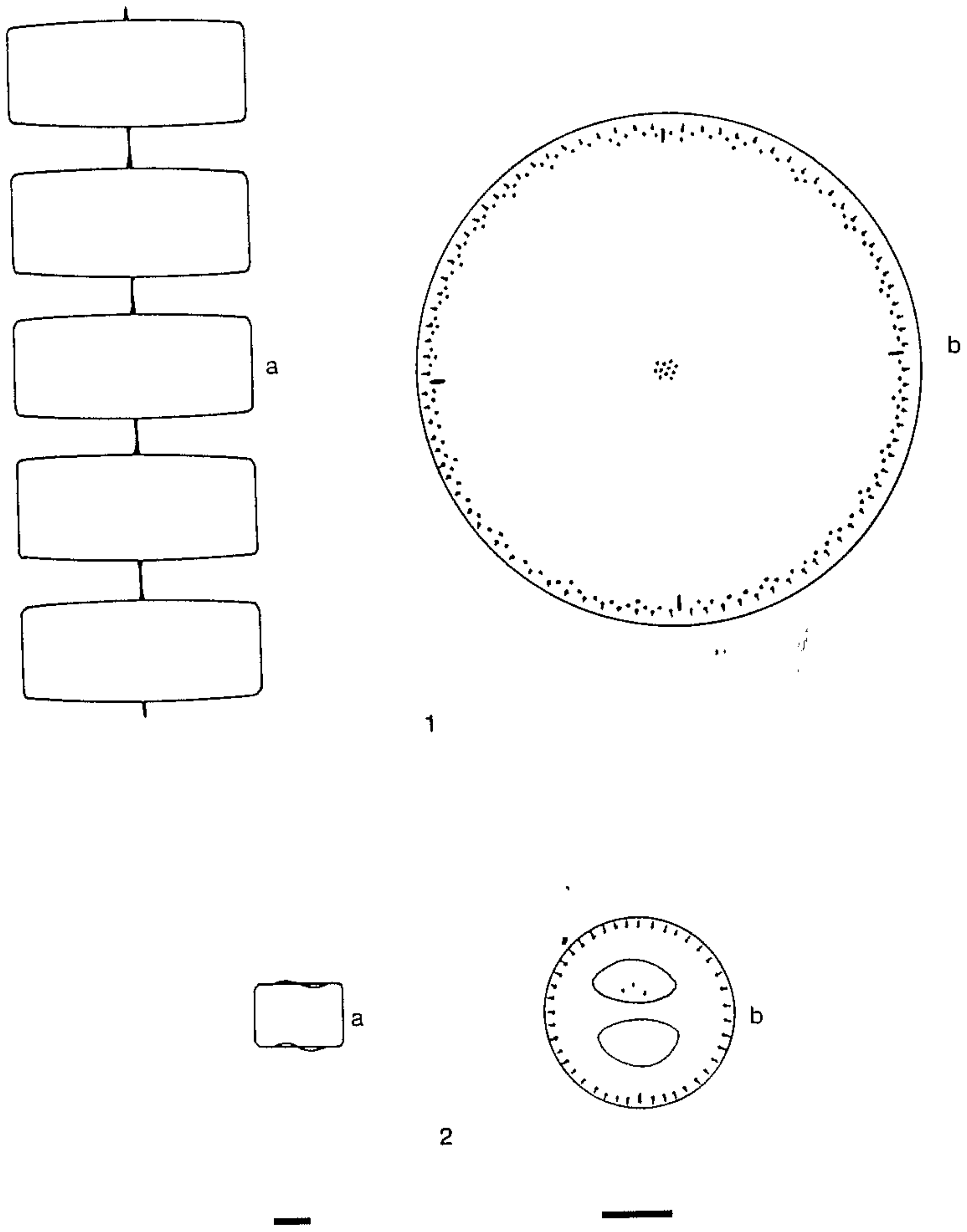


Plate 11.7. Line drawings of species found in Arctic brackish waters: a = colonies in girdle view X500; b = valves with processes X1000. Scale bars = 10 μm.

Fig. 1 *Thalassiosira baltica*

Fig. 2 *Thalassiosira hyperborea*



SECTION 2

THALASSIOSIRA

Key to species and varieties found in the Antarctic

1a Strutted processes scattered evenly over valve face, positioned between areolae; labiate processes not visible due to heavy silicification of valves; areolae pattern linear .... *T. tumida*
1b Not having all characters as described above 2
2a Fasciculated to linear areolae pattern: strutted processes scattered over valve face; 2-10 radially oriented labiate processes .... *T. tumida*
2b Only one labiate process or labiate process not visible 3
3a Labiate process inside and set off from the marginal ring of strutted processes 4
3b Labiate process marginal 13
4a Labiate process more than halfway towards the centre; diameter 42-65 µm; central cluster of processes may be indistinct, as few as one central process present .... *T. ritscheri*
4b Diameter less than 40 µm not having the labiate process more than halfway towards the centre and having central strutted processes either adjacent, often in a row, or solitary 5
5a Areolation fine, 18-22 in 10 µm: central strutted process quite eccentric on larger valves; labiate process usually distinct, eccentric: few marginal strutted processes, diameter 6-15µm .... *T. perpusilla*
5b Areolation coarser than 16 in 10 µm in valve centre, may be as fine as 20 in 10 µm at valve margin 6
6a Central areolae distinctly larger than marginal areolae; only one central strutted process present 7
6b Central areolae not distinctly larger than marginal areolae; 1-8 central strutted processes present 9
7a Areolae 5-10 in 10 µm in the centre, 9-12 in 10 µm near the margin; labiate process 2-3 areolae distant from central strutted process .... *T. oestrupii*
7b Areolae 16-20 in 10 µm near the margin; labiate process almost marginal, often difficult to discern 8
8a Central areolae very coarse, 8-12 in 10 µm .... *T. gracilis*
8b Central areolae not as coarse, 14-15 in 10 µm .... *T. gracilis* var. *expecta*
9a Areolae pattern radial, bifurcating or fasciculated 10
9b Areolae pattern irregularly linear, sublinear, or linear 11
10a Central strutted processes adjacent, usually in a row; marginal strutted processes 1-2 in 10 µm .... *T. poroseriata*
10b Central strutted processes irregularly scattered in a loose cluster on valve face; marginal strutted processes 4-6 in 10 µm .... *T. poro-irregulata*
11a Areolae 5-7 in 10 µm; areolae pattern sublinear to linear; 1-4 adjacent central strutted processes; labiate process 8-9 (5-12) areolae distant from central processes .... *T. trifulta*
11b Areolae 8-18 in 10 µm; areolae pattern irregularly linear or irregularly eccentric 12
12a Operculate strutted processes with pores visible at bases of marginal processes; marginal striae 24-30 in 10 µm .... *T. frenguelliopsis*
12b Trifultate strutted processes with pores not visible at bases of marginal processes; marginal striae 15-18 in 10 µm .... *T. frenguellii*
13a Strutted processes with internal extensions of the tubes .... *T. oliverana*
13b Strutted processes with external extensions of the tubes or extensions absent 14
14a Strutted processes on valve face 15
14b Strutted processes only in the centre and margins, not on the valve face 18
15a Strutted processes in compact clusters on valve face, appearing as patches of heavier silicification; one ring of marginal strutted processes present; one ring of occluded processes may be present .... *T. australis*
15b Strutted processes scattered over the valve face 16
16a One to many central strutted processes, external tubes of the strutted process can be discerned at the valve margin; areolae about 20 in 10 µm .... *T. gravida*
16b No distinct central cluster of strutted processes, no external tubes present on strutted processes; areolae less than 15 in 10 µm 17
17a No extensions on the tubes of strutted process, which look like very small areolae; single labiate process distinctly visible, radially oriented .... *T. lentiginosa*
17b Strutted processes possessing internal extensions of the tubes; single labiate process parallel to marginal tangent may be difficult to discern ...... *T. maculata*
18a Areolae about 30 in 10 µm; diameter 25 µm or less 19
18b Areolae less than 24 in 10 µm 20
19a Single central strutted process, diameter 10-13 µm .... *T. ambigua*
19b Siliceous radial or concentric extensions of areolae walls on valve face often present on the exterior of the valve; 1-6 central strutted processes; diameter 15-25 µm .... *T. dichotomica*
20a Single ring of marginal strutted processes with external tubes, which are clearly visible in the light microscope .... *T. gerloffi*
20b At least two rings of marginal strutted processes present, though may be difficult to discern; occluded processes may be present 21
21a Occluded processes may be present, marginal striae absent; valves flat 22
21b Occluded processes consistently present; marginal striae present, though may be reduced or absent; valves heavily silicified, may be arched 23
22a Areolae 9-16 in 10 µm; occluded processes usually present; central cluster of 8-25 strutted processes .... *T. scotia*
22b Areolae 15-24 in 10 µm; occluded processes may be present, but difficult to discern; central cluster of 4-14 strutted processes .... *T. antarctica*
23a Areolae 5-8 in 10 µm; very heavily silicified .... *T. scotia* (resting spore)
23b Areolae 7-12 in 10 µm; heavily silicified .... *T. antarctica* (resting spore)

Modified from Johansen and Fryxell (1985)

Table 11.3. Morphometric and distributional data on *Thalassiosira* spp. in Antarctic Waters

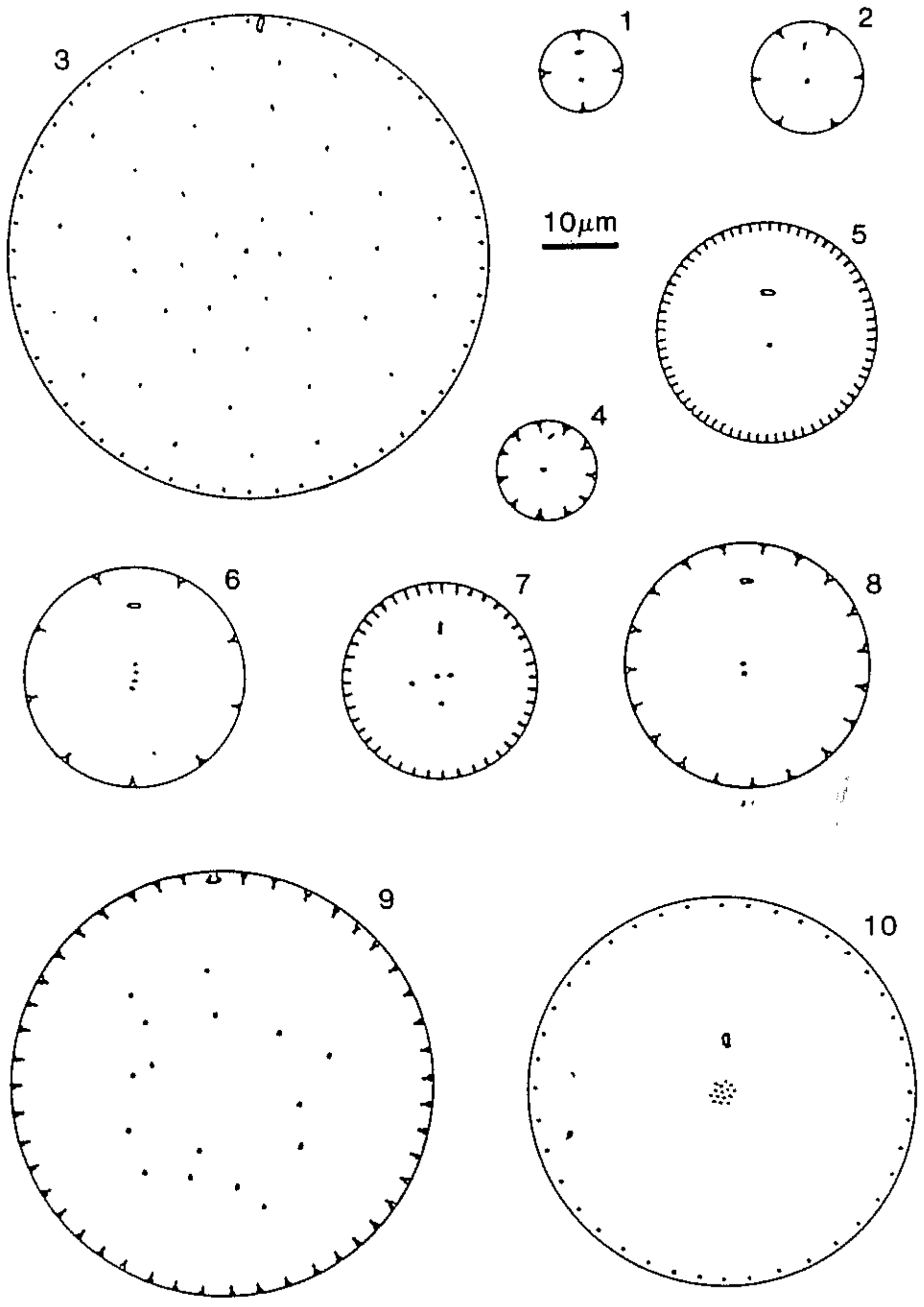
Taxa	Diameter (µm)	Areolae in 10 µm Centre	 Tangential	Pattern	Strutted processes Mantle (in 10 µm)	 Central (No.)	 Greater projection	Labiate processes No.	 Position	Occluded Processes in 10 µm	Polar distribution
T. ambigua Kozlova	6.5–14	24–32	—	Radial	6–10	1–2	Outside, operculate	1	In marginal ring	—	Antarctic plankton
T. antarctica Comber	16–56	15–24	—	Radial, bifurcating	8–16 in outer ring	4–14	Outside, operculate	1	Inside inner ring	0–4	Antarctic, near ice
T. antarctica resting spores	13–44	8–12	—	Radial	3–6 in outer ring	2–6	Outside, operculate	1	In occluded process ring	2–5	Antarctic near ice
T. australis Peragallo	23–56	11–13	14–16	Radial, bifurcating	4-5 (-9)	Clusters on face	Outside, operculate	1	In occluded process ring	3–4 (0–5)	Antarctic often benthic
T. dichotomica (Kozl.). Fryx. & Hasle.	15–22	ca.30	—	Radial	3–7	1–6	Outside, operculate	1	Inside single ring	—	Antarctic often coastal
T. frenguellii Kozlova	12–25	7–16	striae 15–18	Irregular, eccentric	1–2	1–2	Inside, trifultate	1	4–5 areolae from centre	—	Antarctic
T. frenguelliopsis. Fryx. & Johan.	12–34	7.5–16	< 18 striae 24–30	Linear, eccentric	1–2	1	Inside, operculate	1	Away from margin	—	Subantarctic
T. gerloffii Rivera	16–77	13–18	12–20	Fasciculated	6–9 (5–11)	2–9	Outside, operculate	1	In marginal ring	—	Antarctic, subantarctic
T. gracilis (Kars.) Hust.	5–28	8–12	16–20	Coarser in centre	3–4	1	Inside, operculate	1	Away from margin	—	Antarctic, subantarctic
T. gracilis var. *expecta* (Van Land.). Fryx. & Hasle	7–26	14–15	16–20	Radial	3–4	1	Inside, operculate	1	Away from margin	—	Antarctic, subantarctic
T. gravida Cleve	13–62	ca.20	—	Radial, fasciculated	6	Small cluster	Outside, operculate	1	Large, near margin	—	Subantarctic, Antarctic
T. lentiginosa (Jan.). Fryxell	29–120	7–9	—	Fasciculated	3–4	On valve face	No projection, operculate	1	Slit near margin	—	Antarctic plankton
T. maculata. Fryx. & Johan.	23–71	8–12	14	Fasciculated	2–4	On face only	Inside, operculate	1	Parallel to margin	—	Antarctic plankton
T. oestrupii (Ost.) Hasle	7–60	5–10	9–12	Eccentric	6–8	1	Inside, trifultate	1	Away from margin	—	Cosmopolitan
*T. oliverana** (O'Meara) Mak.	23–60	7–8	9–14	Radial, irregular	3	On face only	Inside, operculate	1	Large, near margin	—	Antarctic, subantarctic
T. perpusilla Kozlova	5–15	18–24	—	Irregular	1–2	1 off centre	Inside, operculate	1	Away from margin	—	Antarctic, subantarctic
T. poro-irregulata Hasle & Heim.	17–40.5	10–15	—	Fasciculated	4–6	Irregular 1–8	Inside, trifultate	1	Away from margin	—	Subantarctic, Antarctic
T. poroseriata (Ramsf.) Hasle	14–38	11–16	—	Fasciculated	1–2	Adjacent, 1–8	Inside, trifultate	1	Away from margin	—	Antarctic, subantarctic
T. ritscheri (Hust.) Hasle	42–72	12–16	—	Fasciculated or linear	3–4	Many, cluster	Inside, operculate	1	Near centre, radial	—	Antarctic, ice edge
T. scotia. Fryxell & Hoban	15–53	9–16	—	Fasciculated bifurcate	6–8	8–25	Outside, operculate	1	In occluded process ring	2–5	Subantarctic
T. scotia resting spore	18–46	5–8	striae 10–11	Radial	3–7	7–12	Outside, operculate	1	In occluded process ring	robust, long, 3–5	Subantarctic
T. trifulta. Fryxell	16–58	5–6	6–7	Radial	2–3	1–4	Inside, trifultate	1	Away from margin	—	Subantarctic, Antarctic
T. tumida (Jan.) Hasle	21–137	4–14	—	Linear, sublinear	4–5	6–23	Outside, operculate	2–10	Near margin, radial	—	Antarctic, subantarctic

*Not illustrated

Plate 11.8. Stylized drawings of process patterns of Antarctic *Thalassiosira* species lacking external tubes.

- **Fig. 1.** *T. perpusilla.*
- **Fig. 2.** *T. frenguellii* and *T. frenguelliopsis.*
- **Fig. 3.** *T. lentiginosa.*
- **Fig. 4.** *T. gracilis*, both varieties.
- **Fig. 5.** *T. oestrupii.*
- **Fig. 6.** *T. poroseriata.*
- **Fig. 7.** *T. poro-irregulata.*
- **Fig. 8.** *T. trifulta.*
- **Fig. 9.** *T. maculata.*
- **Fig. 10.** *T. ritscheri.*

Figs from Johansen and Fryxell (1985)



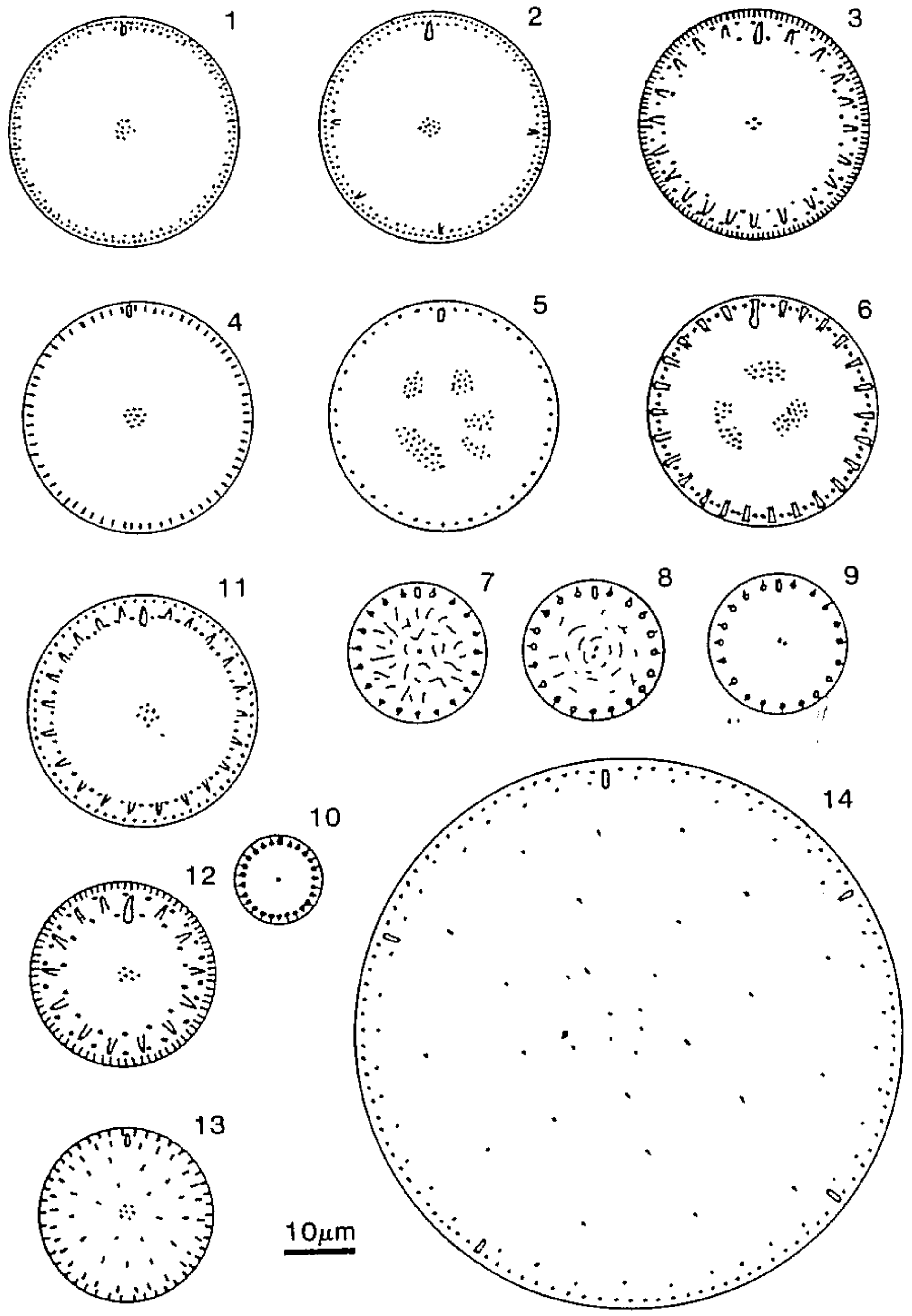


Plate 11.9. Stylized drawings of process patterns of Antarctic *Thalassiosira* species possessing external tubes.

Figs 1, 2. *T. antarctica*, vegetative cells.

Fig. 3. *T. antarctica* var. *antarctica*, resting spore.

Fig. 4. *T. gerloffii*.

Figs 5, 6. *T. australis*.

Figs 7-9. *T. dichotomica*.

Fig. 10. *T. ambigua*.

Fig. 11. *T. scotia*, vegetative cell.

Fig. 12. *T. scotia*, resting spore.

Fig. 13. *T. gravida*.

Fig. 14. *T. tumida*.

Figs from Johansen and Fryxell (1985)

CHAPTER 12

FAMILY LEPTOCYLINDRACEAE

David P. Thomas and P. I. Bonham

GENUS CORETHRON Castracane

Corethron is an unusual diatom, both in the presence of movable spines attached to the valve mantle and for the unidirectional heteropolarity of the division process. This has led some people to suggest that it is not a diatom at all!

The cells are heterovalvate and cylindrical with a cingulum of numerous elements joining upper and lower domed valves. The upper valve carries two types of spines, one long and barbed, the second shorter and terminating with a heavily silicified claw or hook, which fit into chambers along the margin of the valve. These chambers are characteristic for each different type of spine and are best observed in the SEM. The lower valve (hypovalve) carries only barbed spines, slightly different in structure, size and method of attachment, to those of the upper valve. Within the confines of the cingulum prior to cell division, the spines all point in the same direction. Once the cell divides and the cingulum no longer contains the spines in their vertical position, the spines swivel in their chambers until they come to rest at about a 45° angle to the valve. The spines of the lower valves, when released from the maternal cingulum, are constrained to about 60° from the pervalvar axis by projections in the chambers. The structure of the lower valves differs primarily in the structure of these projections. *C. inerme* Karsten (1905, p. 104, pl. 13/11-17) forms an additional 'vegetative' valve type with short spines which assist the cells in forming long colonies.

How to identify to species:
Hendey (1937) proposed that 11 described species of *Corethron* were in fact members of a polymorphic species. We agree with this stance except in the case of *C. inerme*.

The easiest differentiation between the two species is the presence of colony formation in *C. inerme* versus solitary cells in *C. criophilum* Castracane (1886, p. 85, pl. 21/14). Furthermore, a careful observer can differentiate the different hook shapes and discern the more silicified nature of the *C. criophilum* frustule in water mounts. Cells normally lie in girdle view.

Characters to look for in valve view:
1) The valve surfaces are essentially the same, appearing in the light microscope as hyaline and unstructured (i.e. lacking any tube process) except at the margin where the marginal chambers containing the spine bases are evident. *C. inerme* is generally much less robust and more weakly silicified than *C. criophilum*.

Characters to look for in girdle view:
1) The girdle view shows *C. criophilum* (Plate 12, Fig. 1) as solitary whereas *C. inerme* (Plate 12, Fig. 2) is more commonly found in colonies, sometimes up to 30-40 cells long and held together by short, interdigitated spines. In our observations the long-spined valves are rare in *C. inerme* and seem to act as separation valves in this species.
2) The cingulum is visible in wet mounts of *C. criophilum* and composed of ligulate open bands (Plate 12, Fig. 3). The cingulum of *C. inerme* is rarely visible, but can be resolved as being composed of half bands (Plate 12, Fig. 4) if an empty frustule is seen in phase contrast.
3) The hooked spines terminate in robust, hook-like structures which are discernable in the light microscope. In *C. criophilum* the hook has a thickened, finger-like projection at the distal extreme of the spine, and at right angles to the spine, and a second, parallel to the first, which projects out from the spine in the same direction. The net result is a hook with two internal angles (Plate 12, Fig. 5). In *C. inerme* the hook has a single free projection at the distal extreme of the spine and at about 60° to the spine (Plate 12, Fig. 6) to form only one internal angle.
4) The 'intercalary' valves of *C. inerme* are generally less convex than the 'separation' valves. The spines on the intercalary valves are more numerous than those on the separation valves (i.e. 15 in 10 µm vs 3-5 in 10 µm) and are angled at 45° to the valve face while remaining in the plain set by the cingulum.

Key to species:
1a. Cells solitary, robust, forming only separation valves either with both hooked and long spines or just long spines. All cells heterovalvate ....*C. criophilum*
1b. Cells usually in colonies, weakly silicified, forming both separation valves and intercalary valves. The latter with short spines which interlock with those of the same valve type of an adjacent cell. Only end cells of a colony are heterovalvate ....*C. inerme*

Ecology: Both species are marine, planktonic and achieve their greatest densities in the Southern Ocean south of the Antarctic Polar Front. *C. inerme* has been observed in our material as far north as the Subantarctic Front in the region south of Australia but is generally circumpolar in its recorded distribution from other authors. *C. criophilum* has a more cosmopolitan distribution through tropical waters to the Arctic. See also Fryxell and Hasle (1971) for SEM observations.

Plate 12. Line drawings of *Corethron* spp. Scale bars = 10 μm.

Fig. 1. Predivision cell of *C. criophilum* from Tasmanian waters.

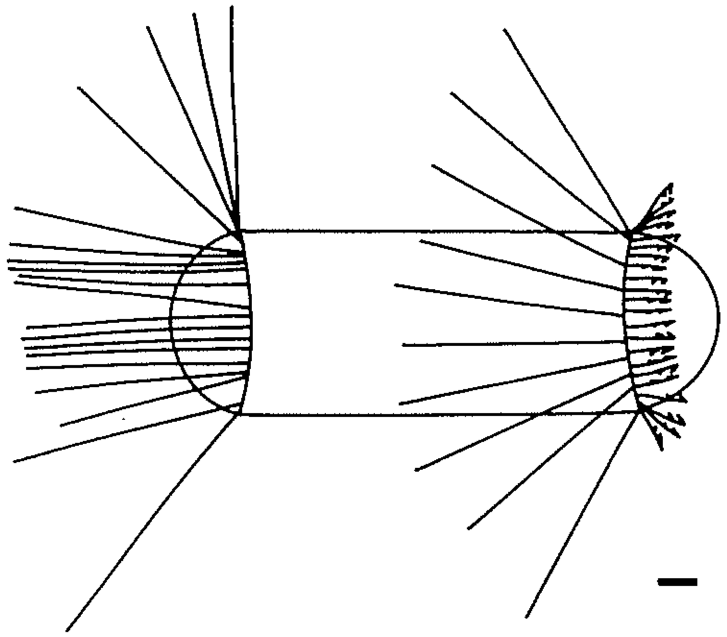
Fig. 2. Cell of *C. inerme* showing separation valves with typical *Corethron* displacement of hooked and long spines.

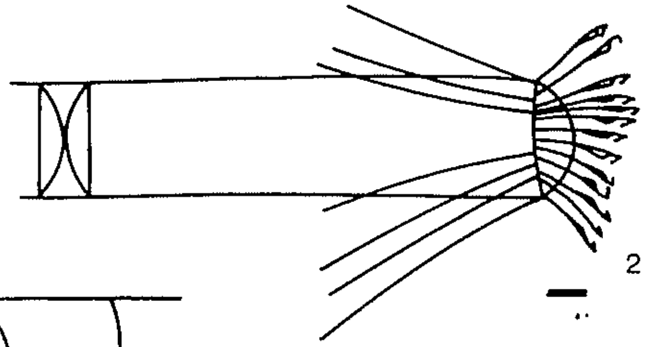
Fig. 3. Cingulum of *C. criophilum* showing the alternating, ligulate, open bands.

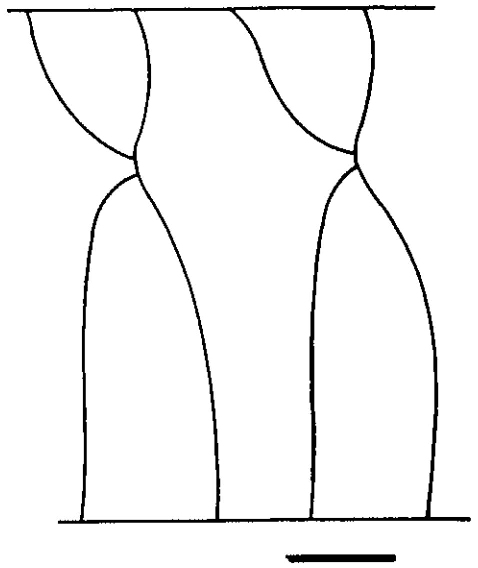
Fig. 4. Cingulum of *C. inerme* showing the parallel rows of half bands with those forming the valvocopula (VC) on the left.

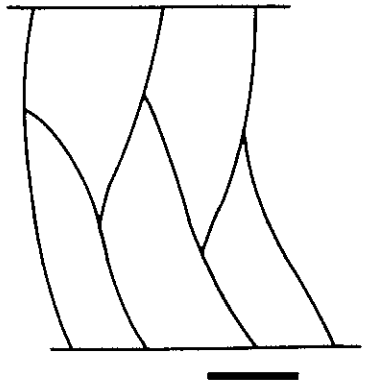
Fig. 5. Detail of the hooked spine of *C. criophilum*.

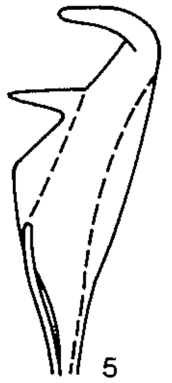
Fig. 6. Detail of the hooked spine of *C. inerme*.


1

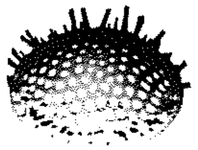

2


3


4


5


6



CHAPTER 13

FAMILY COSCINODISCACEAE

Grethe R. Hasle and Erik E. Syvertsen

GENUS STELLARIMA Hasle & Sims

This genus is represented in the Antarctic by *S.microtrias* (Ehrenberg) Hasle & Sims. The most conspicuous morphological features are the presence of central labiate processes and the absence of marginal processes. Resting spores are frequently present in ice-samples and in net-samples collected in the vicinity of the ice. The vegetative cells and the resting spores were in the past described as two distinct *Coscinodiscus* species: *C. furcatus* with furcate areolation and *C. stellaris* var. *symbolophora* with fasciculate areolation (see Syvertsen, 1985).

How to identify:
Vegetative cells as well as resting spores can be identified in water mounts.

Characters to look for to distinguish between vegetative cells and resting spores:
1. Type of areolation
2. Size of areolae

Table 13.1. Morphometric data on *Stellarima microtrias*

	Diameter in μm	*Areolation*	*Areolae in 10 μm*	*Labiate processes*
Vegetative cells	35–105	furcate	11–16	2–8
Resting spores	40–199	fasciculate	9–12	3–5

For further information see Hasle and others, 1988.

Plate 13.1. Stylized drawings of *Stellarima microtrias*. Scale bar = 10 μm.

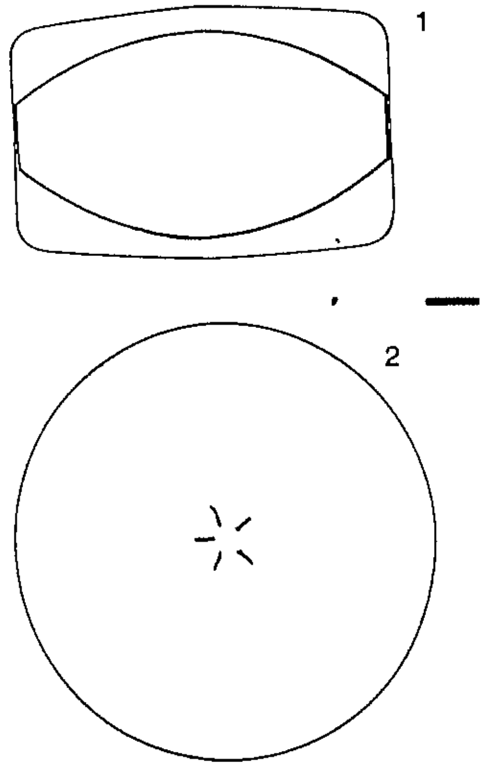


Fig.1. Cell with resting spore, girdle view

Fig.2. Single valve.

CHAPTER 14

FAMILY HEMIDISCACEAE

Greta A. Fryxell

GENUS ACTINOCYCLUS Ehrenb.

Cells are drum-shaped, mostly net plankton (20 µm in diameter), with either no external projections or with external projections very much reduced in living species. Girdle bands are apparently hyaline and few in number (2-3), with the valvocopula providing most of the pervalvar distance on a newly divided cell. Colony formation has not been observed.

Valves have radial, fasciculated, and/or decussating rows of areolae. Usually each valve possesses a pseudonodulus, an opening more or less occluded on the outside or inside by siliceous or organic material (areolate, areolate-operculate, or luminate). Fasciculation, if present, is of two types: rows within a bundle lying parallel to a complete radial row at the edge or lying parallel to a complete row in the middle of the bundle. A central thickened ring (annulus) may be present, enclosing several areolae. The mantle is often deep and is commonly at right angles to the valve face, with areolae on the mantle generally reduced to about half the size of valvar areolae. This change in size can be noted even in valve view with LM, by the number of apparent "marginal striae" observed in 10 µm.

At the near-margin end of some complete radial rows lies a labiate process, lacking an external tube or even with the external opening recessed (at least in the four species discussed here) and an expanded internal anvil- to spade-shaped terminus on a neck of varying length in different species. The fine structure of these processes varies with the species and is best seen with SEM, but in all of the species here, the slits of the processes lie roughly parallel to the margin instead of being radially orientated. They can, however, be slightly canted from the circumference, even giving an apparent polarity to the valve. These observations can be made under favourable conditions with LM or at some angles with SEM.

More detailed SEM and TEM observations on the genus *Actinocyclus* can be found in Andersen, Medlin and Crawford (1986); Simonsen (1975, 1982); Villareal and Fryxell (1983); Watkins and Fryxell (1986).

How to identify to species:
In most cases, whole cells of *Actinocyclus* are very difficult to identify with LM or SEM. Internal views of material gently cleaned of organic matter allow the clearest view of many characters, but there are many similarities in major features as can be seen in Plate 14.1, Figs 1-3. Characters to consider include: diameter; areola size and pattern, including the presence or absence of a central ring; mantle depth and ornamentation; shape and orientation of labiate processes. Processes are usually widely spaced with a great deal of variation in distance apart.

Characters to Look for in Girdle View:
Look for drum-shaped cells with flat valves and rounded edges, sometimes with the valves possessing a deep mantle at right angles to the face of the valve. Projections are lacking, but the processes can be seen, particularly in bright field at low contrast.

Characters to Look for in Valve View:
Specific characters can be considered with species being included here: *Actinocyclus actinochilus*, *A. cholnokyi*, *A. exiguus* and *A. spiritus*.

Small size sets apart *A. exiguus* (Plate 14.1, Fig. 2), and the areola pattern with isolated rows set off by hyaline spaces in *A. actinochilus* is distinctive (Plate 14.1, Fig. 1). The number of areolae in 10 µm on the valves of *A. spiritus* provides a distinctive character (Plate 14.1, Fig. 3). It is not only finer in structure than others in its general size range, but this diatom was named for its "ghostlike" appearance usually encountered in cleaned preparations. Unlike most others in the genus, it is lightly silicified under field conditions. *Actinocyclus cholnokii* is problematic at best (See Priddle and Fryxell, 1985, pp. 104, 105; Hustedt, 1930, figure 218 as *Coscinodiscus divisus* Grunow). The range of areola size and wide geographical distribution we have observed arouses the suspicion that more than one taxon may be involved. But the tendency toward the *Coscinodiscus*-like decussating arcs of areola, plus the slightly fasciculated pattern with the central ring of areolae, set it apart from others in this treatment. Unless the valve is eroded, the areolate pseudonodulus is difficult to see, even in bright field. However, these areolae are smaller and less regular than those adjacent to it. Omitted from this study is *A. curvatulus* Janisch. Unpublished observations of fine structure suggest that several taxa are included in thus taxon and good field characters and geographical distribution have not been well documented.

GENUS AZPEITIA M. Per.

Cells range from drum shaped to coin shaped, with hyaline bands and large valvocopula, similar to *Actinocyclus*. There are few external projections in living species. Valves are generally flat, and mantles of living species are well developed, distinctive, and even ornate. The annulus near the geometrical centre of the valve is well-defined in some species, and a labiate process is at the periphery of this ring. Labiate processes near the mantle/valve interface are mostly simple, large, low-lying forms with the slits running nearly parallel to the circumference of the valve. However, their oblique

Table 14.1. Morphometric data on polar *Actinocyclus* and *Azpeitia* spp.

Species	*Diameter* *µm*	*Labiate* *µm*	*Structure**	*Areolae in 10 µm*	*Pattern*	*Mantle structure*	*Pseudo-nodulus*	*Polar distribution*
Actinocyclus actinochilus (Ehrenb.) Sim.	20–112	9.5–15 apart	Laterally expanded, open abvalarly	5–11	Isolated radial rows	Striae 13–21 in 10µm	Variable	Antarctic, ice edge
A. cholnokyi Van Land.	41–70	8–15 apart	Laterally expanded	7–9	Slightly fasciculated, decussating rows	Striae 20–24 in 10 µm	Areolate or eroded	Antarctic, cosmopolitan
A. exiguus G. Fryx. & Sem.	6.5–13	3–5 per valve	Slightly expanded	15–18	Irregular radial rows	Areolae 21–24 in 10 µm, thin flange	Not visible in LM	Antarctic, Subantarctica
A. spiritus Watkins	27–64	8–12	Slightly expanded	13–15	Fasciculated	Striae 24–29 in 10 µm	Open?	Antarctic, ice edge
Azpeitia tabularis (Grun.) Fryx. & Sims	16–70	7–12	Laterally expanded reduced neck	6–9 (–10)	Slightly fasciculated	Multiple rows of areolae with rhombic chambers	Lacking	Subantarctic, rarely near ice

* Internal fine structure

orientation can give polarity to the valve. Symmetry ranges from a small step away from biradial because of the slightly off-centered labiate processes to a complex overlaying of different symmetries. See Fryxell, Sims and Watkins (1986) for a fuller treatment of this genus.

How to identify to species:
Only one species is in Antarctic waters, and it is more common in subantarctic water north of the Antarctic Convergence Zone (AACZ). *Azpeitia tabularis* has the general characteristics of the genus. It has a short pervalvar axis, even <10 µm. The slightly off-centred labiate process has no external tube, and areolae are arranged in radial rows that generally run parallel to the outside row. At the outer edge of the valve face, there is a narrow hyaline ring adjacent to the processes and the multiple mantle rows of areolae. The processes appear to interrupt the first row of mantle areolae, providing a distinctive feature in LM.

Characters to Look for in Girdle View:
Azpeitia tabularis is coin shaped in girdle view with no external projections. The rhombic-shaped loculate areolae on the mantle can sometimes be resolved.

Characters to Look for in Valve View:
The hyaline ring between the areolae on the valve and the distinctive mantle structure is a good character, and one that is shared with *Actinocyclus actinochilus*. However, there is no separation of the rows of areolae in *Azpeitia tabularis*, and its near-central process can sometimes be resolved in bright field with LM. Because *Azpeitia* and *Actinocyclus* share many characteristics, the key and the table of morphometric measurements for Antarctic species will include both genera.

Key to Species of *Actinocyclus* and *Azpeitia*:
1a Diameter < 20 µm .... *Actinocyclus exiguus*
1b Diameter > 20 µm 2
2a Hyaline ring near interface of mantle and valve face 3
2b Areolae continuous to mantle 4
3a Areolae in isolated radial rows ....
.... *Actinocyclus actinochilus*
3b Areolae not isolated but in fascicles; nearly central labiate process sometimes visible ....
.... *Azpeitia tabularis*
4a Areolae > 12 in 10 µm; valves lightly silicified
.... *Actinocyclus spiritus*
4b Areolae < 10 in 10 µm, areolate pseudonodulus
.... *Actinocyclus cholnokyi**

*not illustrated

Ecology: Planktonic, widespread latitudinally, with both oceanic and neretic species.

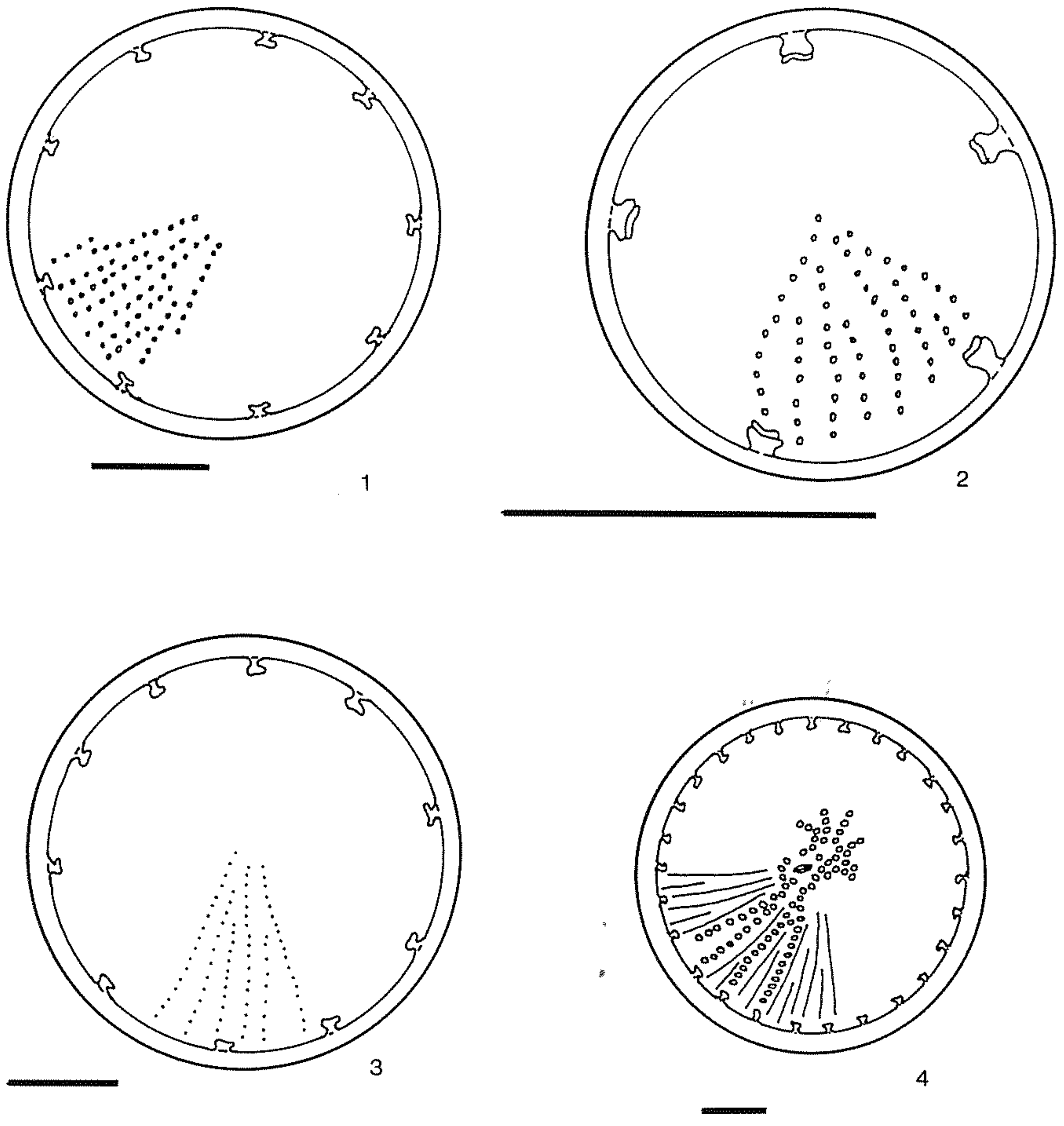


Plate 14.1. Stylized sketches of internal valve views with near-marginal rings of labiate processes. Scales = 10 µm.

Fig. 1. *Actinocyclus actinochilus.*

Fig. 2. *Actinocyclus exiguus.*

Fig. 3. *Actinocyclus spiritus.*

Fig. 4. *Azpeitia tabularis.* Note near-centre labiate process.

CHAPTER 15

FAMILY RHIZOSOLENIACEAE

Julian Priddle, Richard W. Jordan and Linda K. Medlin

GENUS RHIZOSOLENIA Brightwell and related taxa, including the GENUS PROBOSCIA Sundström

Rhizosolenia is an important genus worldwide and may be abundant in both Arctic and Antarctic pelagic communities. In a recent treatment of the genus, Sundström (1986) has identified a number of 'classical' species that fall outside his circumspection of the genus. This is not surprising when one considers that many diagnoses are over a century old and that the criteria used by Sundström are often based on electron- as well as light-microscopical techniques. Unfortunately, he has not been able to complete the necessary descriptions of new species and genera implied by his revision of *Rhizosolenia*, and we refer here to some well-known species in the knowledge that they properly belong to new genera. Such cases are identified below.

According to Sundström (1986), the species list for Antarctic waters is considerably longer than that for the Arctic. This does not appear to reflect density of sampling, as the history of diatom sampling in the Arctic is a long one. The following lists are compiled from his thesis, and from other works.

Rhizosolenia and allied genera from the Antarctic

Section *Rhizosolenia*
  R. antennata f. *antennata* (Ehrenberg) Brown †
  R. antennata f. *semispina* Sundström
  R. crassa Schimper in Karsten
  R. curvata Zacharias
  R. polydactyla f. *polydactyla* Castracane
  R. polydactyla f. *squamosa* Sundström †
  R. sima f. *silicea* Sundström †
  R. sima f. *sima* Castracane
  R. simplex Karsten
  R. styliformis Brightwell ‡

Section *Imbricatae*
  R. chunii Karsten

Proboscia (including *Rhizosolenia* spp. that probably belong in this genus)
  Proboscia sp. cf. *P. alata* (Brightwell) Sundström *
  Rhizosolenia inermis Castracane
  Rhizosolenia truncata Karsten

Other species assigned to *Rhizosolenia* that should be transferred to new genera
  R. cylindrus Cleve
  R. rhombus Karsten

† Sundström (1986) accords form rank to taxa that are almost certainly resting spores of the type form. In some instances he has given the probable spore the type name, while in others the spore carries the form name.

‡ Sundström (1986) regards this species as being easily confused with others and suggests that *R. styliformis* may be restricted to the North Atlantic. This is discussed below.

* Sundström (1986 and personal communication) is of the opinion that his species *Proboscia alata* does not correspond to those specimens commonly described as *Rhizosolenia alata* Brightwell in Antarctic samples. The species name is retained here for light microscope identifications as the distinction is based on fine structural differences visible only with TEM.

Rhizosolenia and allied genera from the Arctic

Section *Rhizosolenia*
  R. borealis Sundström
  R. hebetata f. *hebetata* Bailey†
  R. hebetata f. *semispina* (Hensen) Gran
  R. styliformis Brightwell

Proboscia (including *Rhizosolenia* that probably belong to this genus)
  Proboscia alata Sundström
  Rhizosolenia cf. *R. inermis* Castracane ‡

Other species allied to *Rhizosolenia* which should be transferred to another genus
  R. setigera Brightwell

† As noted above, Sundström (1986) has assigned form rank to the resting spore of the type form.

‡ Sundström (personal communication) notes that a species 'almost indistinguishable from *P. inermis* [sic] in the vegetative stage is found in the Arctic and in the Bering Sea'. Again, we have not attempted to distinguish between this taxon and the nominal species.

How to identify to species:

Identifications using light microscopy are based on the shape of the valve and its process and associated structures, and on the character of the girdle bands (see Fig. 10.5.12). Valves vary in shape from symmetrically conical or rounded to markedly asymmetrical. The girdle bands may be in two or more series, with striation visible in some taxa but not resolvable in others or in lightly silicified specimens. The orientation of girdle bands is referred to the position of the process on the valve - thus the side of the cell where the process is located is designated the dorsal side. Where two rows of girdle bands are present, they commonly form dorsi-ventral rows (where the openings of the valve are in the plane of the apical axis of the valve, e.g. Fig. 15.1.1). Some species have bilateral rows where the band openings are at right angles to this plane (Fig. 15.3.2). The process or projection from the valve in *Rhizosolenia* and allied genera varies in size and shape between species and may carry conspicuous otaria. The contiguous area, where the valve and process of the sibling valve are adpressed when cells are joined, may have a complex structure with siliceous flaps, the claspers, that unite the cells by wrapping around the otaria and the process. In such cases, the ventral part of the valve may be extended and the valve departs from the simple conical form. Valves in some species may bear twin or bifurcated processes; their precise significance is unclear. The genus *Proboscia* lacks a process and the valve apex is elongated into a proboscis. Further details of the morphology of these genera are given by Hustedt (1958), Manguin (1960), Hasle (1975) and Sundström (1986)

Two dichotomous keys are given below, one for the Antarctic and one for the Arctic because of the differing variety of species in the two regions, resulting in different emphasis on certain characters.

Artificial key to Antarctic *Rhizosolenia* and allied genera

1a Valve terminates in a proboscis 2
1b Valves terminate in one, or rarely two, processes ..4
2a Proboscis stout, markedly truncate, more or less parallel to the pervalvar axis of the cell ....*Rhizosolenia inermis*
2b Proboscis less massive and tapering, commonly slightly curved 3
3a Valve acutely conical, proboscis gradually tapering and with a slit at the end ....*Proboscia alata*
3b Valve rounded, proboscis clearly demarcated from the valve and markedly curved ....*Rhizosolenia truncata*
4a Valve bearing two processes ....*R. antennata* f. *antennata*
4b Valve with a single process 5
5a Copulae arranged bilaterally, with a distinct chevron pattern. Cell more or less rectangular in girdle view, with the valve markedly asymmetrical, having an almost flattened face with the process on one edge ....*R. chunii*
5b Copulae in dorsi-ventral columns. Cells with no recognizable symmetry 6
6a Otaria or comparable structures (and claspers) absent, or impossible to resolve using light microscopy 7
6b Otaria (and claspers) present 10
7a Process tubular, ± sigmoid. Copulae in a single pair of columns .....*R. cylindrus* (includes *R. antarctica*)
7b Process straight, tapering uniformly. Copulae in one or more pairs of columns 8
8a Cells large, diameter > 50 µm, and very heavily silicified. Process visibly rough. Copulae in several pairs of columns ....*R. polydactyla* f. *squamosa*
8b Cells generally < 50 µm in diameter. Copulae in one or two pairs of columns 9
9a Valves weakly silicified. Copulae in one or two pairs of columns but very difficult to resolve using light microscopy ....*R. simplex*
9b Valves heavily silicified. Apex of valve and base of uniformly-tapering process rough. Copulae in a pair of columns, easily resolved using light microscopy .. ..*R. sima* f. *silicea*
10a Otaria pointed or angular with part of the margin concave, extending along the basal part of the process 11
10b Otaria not pointed, margin convex 12
11a Otaria relatively small, straight-edged. Process long and slender. Cells not exceeding 45 µm in diameter ....*R. antennata* f. *semispina*
11b Otaria rounded. Process robust and long (about 50 µm). Cells 100-165 µm in diameter ....*R. crassa*
12a Cells 110-280 µm in diameter. Process stout, displaced to valve margin, giving the cell a rhombic shape in girdle view ....*R. rhombus*
12b Cells < 100 µm in diameter, process position and cell shape not as above 13
13a Cells markedly curved, usually solitary, occasionally in pairs or occurring as 'rafts'. Process positioned centrally ....*R. curvata*
13b Cells straight or only slightly curved 14
14a Otaria very conspicuous, extending well away from the swollen base of the otherwise fine process ....*R. sima* f. *sima*
14b Otaria not nearly as wide as long, barely extending onto the process 15
15a Process tapering uniformly ....*R. styliformis*
15b Process of uniform thickness proximally, then tapering rapidly in the distal portion ....*R. polydactyla* f. *polydactyla*

Artificial key to Arctic *Rhizosolenia* and allied genera

1a Valve with a proboscis 2
1b Valve with a process 3
2a Valve conical, merging into a tapering, sometimes slightly curved proboscis ....*Proboscia alata*
2b Valve bearing a massive, straight, truncate proboscis. ....*Rhizosolenia inermis*
3a Process short and stout, rounded ....*R. hebetata* f. *hebetata*
3b Process not as above 4
4a Otaria absent, process very long and needle-like ....*R. setigera*
4b Otaria present 5
5a Otaria pointed, extending a significant distance along the base of the process. Process long and slender. Valve acutely conical, the ventral part prolonged ....*R. hebetata* f. *semispina*
5b Otaria not pointed 6
6a Otaria rounded and extending half-way up the base of the process. Process 15-28 µm, wide at the base and only tapering significantly after half of its length. Valve asymmetrical ....*R. borealis*
6b Otaria inconspicuous, rarely extending onto the process. Process 30-50 µm, tapering more or less uniformly. Valve markedly asymmetrical, with the ventral margin greatly prolonged ......*R. styliformis*

The following species descriptions, derived mainly from Sundström (1986), Cupp (1943), and from personal observations, provide more details to use in identifying *Rhizosolenia* and allied species. A number of species and subspecific taxa present similar features when examined using the light microscope, so we have dealt with these in groups, each introduced by a short note, so as to highlight comparisons. Unlike the keys, we have not separated Antarctic and Arctic taxa.

GENUS RHIZOSOLENIA Brightwell

Section *Rhizosolenia*

Species with the segmented girdle bands (copulae) arranged in two dorsi-ventral columns, or exceptionally in several columns. In many species the copulae closest to the valve bear the impression of the sister-cell valve process.

Note 1. We start the section with descriptions of a complex of four related taxa. *R. hebetata* has long been recorded from both the Arctic and Antarctic as the form *semispina*. In each locality the '*semispina*' cells are associated with two completely different, but distinctive, cell types (? spores). In the Arctic, '*semispina*' cells are associated with *R. hebetata* f. *hebetata* (sometimes referred to as f. *hiemalis*). In the Antarctic, '*semispina*' cells are associated with valves bearing two processes. Sundström (1986) has assigned the Antarctic '*semispina*' cells as a form of an earlier described species, *R. antennata*, which characteristically bears two processes on its valve. The *semispina* forms of the two species remain essentially indistinguishable except on biogeographic grounds. Although the distinctive valves of the different forms of each species are usually found at both ends of cells, occasionally a cell is found which bears one valve of each form. An example for *R. hebetata* is given by Drebes (1974, Fig. 41a-c), and JP has observed similar behaviour in *R. antennata* from the Bransfield Strait.

Rhizosolenia antennata (Ehrenberg) Brown f. *antennata* (Plate 15.1, Fig. 5a,b,c)

This taxon has often been noted in Antarctic samples under a number of names of which *Rhizosolenia bidens* and *Rhizosolenia hebetata* f. *bidens* are the most common. Cells are long, cylindrical or slightly swollen, and solitary. The valve bears two central symmetrical processes and lacks the contiguous area, otaria and claspers.

Rhizosolenia antennata f. *semispina* Sundström (Plate 15.1, Fig. 6)

Cells are long and cylindrical, either solitary, in pairs or forming long chains. The valve is acutely conical and bilaterally symmetrical, with the ventral part much longer than the dorsal. The marginal ridges of the contiguous area are usually readily discernible towards the proximal part of the valve and claspers are visible in permanent mounts. The single process is comparatively long, although usually broken in permanent preparations. It is widest basally, tapering into a long narrow tube. Otaria are small but conspicuous, being pointed and extending at least 3 µm along the basal part of the process. In narrow cells, the otaria may not reach the valve whereas they extend onto the valve face on more robust cells (Sundström, 1986). The quincuncial pattern of the areolation may be visible in heavily-silicified specimens.

Rhizosolenia hebetata f. *hebetata* Bailey (Plate 15.1, Fig. 3a,b)

The long cylindrical cells occur solitary or in pairs. The valve is acutely conical with the valve margin in a plane slightly oblique to the pervalvar axis. It is fairly heavily silicified, especially close to the apex. Contiguous area, otaria and claspers are lacking, so the mechanism holding cells together must differ from the *semispina* form. The process is heavily silicified, 15-25 µm long, tapering only slightly from the base and with a rounded tip.

Rhizosolenia hebetata f. *semispina* (Hensen) Gran (Plate 15.1, Fig.4)

These long cylindrical cells also occur solitarily or in pairs. The valve is acutely conoidal and bilaterally symmetrical, with the ventral margin prolonged. The marginal ridges of the contiguous area and claspers can be seen in permanent mounts. The process is comparatively long, but again usually broken in preserved material. It is wide at the base and then tapers into a narrow tube. The otaria are indistinguishable from those of *R. antennata* f. *semispina*, being pointed and extending at least 3 µm along the base of the process. As with *R. antennata* f. *semispina*, the degree to which the otaria extend onto the valve varies with cell size.

Note 2. Sundström (1986) points out that *R. styliformis* is commonly misidentified and this has led to world-wide reports. He concluded that reliable records come only from the North Atlantic but acknowledges that this may not describe the complete range of *R. styliformis*. As it has been recorded in the past from both the Arctic and Antarctic, we have included it here in the hope that future workers will examine material more carefully. Two similar species are presented alongside *R. styliformis*: *R. borealis* from the Arctic and *R. polydactyla* from the Antarctic.

Rhizosolenia styliformis Brightwell (Plate 15.3, Fig. 4)

Cells are long, cylindrical and occur singly or in pairs. The valve is markedly asymmetrical, with the ventral margin prolonged so as to account for nearly half of the pervalvar length (excluding the process). Claspers are visible. The process is usually 30-50 µm long, although seldom intact in preserved material. Sundström's (1986) micrographs and line drawing suggest that the process tapers more or less uniformly from the basal part – an important distinction from the next two species. The otaria are rounded and usually terminate below the process or only extend 1-2 µm along it. Because of the asymmetry of the valve, the first two copulae differ from the rest.

Rhizosolenia borealis Sundström (Plate 15.1, Figs 1,2)

Cells are long and cylindrical, usually solitary or in pairs. The valve is asymmetrical with the ventral part longer than the dorsal. The contiguous area is distinct, at least towards the proximal part, and claspers are prominent. The process is 15-28 µm long. It is widest at the base and narrows abruptly about half way along. This character and the shape of the otaria separate it reliably from *R. styliformis* (although this opinion is based on published information and not on our own observations). The conspicuous otaria with rounded lateral edges arise at the valve apex and extend almost half way up the basal part of the process.

Rhizosolenia polydactyla Castracane f. *polydactyla* (Plate 15.2, Figs 4,5)

Cells are long, cylindrical, and usually solitary. The valve is bilaterally symmetrical, with the ventral part longer than the dorsal. The contiguous area is conspicuous in the proximal part of the valve, with prominent claspers. The process is 18-34 µm long and resembles that of *R. borealis* in that it is of more or less uniform thickness at the base and only begins to taper half way along its length. The otaria arise at the valve apex and extend half way along the thicker basal part of the process. The distal ends of the otaria join the process at right angles.

Rhizosolenia polydactyla f. *squamosa* Sundström (Plate 15.2, Fig. 6)

This taxon is distinguished from the type form in that the copulae form several pairs of columns. The valve is also heavily silicified, with ridges on the distal part which may extend onto the base of the process. Claspers are lacking.

Note 3. The remaining taxa in the Section *Rhizosolenia* do not fall into any morphologically similar groups and are covered in alphabetical order.

Rhizosolenia crassa Schimper in Karsten (Plate 15.3, Fig. 1)

Cells are large, cylindrical, heavily silicified, and occur solitary or in pairs. The valve is bilaterally symmetrical with the ventral part approximately twice as long as the dorsal. The marginal ridges of the contiguous area are distinct over the entire length of the valve. The claspers are prominent. The process is robust, 50 µm long when intact but usually broken in preserved material. The prominent otaria are continuous with the marginal ridges of the contiguous area and have distinctive convex lateral margins extending to a slight point distally. They extend along the base of the process. Some cells possess a girdle with two-columns of copulae and the other composed of four columns. Cells with four columns of copulae were those in the larger part of the size range, whilst Karsten (1905 Plate XI Fig 6a) illustrated cells with at least six columns of copulae.

Rhizosolenia curvata Zacharias (Plate 15.2, Fig. 3)

This distinctive curved cell is usually solitary in preserved material, but Hart (1937) gives several illustrations of cell pairs and rafts composed of several individuals. The valve is bilaterally symmetrical with the ventral part longer than the dorsal. The marginal ridges of the contiguous area are usually distinct with comparatively small claspers. The process tapers uniformly from the base and is seldom intact in preserved samples. The small rounded otaria arise on the distal part of the valve, continuous with the marginal ridges and end below the valve apex.

Rhizosolenia sima Castracane f. *sima* (Plate 15.2, Fig. 1)

Cells are long and straight or slightly curved, usually solitary or in pairs. The valve is conical but not strongly acute, bilaterally symmetrical with the ventral part longer than the dorsal. The contiguous area is only distinct near the beginning of the sister-cell process. Claspers are prominent. The basal part of the process is bulbous and thick-walled, and tapers abruptly into a fairly long, narrow, thin-walled distal tube. In valves not attached to the sister valve, the tube is usually broken off near the base. The rounded otaria are comparatively large and extend laterally almost as much as their length. They arise on the valve apex and extend along the basal part of the process.

Rhizosolenia sima f. *silicea* Sundström (Plate 15.2, Fig. 2)

This form can be distinguished from the type form by its heavier silicification; lack of contiguous area, claspers and otaria; and the robust process arising from the thickened valve apex. The valve is more or less radially symmetrical and Sundström (1986) suggests that f. *silicea* is the resting spore of the type form, with some cells having been observed with one valve identifiable as f. *silicea* and the other as f. *sima*. Mangin (1915) observed intermediate stages.

Rhizosolenia simplex Karsten (Plate 15.3, Fig. 3)

Cells are small and comparatively weakly silicified. The valve lacks a contiguous area and claspers. The process is approximately 15-20 µm long, and tapers so that it appears to be an extension of the valve. Otaria are lacking.

The valve shape, lack of otaria and related structures, and the multiple columns of copulae may suggest that *R. simplex* is a resting spore (by analogy with *R. polydactyla* f. *squamosa* and *R. sima* f. *silicea*), although the weak silicification is anomolous. If this is correct, the identity of the corresponding vegetative cell is unknown. The similar taxon *R. torpedo* Karsten falls within the range of *R. simplex* and is probably identical to it. In the case of both species, Karsten (1905, Plate X Figs 1c and 2a) illustrates pairs of cells within the mother-cell girdle. The opposed valves apparently differ in shape from the free ends of the cells, being bilaterally symmetrical.

Section *Imbricatae*
This section of the genus has the copulae of the girdle arranged in two lateral, rather than dorsi-ventral, columns.

Rhizosolenia chunii Karsten (Plate 15.3, Fig. 2)

Cells are cylindrical, almost rectangular in girdle view, and form short chains. The stout process, hollow at the base, is displaced to the edge of the slightly convex valve. Copulae are short and 'boomerang-shaped' (Sundström, 1986). The interleaving of the ends of the copulae presents the characteristic chevron pattern of this group when seen in girdle view in dorsal or ventral aspect. The bands are finely striate.

Table 15.1. Morphometric and distributional data on *Rhizosolenia* species occurring in polar waters.

Species	*Diameter, in µm*	*Process*	*Otaria*	*Copulae rows*[1]	*Polar distribution*
SECTION RHIZOSOLENIA					
R. antennata f. *antennata**	18–45	Paired	none	2	Antarctic
R. antennata f. *semispina*	6.5–42	long, tapering	small, pointed	2	Antarctic
R. hebetata f. *hebetata**	15–44	heavily silicified, rounded tip	none	2	Arctic
R. hebetata f. *semispina*	4.2–25	long, tapering	small, pointed	2	Arctic
R. styliformis	23–90	long, uniformly tapering	small, rounded	2	Arctic ? Antarctic
R. borealis	13–5	long, tapering distally	large, rounded	2	Arctic
R. polydactyla f. *polydactyla*	15–105	long, tapering	large, pointed distally	2	Antarctic
R. polydactyla f. *squamosa**	56–105	short	none	Several pairs	Antarctic
R. crassa	100–165	long, robust	large, slightly pointed	2 or 4 (6)	Antarctic
R. curvata	20–135	uniformly tapering	small, rounded	2	Antarctic
R. sima f. *sima*	12–39	bulbous, tapering distally	large, rounded	2	Antarctic
R. sima f. *silicea**	18–40	robust, heavily silicified	none	2	Antarctic
R. simplex	5–48	uniformly tapering	none	2–4	Antarctic
SECTION IMBRICATAE					
R. chunii	20–28	short, stout	none	2	Antarctic
OTHER RHIZOSOLENIA SPP.					
R. cylindrus	8–20	tubular, slightly sigmoid	none	2	Antarctic
R. rhombus	110–280	stout, eccentric	large, rounded	2	Antarctic
R. setigera	4–20	long, needle-like	none	2	Arctic

[1] where there are two rows of copulae, these are usually dorsi-ventral
* probable resting spores

GENUS PROBOSCIA Sundström, and related species

This new genus includes a number of species previously referred to *Rhizosolenia alata* Brightwell and to its subspecific and related taxa. These share the distinctive feature of having the valve prolonged into a tubular feature – the 'proboscis' which gives the generic name. A process and its associated external structures are absent. Unfortunately, Sundström (1986) circumscribes only one species in this genus, *Proboscia alata* (Brightwell) Sundström, and excludes from it Antarctic records. Thus, similar *Rhizosolenia* species that possess the proboscis await redescription and transfer to *Proboscia* and this is beyond the scope of this manual. Therefore, this section contains some species still in *Rhizosolenia*. We are also unable to present diagnostic features which delimit Antarctic *R. inermis* from the similar form in the Arctic, or *Proboscia alata* in the Arctic from a nearly identical un-named species in the Antarctic. Therefore we present simple diagnoses for the three taxa noted in the species lists, based on features visible in the light microscope. The major distinguishing features used are the size and shape of the proboscis. Copulae are in two columns.

Proboscia alata (Brightwell) Sundström (Plate 15.3, Figs 5a,b)

The cells are long, cylindrical, commonly solitary but may form chains. The conical valve is asymmetrical and tapers into a truncate or slightly rounded and often curved proboscis. The proboscis bears a short longitudinal slit just below the tip. The contiguous area is developed into a groove proximally, and this is occupied by the distal end of the sister-cell valve proboscis in linked cells.

The species is well documented and includes some unusual specimens. Karsten (1905, Plate IX, Figs 13a,b) illustrates two valves which are probably referrable to *P. alata* but are grouped by him with a cell of *R. antennata* f. *antennata* as '*R. bidens*'. The proboscis of these cells is apparently bifurcated for about two-thirds of its length.

Rhizosolenia inermis Castracane (Plate 15.3, Figs 6a,b)

The cells are long and cylindrical. The valve is only moderately prolonged with a stout and markedly truncate proboscis, which is slightly expanded distally (*sensu* Cupp 1943, Fig 52E). The contiguous area has a proximal groove as in *P. alata*. It is distinguished from that species in the light microscope by the valve shape, proboscis size and shape.

Rhizosolenia truncata Karsten (Plate 15.4, Fig. 4)

Karsten's (1905) description of this species is sketchy. The valve is noticeably rounded, especially by comparison with the preceding species. The proboscis is strongly curved over the valve face and this appears also to be diagnostic (e.g. Karsten, 1905, Plate X, Figs 3, 3a). Cells form chains linked by the probosces. Karsten however notes a possible dimorphism in valve type, and his figure 3a shows one proboscis straight and about half of the cell length. Some later illustrations of this species (e.g. Sournia and others, 1979, Fig. 30) show this as the typical form. No details of the girdle are visible, an impression confirmed by the two light micrographs in Krebs (1983) and in comments by Hendey (1937).

The remaining taxa are a mixed group, most of which fall outside Sundström's (1986) description of *Rhizosolenia sensu stricto* and should probably be placed in new genera.

Rhizosolenia cylindrus Cleve (Plate 15.4, Figs 1, 2)

Cells are small and cylindrical and occur solitary or in pairs, united by the mother cell girdle. The valve is variable in shape, ranging from conical to almost flat. The latter is referred to a separate species, *R. antarctica* (Plate 15.4, Fig. 2), by Karsten (1905) but this is regarded as conspecific with *R. cylindrus* by Hasle (1969). The process is tubular, and slightly sigmoid in shape.

Rhizosolenia rhombus Karsten (Plate 15.2, Fig. 7)

Cells large and usually solitary. The valve is moderately convex to more or less flat, and bears a stout process displaced to one side giving the characteristic rhombic shape of the cell in girdle view. Karsten (1905) shows lightly silicified otaria with rounded margins which arise on the valve face and extend for most of the length of the process.

Rhizosolenia setigera Brightwell (Plate 15.4, Fig. 5)

The cell is notable for its long process, being up to 80% of the cell length (Cupp 1943 Fig. 49). The cell is cylindrical, weakly silicified with conical valves lacking otaria. The process is thickened at the base, becoming needle-like in the distal half. The impression of the sister-cell process runs across more than one girdle segment.

Table 15.2. Morphometric and distributional data of *Proboscia* species (see text for taxonomy)

Species	*Diameter in μm*	*Proboscis shape*	*Polar distribution*
P. alata	2.5–13	slightly curved, end truncate or slightly rounded	Arctic, ?Antarctic
'*R. inermis*'	10–19	stout, markedly truncate	Antarctic, ?Arctic
'*R. truncata*'	16–30	dimorphic – either curved or straight and long	Antarctic

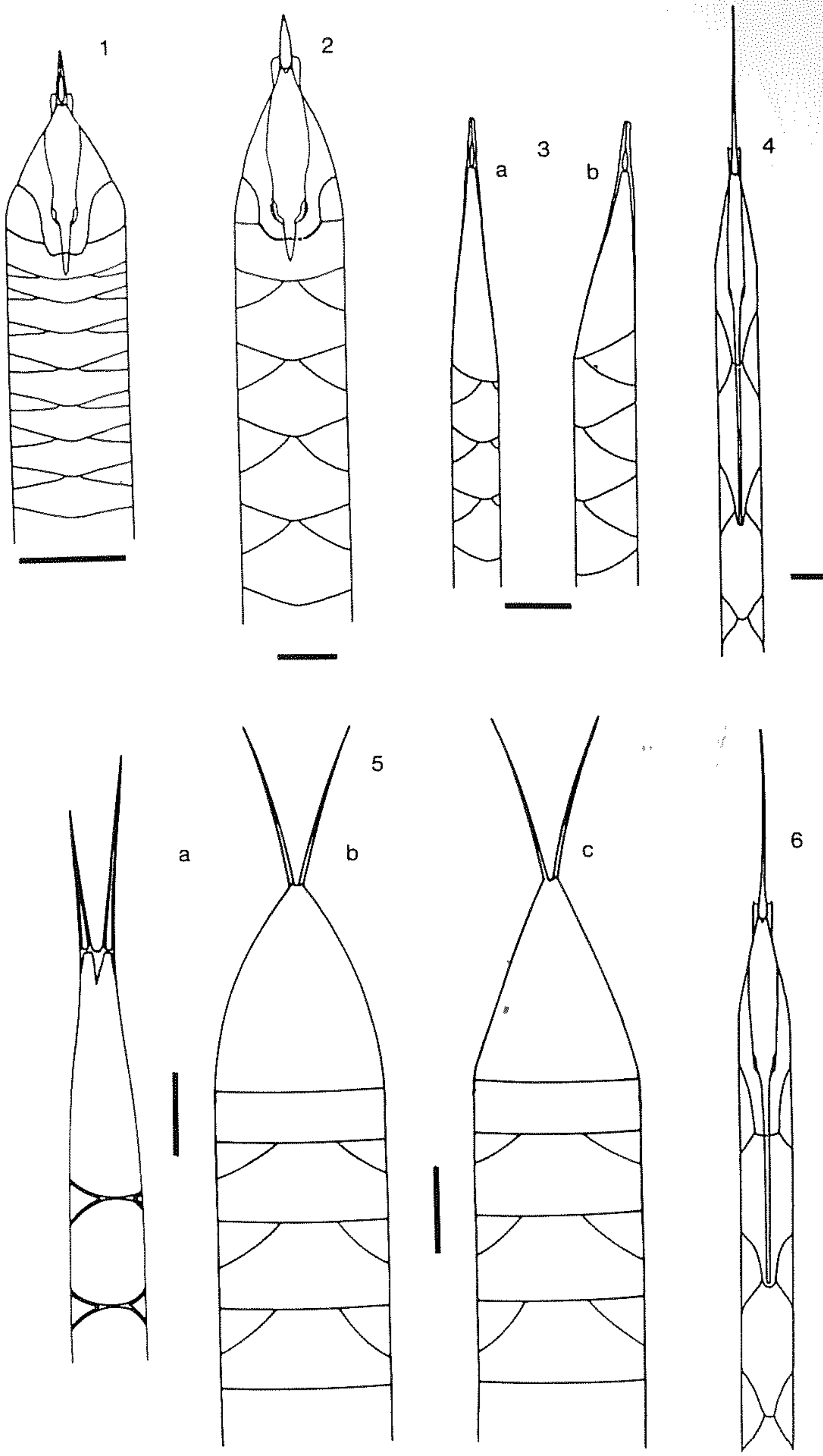


Plate 15.1. Line drawings of *Rhizosolenia*

Figs 1, 2 *Rhizosolenia borealis*

Fig. 3a, b *Rhizosolenia hebetata* f. *hebetata*

Fig. 4 *Rhizosolenia hebetata* f. *semispina*

Fig. 5a, b, c *Rhizosolenia antennata* f. *antennata*

Fig. 6 *Rhizosolenia antennata* f. *semispina*

Scale bar = 50 μm Fig 1; = 25 μm Figs 2, 3; = 20 μm Fig. 5; = 10 μm Figs 4, 6.

Figs 1-4, 6 from Sundström (1986); others are redrawn from a compilation of previously published figures.

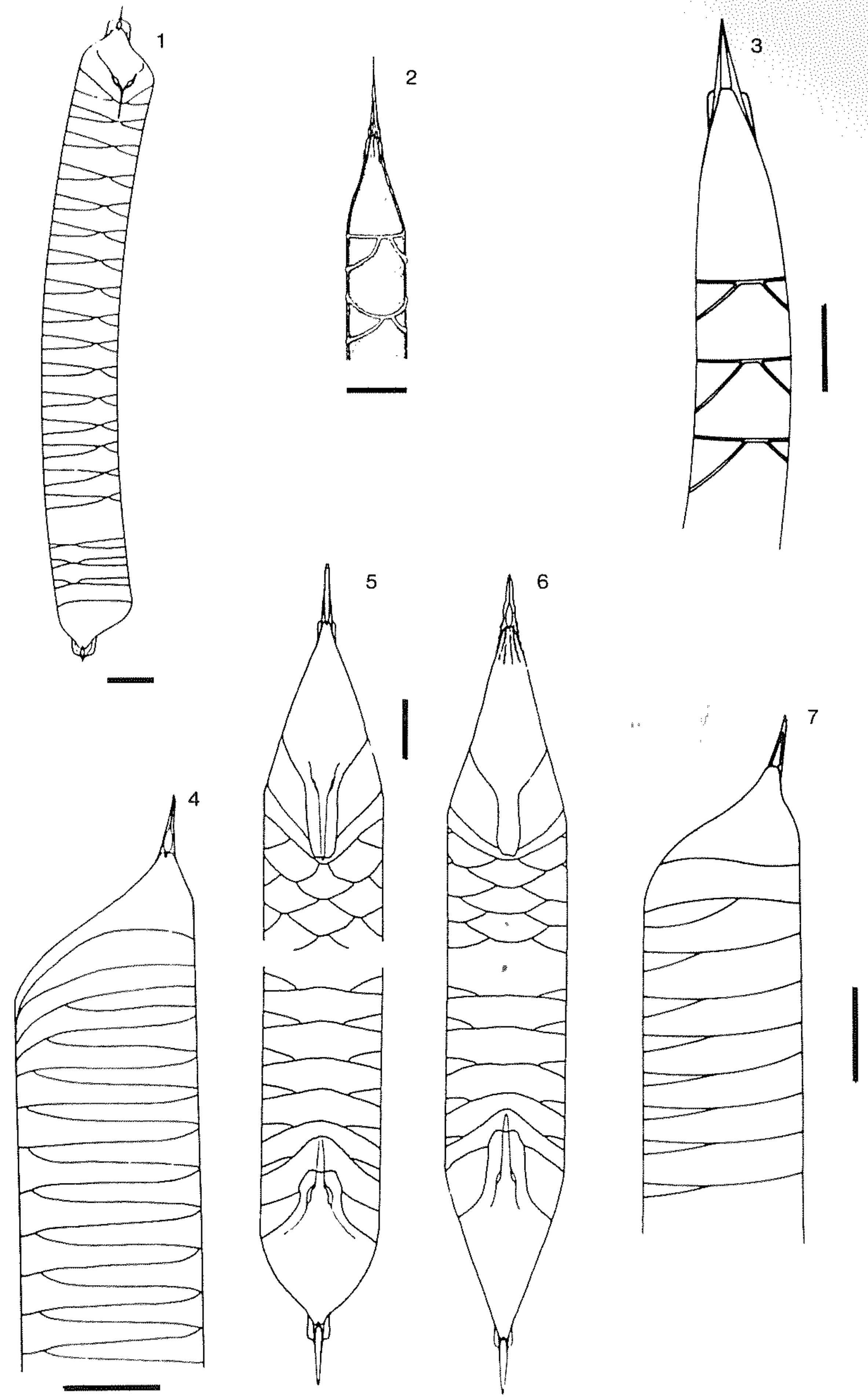


Plate 15.2. Line drawings of *Rhizosolenia*

Fig. 1 *Rhizosolenia sima* f. *sima*

Fig. 2 *Rhizosolenia sima* f. *silicea*

Fig. 3 *Rhizosolenia curvata*

Fig. 4 *Rhizosolenia polydactyla* f. *polydactyla*

Fig. 5 *Rhizosolenia polydactyla*
bottom valve = f. *polydactyla*
top valve = intermediate between f. *polydactyla* and f. *squamosa*

Fig. 6 *Rhizosolenia polydactyla*
bottom valve = intermediate between f. *polydactyla* and f. *squamosa*
top valve = f. *squamosa*

Fig. 7 *Rhizosolenia rhombus*

Scale bar = 200 µm Fig 7; = 50 µm Figs 3, 4; = 25 µm Figs 1, 2, 5, 6.

Figs 1, 2, 4-6 from Sundström (1986); others are redrawn from a compilation of previously published figures.

Plate 15.3. Line drawings of *Rhizosolenia* and *Proboscia*

Fig. 1 *Rhizosolenia crassa*

Fig. 2 *Rhizosolenia chunii*

Fig. 3 *Rhizosolenia simplex*

Fig. 4 *Rhizosolenia styliformis*

Fig. 5a, b *Proboscia* (= *Rhizosolenia*) *alata*

Fig. 6a, b *Rhizosolenia inermis* (not transferred to *Proboscia* by Sundström, pending further investigations)

Scale bar = 50 μm Fig 1; = 25 μm Figs 2, 3, 4; = 10 μm Figs 5, 6.

Figs 1, 3, 4 from Sundström (1986); all others are redrawn from a compilation of previously published figures.

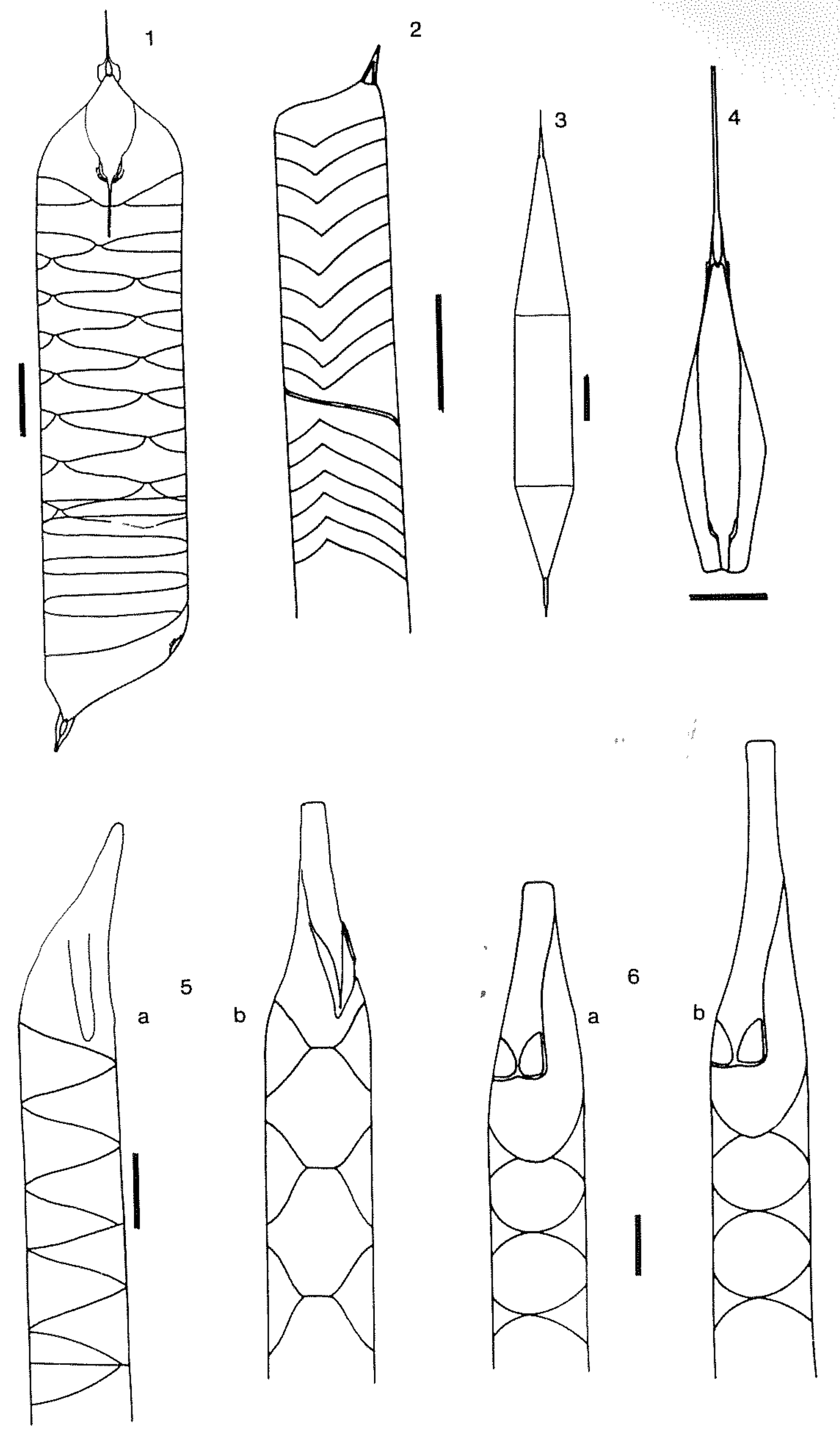


Plate 15.4. Line drawings of *Rhizosolenia*

Fig. 1 *Rhizosolenia cylindrus*

Fig. 2 *Rhizosolenia cylindrus* (*antarctica* type valve)

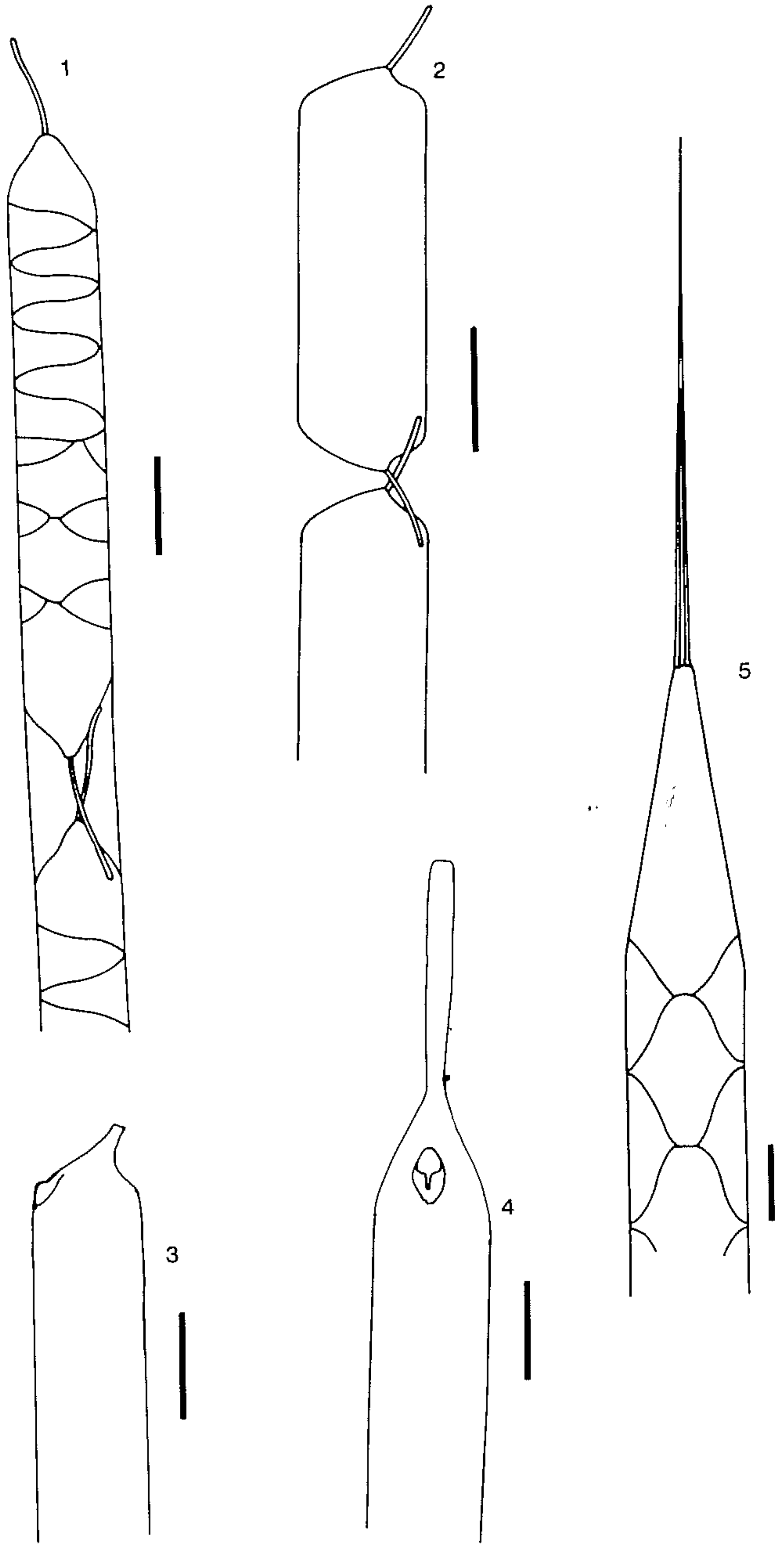
Fig. 3 *Rhizosolenia truncata* (valve with short proboscis)

Fig. 4 *Rhizosolenia truncata* (valve with long proboscis)

Fig. 5 *Rhizosolenia setigera*

Scale bar = 20 µm Figs 3, 4; = 15 µm Fig. 1; = 10 µm Figs 2, 5.

All illustrations are redrawn from a compilation of previously published figures.



CHAPTER 16

FAMILY BIDDULPHIACEAE

Grethe R. Hasle and Erik E. Syvertsen

GENUS EUCAMPIA Ehrenberg

This genus is represented in polar waters by two species, *E.groenlandica* Cleve in the Arctic and *E.antarctica* Castracane in the Antarctic. The characteristic morphological feature is the presence of the bipolar elevations (horns) without spines. The top of the horns of sibling valves abut to form chains of cells. The Antarctic species forms coarsely silicified resting spores.

How to identify to species:
E.groenlandica and *E.antarctica* are distinguished by differences in size, silicification, the proportion between the length of the pervalvar and apical axes, and resting spore formation; *E.groenlandica* being the smaller, more weakly silicified diatom with generally higher cells and no resting spores. The species are readily identified in water mounts. The location of the single labiate process, central in *E.groenlandica* and marginal in *E.antarctica*, is resolved in specimens mounted in a medium of high refractive index.

Characters to look for to distinguish between species:
1. Size of cells
2. Degree of silicification
3. Location of labiate process

Table 16.1. Morphometric data on *Eucampia*

	Apical axis μm	*Valve areolae in 10 μm*	*Labiate process*	*Polar Distribution*
E. groenlandica	10–33	38–42	central	Arctic
E. antarctica	18–92	3–10	marginal	Antarctic

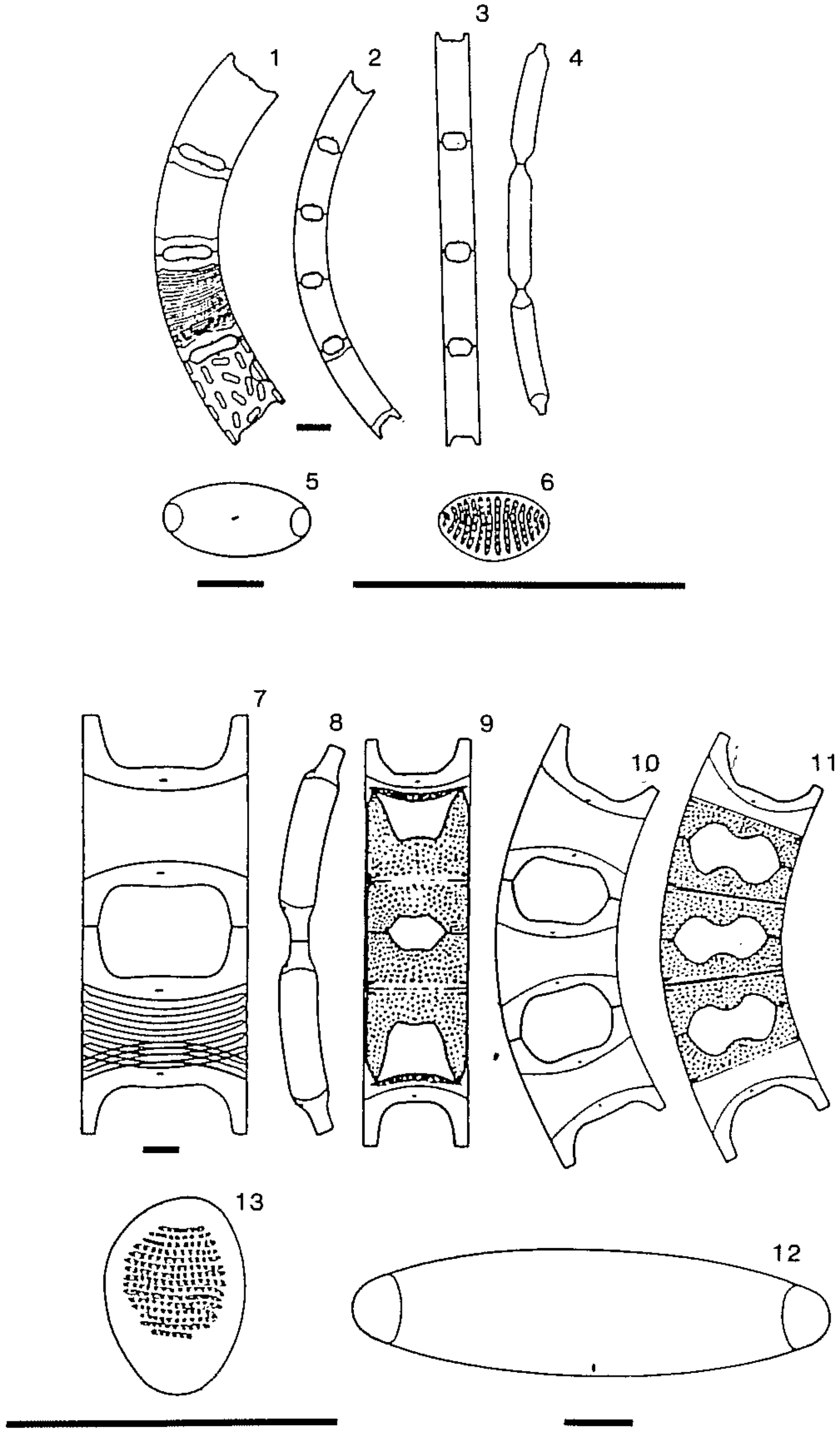
For further information see Syvertsen and Hasle (1983).

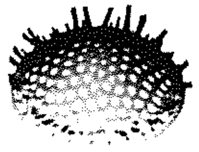
Editors' note: two recent papers deal with Antarctic *Eucampia*, with particular reference to nomenclature (Fryxell, Prasad and Fryxell, 1989) and intraspecific variation (Fryxell and Prasad, 1990).

Plate 16.1. Line drawings of *Eucampia*.Scale bars = 10μm.

Figs. 1–6. *Eucampia groenlandica*
Figs. 1–3. Broad girdle view
Fig. 4. Narrow girdle view
Fig. 5. Valve view
Fig. 6. Top of a horn.

Figs. 7–13. *E. antarctica*
Figs 7, 9, 10, 11. Broad girdle view
Figs 9 & 11. Colonies with resting spores
Fig. 8. Narrow girdle view
Fig. 12. Valve view
Fig. 13. Top of horn





CHAPTER 17

FAMILY DIATOMACEAE

Grethe R. Hasle

GENUS THALASSIOTHRIX Cleve *et* Grunow

The genus is characterized by long twisted cells, slightly inflated in the middle. The valve has short marginal striae and more or less distinct marginal spines. Numerous disc-shaped chloroplasts are present.

How to identify to species:
Thalassiothrix antarctica Schimper *ex* Karsten can be readily distinguished from other genera as well as from other species of the genus, if appearing in colonies in water mounts. Cells in colonies are joined by characteristically bent foot-poles and a shorter or longer part of the cell length, whereas the head-poles are distinctly separated. Because *T.antarctica* can occur as either curved or straight *single* cells, the distinction between the straight form and *T. longissima* Cleve & Grunow becomes critical when examining water mounts. A comparison of well-developed cell apices (best seen in cleaned valves in a permanent mount) is the most reliable means by which the two species can be distinguished.

Characters to look for:
1. Colony formation
2. Shape of cell
3. Shape of cell/valve apices
4. Presence/absence/shape of apical protrusions

Key to species:
1a Cells straight or slightly curved, no colonies 2
1b Cells sigmoid with distinct bend near one pole ....*T. antarctica*
2a Both apices with "cock's comb" protrusions ....*T. longissima*
2b One apex rounded without spines, the other with two winged spines ....*T. antarctica*

GENUS TRICHOTOXON Reid *et* Round

Trichotoxon reinboldii (Van Heurck) Reid *et* Round
Basionym: *Synedra reinboldii* Van Heurck

This species very often occurs in association with *Thalassiothrix antarctica*. They are approximately of the same length and width and are similar in cell shape, with *Trichotoxon reinboldii* being curved but not sigmoid. *T.reinboldii* also forms colonies but unlike *Thalassiothrix antarctica* the cells are attached at either end resulting in pointed, ovoid colonies (Reid and Round, 1987).

How to identify:
Whole cells/valves may be identified in water mounts but like the two *Thalassiothrix* species cleaned material in permanent mounts may be needed in critical cases.

Characters to look for:
1. Shape of colony
2. Shape of cell
3. Shape of cell apices
4. Location of labiate processes
5. Absence of spines

Key to *Thalassiothrix antarctica* and *Trichotoxon reinboldii* based on cleaned material:
1a No marginal spines, spineless rounded cell apices, labiate process close to each apex with low mantle ....*T. reinboldii*
1b Marginal spines turned towards spined apex, the other apex rounded and spineless, labiate process away from the apex ....*T. antarctica*

Table 17.1. Morphometric data on *Thalassiothrix* and *Trichotoxon*

	Apical axis in µm	*Transapical axis in µm*	*Marginal spines in 10 µm*	*Striae/Areolae in 10 µm*	*Distribution planktonic*
T. longissima	530-4000	2.5-6	1-3	11-16	Arctic
T. antarctica	420-5680	1.5-6	1-2	12-17	Antarctic
T. reinboldii	904-3600	3-10	absent	8-10	Antarctic

For further information see Hasle and Semina (1987) and Reid and Round (1987).

Plate 17.1. Line drawings of *Thalassiothrix* and *Trichotoxon*. Scale bars: Figs 1, 4, 7 = 100 μm, Figs 2, 3, 5, 6, 8, 9 = 10 μm.

Figs 1–3. *Thalassiothrix longissima*

Fig. 1. Whole cell

Fig. 2. Terminal part of cell in valve view

Fig. 3. Terminal part of cell in girdle view.

Figs 4–6. *Thalassiothrix antarctica*

Fig. 4. Colony

Fig. 5. Part of cell with foot-pole in valve view

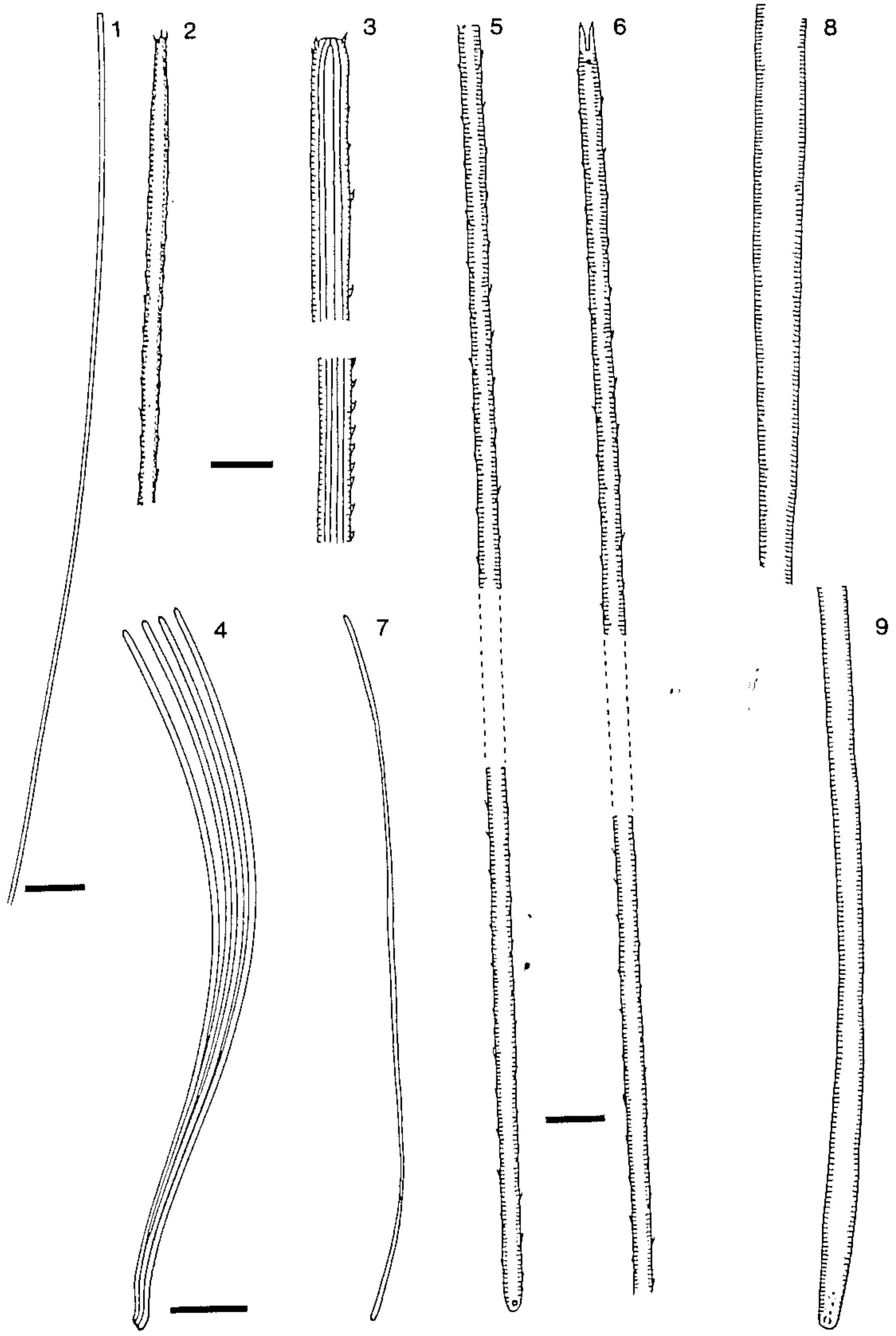
Fig. 6. Part of cell with head-pole in valve view

Figs 7–9. *Trichotoxon reinboldii*

Fig. 7. Whole cell

Fig. 8. Middle part of valve

Fig. 9. Terminal part of valve.



CHAPTER 18

FAMILY NAVICULACEAE:

ARCTIC SPECIES

Michel Poulin

In polar regions, extensive taxonomic works have focused on phytoplanktonic assemblages, while the sea ice habitat has been severely neglected. The identification of bottom sea ice diatoms from the Arctic is still a problem for most of the scientists working in polar regions because they have to rely on out-of-date literature such as Cleve and Grunow (1880), Cleve (1883), Grunow (1884) and Østrup (1895). The few modern but purely taxonomic studies that do exist (i.e. Heimdal, 1970; Poulin and Cardinal, 1982a, 1982b, 1983; Syvertsen, 1984; Medlin and Round, 1986; Poulin, 1990a, b) do not help to answer questions asked by the ecologists. Thus, further thorough taxonomic studies are needed to standardize the identification of the diatoms from the Arctic regions.

This section on the Naviculaceae of the Arctic is an attempt to clarify and simplify the different steps involved in the identification process of the diatoms. Unfortunately only a few taxa are represented but they are those found most commonly in the bottom sea ice assemblage. The most important ice diatom genera are *Navicula* with 24 taxa and *Pinnularia* with 11 taxa. Additional species typical of sea ice biota are included and belong to the following genera: *Diploneis* (1 taxon), *Gyrosigma* (2 taxa), *Haslea* (3 taxa), *Pleurosigma* (2 taxa), *Stauroneis* (1 taxon), and *Stenoneis* (1 taxon). For most of the diatom taxa recorded in the present study, frustules have to be cleaned of organic matter and mounted in a medium of a high refractive index for light microscopy in order to distinguish the characteristics used in the keys. It is also preferable to examine the cells in valve view.

The following keys are incomplete in as much as only the 45 most common and conspicuous sea ice diatom taxa are considered. Additional taxa that might be found can be identified by using more comprehensive taxonomic studies (e.g. Cleve and Grunow, 1880; Cleve, 1883; Grunow, 1884; Østrup, 1895). The identification keys should be used in conjunction with the morphometric data in Table 18.1 and the corresponding figures. Genera with only one or two species treated are not provided with a key. Instead, the main distinguishing characteristics are listed.

TAXONOMY

Key to genera:

1a Valve sigmoid 2
1b Valve not sigmoid 3
2a Transverse and longitudinal striae crossed at right angles .... *Gyrosigma*
2b Transverse and oblique striae crossed at an angle other than 90° .... *Pleurosigma*
3a Transverse and longitudinal striae crossed at right angles .... *Haslea*
3b Valve with only one pattern of striae 4
4a Raphe bordered by longitudinal canals .... *Diploneis*
4b Raphe not bordered by such canals 5
5a Central area laterally expanded into a stauros .... *Stauroneis*
5b Central area not so developed 6
6a Striae alveolate or multiseriate .... *Pinnularia*
6b Striae uniseriate 7
7a Raphe enclosed between two longitudinal axial costae, with central pores very close to each other and terminal pores ending sub-terminally .... *Stenoneis*
7b Raphe sometimes enclosed between axial costae, but never in conjuction with such central and terminal pores .... *Navicula*

GENUS DIPLONEIS Ehrenberg

Cells solitary. Valves usually elliptical, sometimes panduriform. Raphe bordered by longitudinal canals of variable width, unornamented or perforated by small areolae. Striae complex, consisting of loculate areolae.

Features to look for in valve view:
1. Valve outline: shape of the valve and its middle part.
2. Longitudinal canals: shape and width of the longitudinal canals.
3. Striae: nature of the striation, number of striae in 10 µm.

Species illustrated:
D. litoralis var. *clathrata* (Plate 18.1 Fig. 1)
Main features: Valve linear-elliptical.
Longitudinal canals straight and narrow.
Striae close to one another and formed by a double row of areolae.

Ecology:
Marine, bottom sea ice species endemic to the Arctic.

GENUS GYROSIGMA Hassall

Cells solitary. Valves sigmoid. Transverse and longitudinal areolate striae crossed at right angles.

Table 18.1. Morphometric and distributional data on the most common sea ice diatom taxa belonging to the Naviculaceae present in the Arctic, and their ecological distribution.

Taxa	*Apical axis in µm*	*Transapical axis in µm*	*Striae in 10 µm*	*Polar distribution*
Diploneis				
litoralis v. *clathrata* (Østr.) Cleve	26–40	10–12	15–17	Arctic
Gyrosigma				
hudsonii Poul. & Card.	78–114	17–21	23–24(T)[1] 32–34(L)	Subarctic
tenuissimum v.*hyperborea* (Grun.) Cleve	94–152	5–7	20–23(T) 26–30(L)	Arctic-subarctic
Haslea				
crucigeroides (Hust.) Sim.	61–168	8–14	22–24	Arctic-subarctic
kjellmanii (Cleve) Sim.	128–190	27–32	14–16	Arctic-subarctic
vitrea (Cleve) Sim.	131–190	17–20	18–19(T) 21–22(L)	Arctic-subarctic
Navicula				
algida Grun.	34–141	16–51	10	Arctic-subarctic
directa (W.Sm.) Ralfs	52–137	7–11	9–10	Arctic-Antarctic
directa v. *javanica* Cleve	65–165	10–12	7	Arctic-Antarctic
forcipata v. *densestriata* Schmidt	16–36	6–13	18–24	Arctic-subarctic
imperfecta Cleve	65–115	31–37	7	Arctic-subarctic
kariana v. *detersa* Grun.	62–113	21–25	10–11	Arctic-subarctic
kryokonites Cleve	19–37	6–11	20–22	Arctic-subarctic
kryophila Cleve	42–119	18–40	8–12	Arctic-subarctic
novadecipiens Hust.	40–88	16–18	12–13	Arctic-subarctic
obtusa Cleve	45–117	12–16	10–12	Arctic
oestrupioides Hust.	33–92	6–7	22–23	Arctic-subarctic
pellucidula Hust.	45–74	18–22	15	Arctic
recurvata Gran	29–50	8–9	11–13	Arctic
solitaria Cleve	22–78	7–8	10	Arctic-subarctic
superba Cleve	44–105	19–25	8–10	Arctic-subarctic
superba v. *crassa* (Østr.) Gran	40–102	21–25	9–10	Arctic
superba v. *subacuta* Gran	42–98	18–20	8–9	Arctic-subarctic
transfuga v. *septentrionalis* Østr.	60–67	27–30	12	Arctic
transitans Cleve	71–134	16–20	7–9	Arctic-subarctic
transitans v. *derasa* (Grun.) Cleve	45–93	10-18	9–11	Arctic-subarctic
trigonocephala Cleve	28–62	11–14	10–11	Arctic
trigonocephala v. *depressa* Østr.	50–83	12–13	8–9	Arctic-subarctic
valida Cleve & Grun.	33–126	15–26	6–8	Arctic-subarctic
valida v. *minuta* Cleve	15–32	11–15	8–9	Arctic-subarctic
Pinnularia				
ambigua Cleve	41–75	6–10	7–8	Arctic-subarctic
quadratarea v. *bicontracta* (Østr.) Heid.	41–103	10–15	9–11	Arctic-subarctic
quadratarea v. *capitata* Heid.	54-90	12-15	10-11	Arctic-subarctic
quadratarea v. *constricta* (Østr.) Heid.	35–96	11–19	10–11	Arctic-Antarctic
quadratarea v. *cuneata* (Østr.) Østr.	46–84	16–22	8–9	Arctic-subarctic
quadratarea v. *densestriata* Cleve	32–57	9–10	12	Arctic-subarctic
quadratarea v. *dubia* Heid.	35–62	12–19	9–11	Arctic-subarctic
quadratarea v. *maxima* (Østr.) Boyer	60–119	14–17	8–9	Arctic-subarctic
quadratarea v. *minor* (Østr.) Heid.	23–41	8–10	12–13	Arctic-subarctic
quadratarea v. *subglabra* (Østr.) Poul. & Card.	65–94	15–20	8–9	Arctic-subarctic
semiinflata (Østr.) Gran	22–70	8–10	13–14	Arctic-subarctic
Pleurosigma				
siberica (Grun.) Card. et al.	140-230	12	26–27(T) 26–27(O)	Arctic-subarctic
stuxbergii v. *rhomboides* (Cleve) Cleve	83–166	26-33	22–24(T) 25–26(O)	Arctic-subarctic
Stauroneis				
radissonii Poul. & Card.	21–27	3-5	40–44	Subarctic
Stenoneis				
inconspicua v. *baculus* (Cleve) Cleve	40–95	7–11	18–19	Arctic-subarctic

[1] T: transverse striae; L: longitudinal striae; O: oblique striae.

Features to look for in valve view:
1. Valve outline: careful examination of the shape of the valve.
2. Raphe: orientation of the raphe system on the valve surface.
3. Striae: number of striae in 10 µm on both transverse and longitudinal patterns.

Species illustrated:
G. hudsonii (Plate 18.1 Fig. 2)
Main features: Valve strongly sigmoid and lanceolate.
Raphe straight or almost straight from one apex to the other.
Longitudinal striae finer and denser than the transverse striae.

G. tenuissimum var. *hyperborea* (Plate 18.1 Fig. 3)
Main features: Valve narrow, linear and very slightly sigmoid.
Raphe straight, slightly bent in contrary directions at the apices.
Longitudinal striae clearly finer and denser than the transverse striae.

Ecology:
Marine, periphytic and bottom sea ice species, common in the Arctic and also present at temperate latitudes.

GENUS HASLEA Simonsen

Cells solitary, sometimes or in mucilage tubes. Valves typically lanceolate (fusiform) with acute apices. Pseudostauros sometimes present. Transverse and longitudinal areolate striae crossed at right angles.

Features to look for in valve view:
1. Valve outline: especially the width of the valve.
2. Pseudostauros: occurrence and nature of the pseudostauros at the centre of the valve.
3. Striae: number of striae in 10 µm in both longitudinal and transverse patterns.

Key to species:
1 Pseudostauros present .... *H. crucigeroides* (Plate 18.1 Fig. 4)
1 Pseudostauros absent 2
2 Valve broad, coarsely striate .... *H. kjellmanii* (Plate 18.1 Fig. 5)
2 Valve narrow, densely striate .... *H. vitrea* (Plate 18.1 Fig. 6)

Ecology:
Marine, periphytic or bottom sea ice species common in the Arctic and present in coastal environments of tropical or temperate latitudes.

GENUS NAVICULA Bory

This genus shows the highest degree of morphological variation in almost all the valve features. Cells usually solitary. Valves basically linear, elliptical or lanceolate. Raphe usually straight. Axial and central areas variable. Striation is also variable: areolate, alveolate or lineate, uniseriate or biseriate, in longitudinal or decussating rows, radiate, parallel or convergent.

Features to look for in valve view:
1. Valve outline: shape of the valve, shape of the apices.
2. Areas: shape of the axial, central, terminal, and lateral areas.
3. Striae: nature, orientation, and interruption of the striae, number of striae in 10 µm.

Key to species:
1a Valve with marginal multiseriate striae .... *N. kryophila* (Plate 18.1 Fig. 7)
1b Valve without marginal multiseriate striae 2
2a Valve with narrow lyre-shaped lateral areas .... *N. forcipata* var. *densestriata* (Plate 18.1 Fig. 8)
2b Valve without lyre-shaped lateral areas 3
3a Striae areolate 4
3b Striae consisting of apically elongate linear poroids 8
4a Distal raphe ends curved in opposite directions .... *N. oestrupioides* (Plate 18.1 Fig. 9)
4b Distal raphe ends straight 5
5a Valve margin with short inserted rows of areolae .... *N. algida* (Plate 18.1 Fig. 10)
5b Valve margin without short inserted rows of areolae 6
6a Valve asymmetrical to the apical axis .... *N. novadecipiens* (Plate 18.1 Fig. 11)
6b Valve symmetrical to the apical axis 7
7a Valve narrow, asymmetrical central area .... *N. kryokonites* (Plate 18.1 Fig. 12)
7b Valve broad, narrow transapical central area .... *N. pellucidula* (Plate 18.1 Fig. 13)
8a Valve surface deeply concave toward the centre 9
8b Valve surface not concave 10
9a Valve large, butterfly-shaped central area .... *N. obtusa* (Plate 18.1 Fig. 14)
9b Valve small, broad axial area .... *N. recurvata* (Plate 18.1 Fig. 15)
10a Valve with distinct lateral areas 11
10b Valve without lateral areas 12
11a Valve broadly lanceolate .... *N. kariana* var. *detersa* (Plate 18.1 Fig. 16)
11b Valve narrowly lanceolate .... *N. transitans* var. *derasa* (Plate 18.1 Fig. 17)
12a Valve linear 13
12b Valve elliptical and/or lanceolate 16
13a Striae interrupted 14
13b Striae uninterrupted 15
14a Apices apiculate and produced .... *N. trigonocephala* (Plate 18.1 Fig. 18)
14b Apices apiculate .... *N. trigonocephala* var. *depressa* (Plate 18.1 Fig. 19)
15a Apices rounded .... *N. solitaria* (Plate 18.1 Fig. 20)
15b Apices cuneate .... *N. directa* var. *javanica* (Plate 18.1 Fig. 21)
16a Central striae alternately longer and shorter 17
16b Central striae not alternately longer and shorter 18
17a Valve broadly elliptical, striae interrupted .... *N. imperfecta* (Plate 18.1 Fig. 22)
17b Valve narrowly elliptical, striae complete .... *N. valida* (Plate 18.1 Fig. 23)
18a Valve lanceolate 19
18b Valve not lanceolate 20
19a Striae parallel .... *N. directa* (Plate 18.1 Fig. 24)
19b Striae radiate .... *N. transitans* (Plate 18.1 Fig. 25)
20a Valve rhombic .... *N. superba* (Plate 18.1 Fig. 26)
20b Valve elliptical 21
21a Striae interrupted 22
21b Striae uninterrupted 23
22a Apices apiculate, densely striate .... *N. transfuga* var. *septentrionalis* (Plate 18.1 Fig. 27)
22b Apices sub-rostrate, coarsely striate .... *N. superba* var. *crassa* (Plate 18.1 Fig. 28)

23a Striae parallel at centre .... *N. superba* var. *subacuta* (Plate 18.1 Fig. 29)
23b Striae radiate at centre ....*N. valida* var. *minuta* (Plate 18.1 Fig. 30)

Ecology:
Marine, periphytic, bottom sea ice species common in the Arctic and some are also present at temperate latitudes.

GENUS PINNULARIA Ehrenberg

Cells solitary, sometimes in filamentous colonies. Valves linear to linear-lanceolate. Axial and central areas of variable width. Striae multiseriate or alveolate.

Features to look for in valve view:
1. Valve outline: shape and contraction of the valve, shape of the apices.
2. Central area: shape of the central area.
3. Striae: number of striae in 10 μm.

Key to species:
1a Valve asymmetrical with respect to the apical axis .... *P. semiinflata* (Plate 18.1 Fig. 31)
1b Valve symmetrical with respect to the apical axis 2
2a Broad axial area, marginal alveolate striae .... *P. ambigua* (Plate 18.1 Fig. 32)
2b Narrow axial area, multiseriate striae 3
3a Apices capitate ....*P. quadratarea* var. *capitata* (Plate 18.1 Fig. 33)
3b Apices not capitate 4
4a Valve constricted at centre 5
4b Valve not constricted at centre 6
5a Valve large, coarsely striate ....*P. quadratarea* var. *constricta* (Plate 18.1 Fig. 34)
5b Valve small, finely striate ....*P. quadratarea* var. *minor* (Plate 18.1 Fig. 35)
6a Valve inflated at centre ....*P. quadratarea* var. *maxima* (Plate 18.1 Fig. 36)
6b Valve not inflated at centre 7
7a Valve bicontracted 8
7b Valve not bicontracted 9
8a Apices cuneately rounded ....*P. quadratarea* var. *bicontracta* (Plate 18.1 Fig. 37)
8b Apices rounded ....*P. quadratarea* var. *densestriata* (Plate 18.1 Fig. 38)
9a Valve linear-elliptical ....*P. quadratarea* var. *dubia* (Plate 18.1 Fig. 39)
9b Valve not linear-elliptical 10
10a Valve elliptical-lanceolate ....*P. quadratarea* var. *cuneata* (Plate 18.1 Fig. 40)
10b Valve lanceolate .....*P. quadratarea* var. *subglabra* (Plate 18.1 Fig. 41)

Ecology:
Marine, periphytic, bottom sea ice species, common in the Arctic, some are also present at temperate latitudes, others are bipolar.

GENUS PLEUROSIGMA W. Smith

Cells solitary. Valves sigmoid. Areolate striae arranged in oblique and transverse rows crossed at an angle.

Features to look for in valve view:
1. Valve outline: careful examination of the shape of the valve.
2. Raphe: orientation of the raphe system on the valve surface.
3. Striae: number of striae in 10 μm on both transverse and oblique patterns.

Species illustrated:
P. siberica (Plate 18.1 Fig. 42)
Main features: Valve slightly sigmoid, linear and narrow.
Striae very fine, oblique pattern denser than the transverse pattern.
P. stuxbergii var. *rhomboides* (Plate 18.1 Fig. 43)
Main features: Valve strongly sigmoid, lanceolate and broad.
Striae fine, oblique pattern slightly denser than the transverse pattern.

Ecology:
Marine and bottom sea ice species endemic to the Arctic.

GENUS STAURONEIS Ehrenberg

Cells solitary. Valves usually lanceolate or elliptical. Stauros of variable width at the centre of the valve.

Features to look for in valve view:
1. Valve outline: shape of the valve and the apices.
2. Stauros: shape and width of the stauros.
3. Striae: orientation and number of striae in 10 μm.

Species illustrated:
Stauroneis radissonii (Plate 18.1 Fig. 44)
Main features: Valve small, narrow with capitate apices.
Stauros very narrow.
Striae indistinct under the light microscope.

Ecology:
Marine and bottom sea ice species endemic to the Arctic.

GENUS STENONEIS Cleve

Cells solitary or in short aborescent colonies. Valves linear. Apices rounded. Raphe enclosed between two longitudinal axial costae. Axial area very narrow. Striae finely aerolate, interrupted and parallel.

Features to look for in valve view:
1. Valve outline: shape of the valve and the apices.
2. Central area: shape of the central area.
3. Striae: degree of interruption in the striae, number of striae in 10 μm.

Species illustrated:
Stenoneis inconspicua var. *baculus* (Plate 18.1 Fig. 45)

Ecology:
Marine and bottom sea ice species endemic to the Arctic.

Plate 18.1. Photomicrographs of Naviculaceae

Fig. 1 *Diploneis litoralis* var. *clathrata*

Fig. 2 *Gyrosigma hudsonii*

Fig. 3 *Gyrosigma tenuissimum* var. *hyperborea*

Fig. 4 *Haslea crucigeroides*

Fig. 5 *Haslea kjellmanii*

Fig. 6 *Haslea vitrea*

Fig. 7 *Navicula kryophila*

Fig. 8 *Navicula forcipata* var. *densestriata*

Fig. 9 *Navicula oestrupioides*

Fig. 10 *Navicula algida*

Fig. 11 *Navicula novadecipiens*

Fig. 12 *Navicula kryokonites*

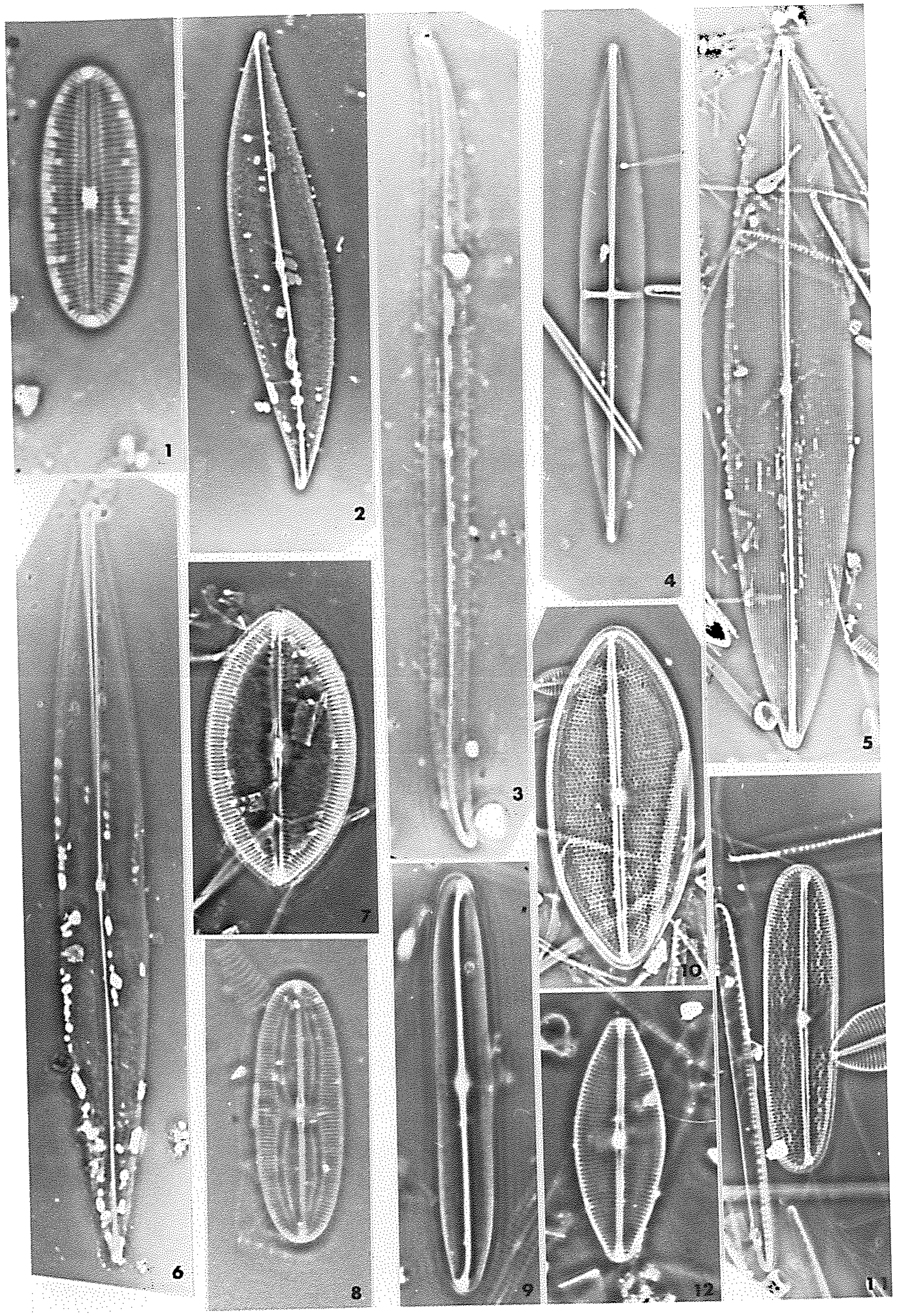


Fig. 13 *Navicula pellucidula*

Fig. 14 *Navicula obtusa*

Fig. 15 *Navicula recurvata*

Fig. 16 *Navicula kariana* var. *detersa*

Fig. 17 *Navicula transitans* var. *derasa*

Fig. 18 *Navicula trigonocephala*

Fig. 19 *Navicula trigonocephala* var. *depressa*

Fig. 20 *Navicula solitaria*

Fig. 21 *Navicula directa* var. *javanica*

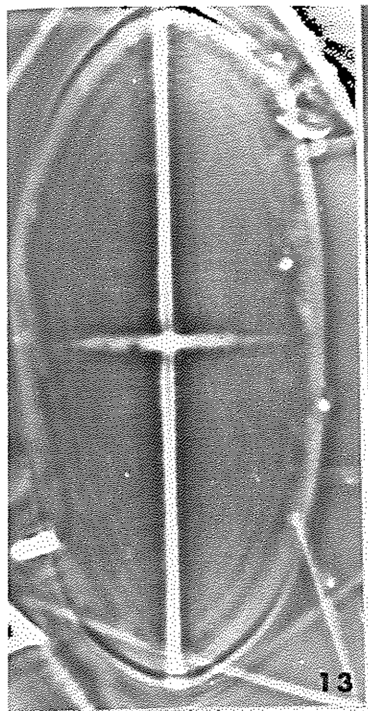
Fig. 22 *Navicula imperfecta*

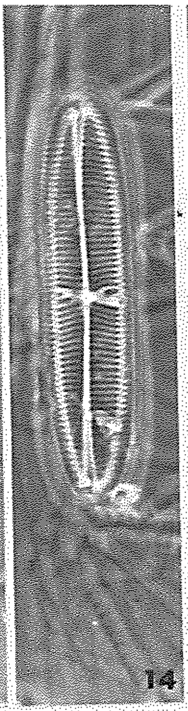
Fig. 23 *Navicula valida*

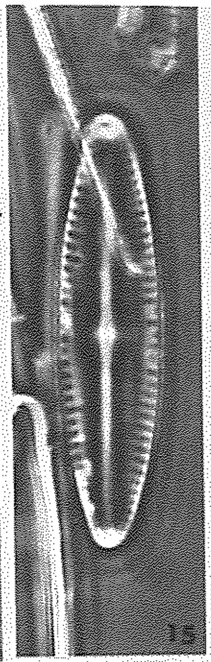
Fig. 24 *Navicula directa*

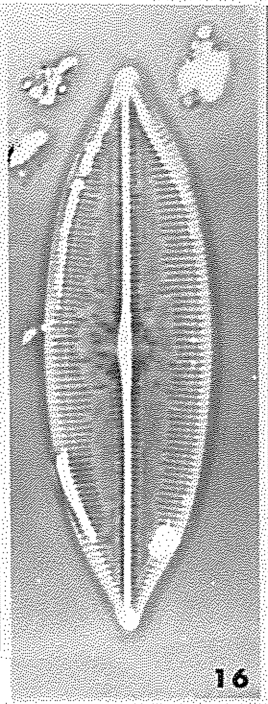
Fig. 25 *Navicula transitans*

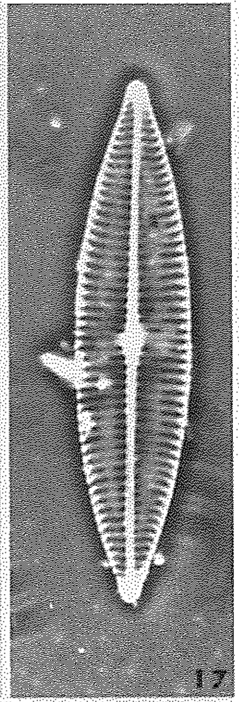
Fig. 26 *Navicula superba*


13

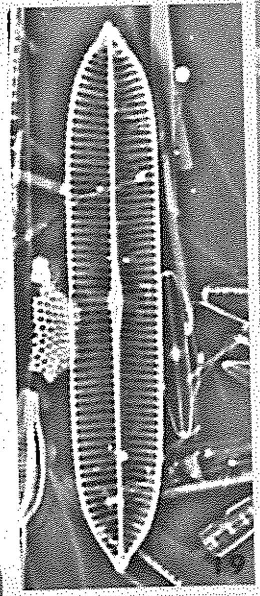

14

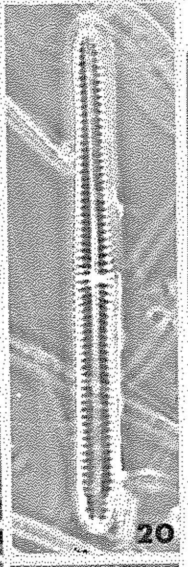

15

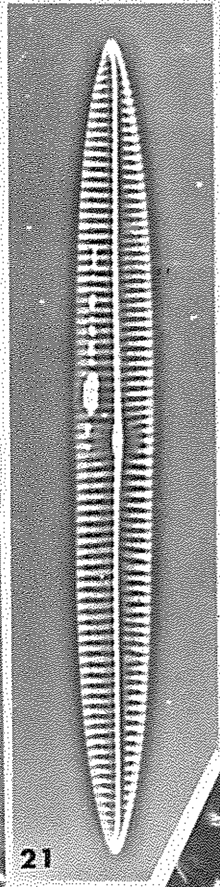

16

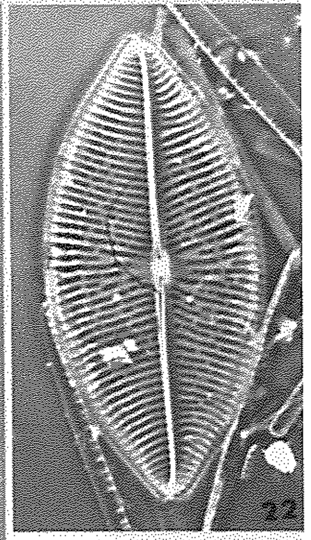

17

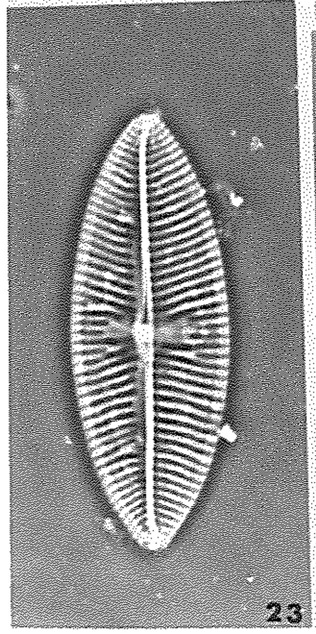

18

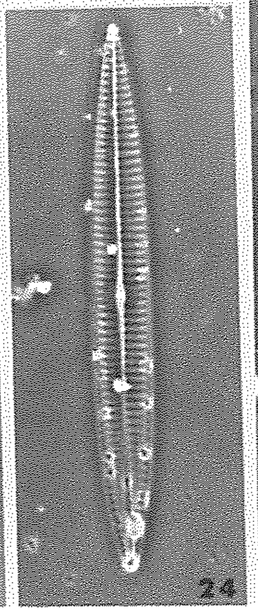

19

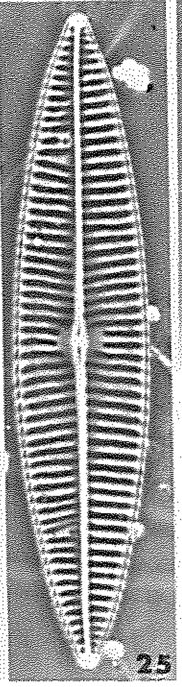

20

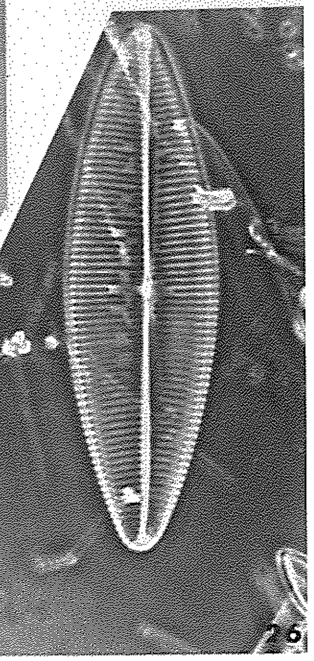

21


22


23


24


25


26

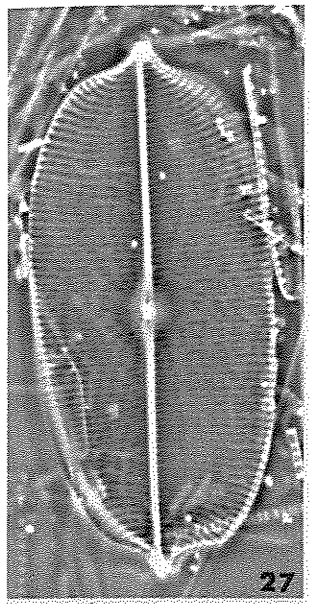


Fig. 27 *Navicula transfuga* var. *septentrionalis*

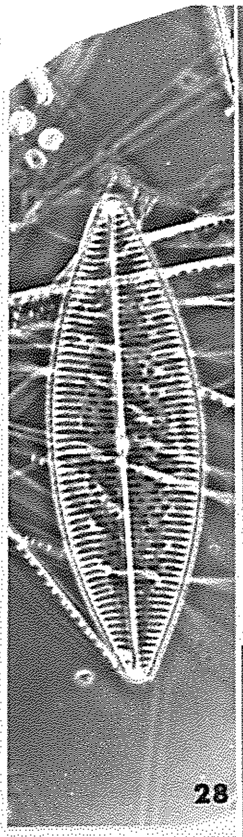


Fig. 28 *Navicula superba* var. *crassa*

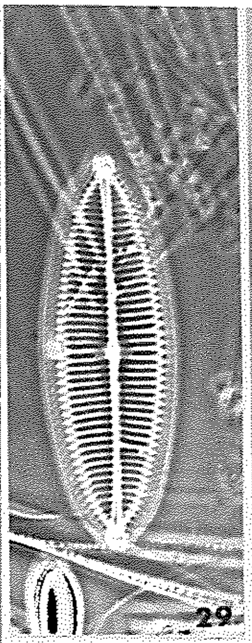


Fig. 29 *Navicula superba* var. *subacuta*

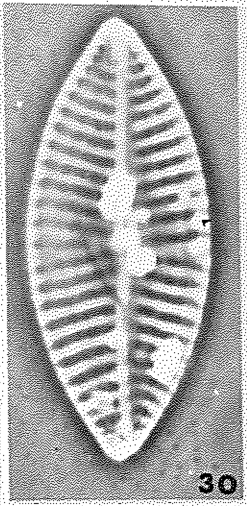


Fig. 30 *Navicula valida* var. *minuta*

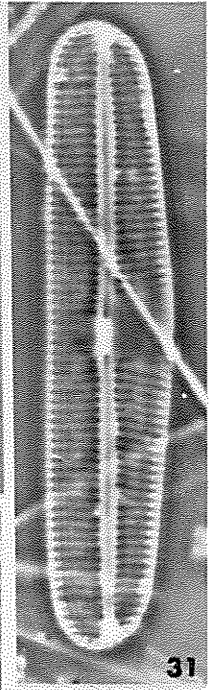


Fig. 31 *Pinnularia semiinflata*

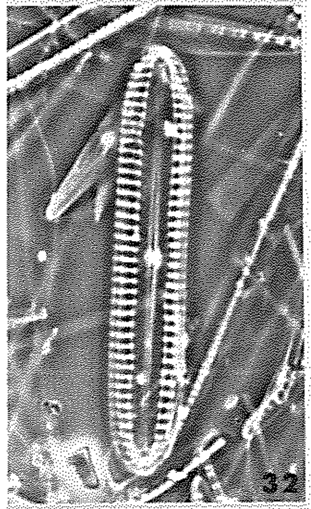


Fig. 32 *Pinnularia ambigua*

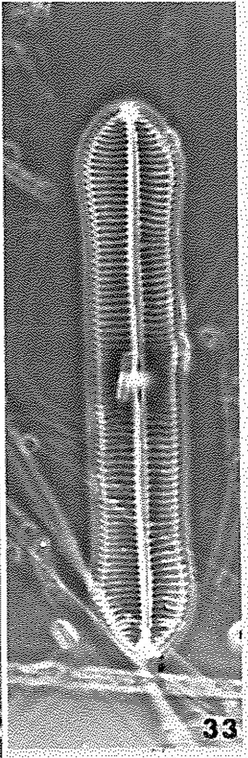


Fig. 33 *Pinnularia quadratarea* var. *capitata*

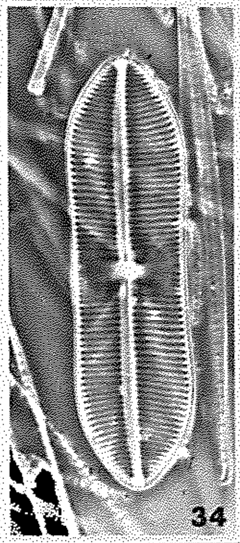


Fig. 34 *Pinnularia quadratarea* var. *constricta*

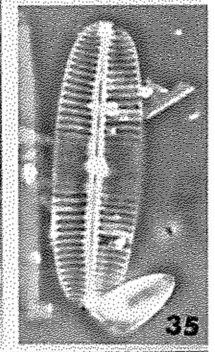


Fig. 35 *Pinnularia quadratarea* var. *minor*

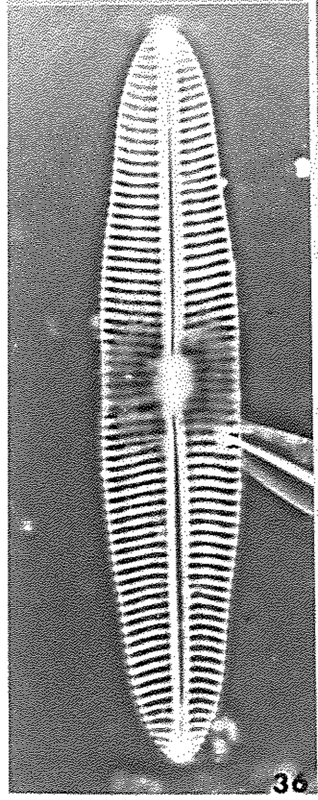


Fig. 36 *Pinnularia quadratarea* var. *maxima*

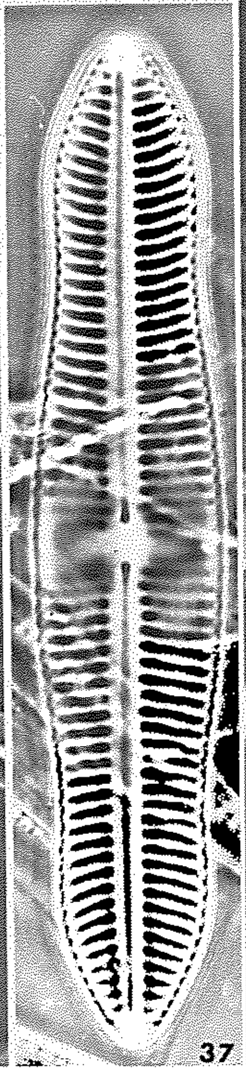


Fig. 37 *Pinnularia quadratarea* var. *bicontracta*

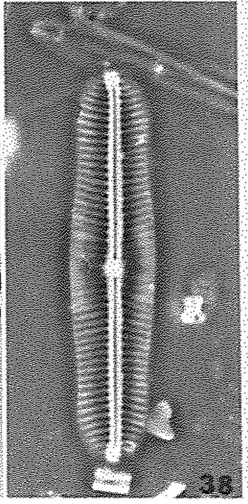


Fig. 38 *Pinnularia quadratarea* var. *densestriata*

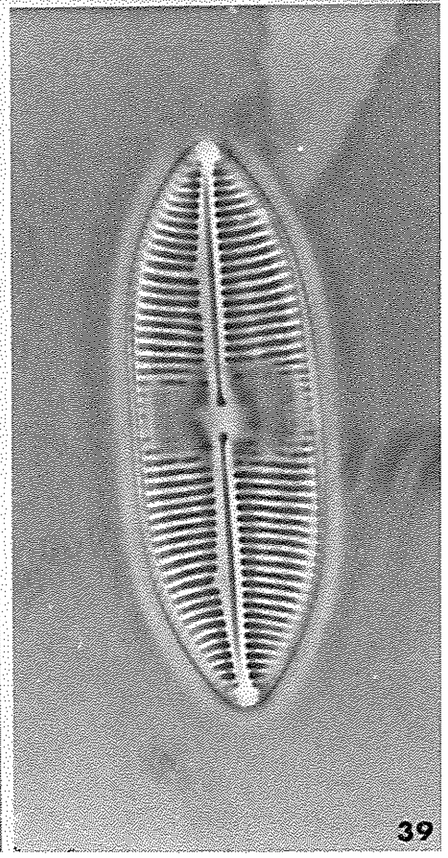


Fig. 39 *Pinnularia quadratarea* var. *dubia*

Fig. 40 *Pinnularia quadratarea* var. *cuneata*

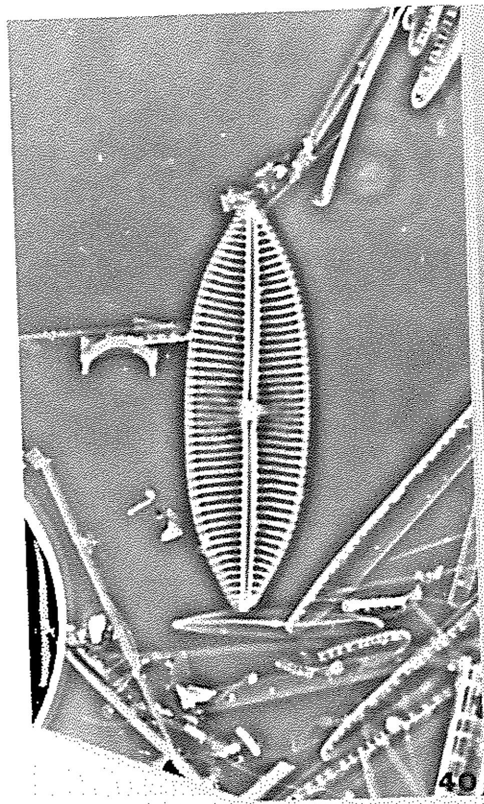
Fig. 41 *Pinnularia quadratarea* var. *subglabra*

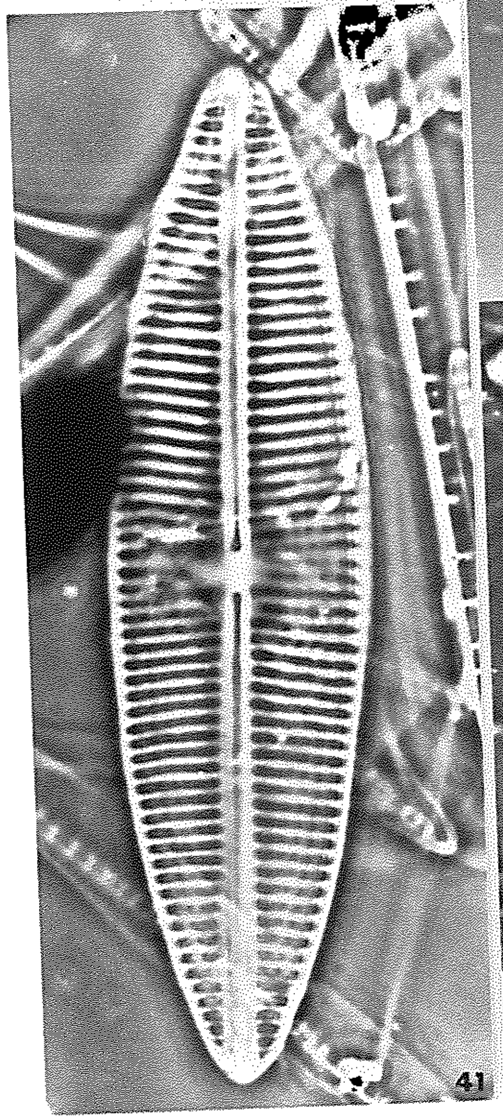
Fig. 42 *Pleurosigma siberica*

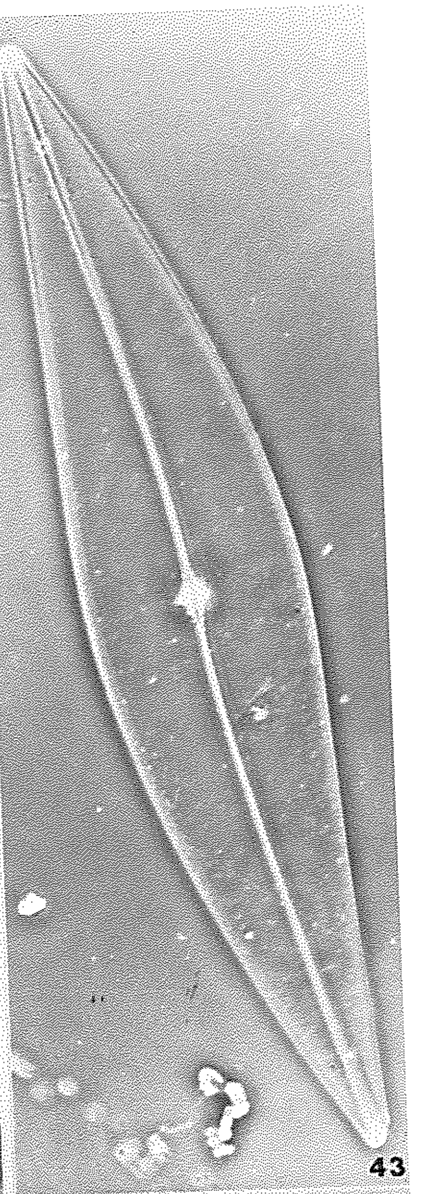
Fig. 43 *Pleurosigma stuxbergii* var. *rhomboides*

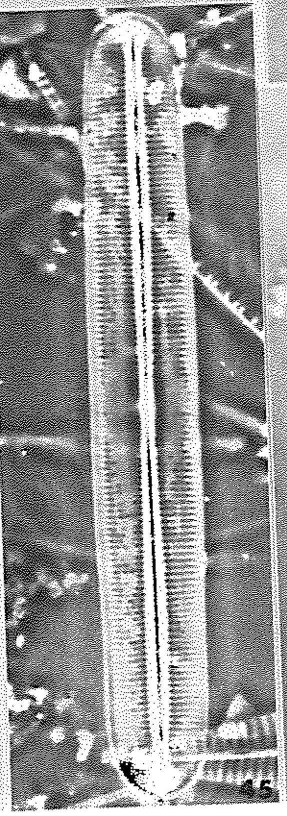
Fig. 44 *Stauroneis radissonii*

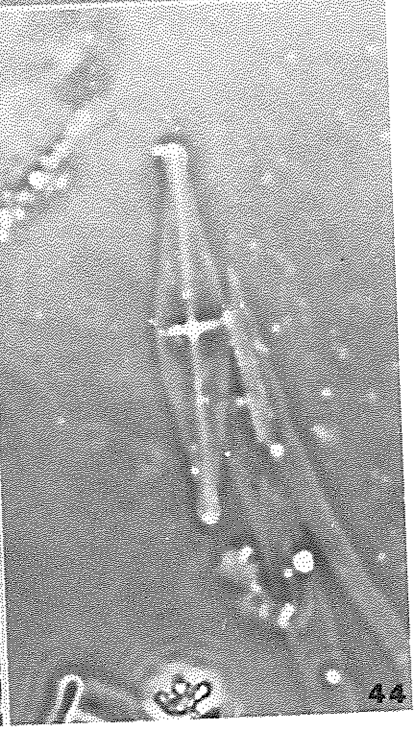
Fig. 45 *Stenoneis inconspicua* var. *baculus*

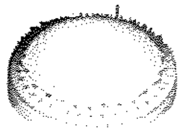












CHAPTER 19

FAMILY NAVICULACEAE:

THE GENERA PLAGIOTROPIS, BANQUISIA, MEMBRANEIS, AND MANGUINEA

T.B.B. Paddock

This section deals with polar species of *Plagiotropis* Pfitzer, *Banquisia* Paddock, *Membraneis* Paddock and *Manguinea* Paddock. Although a separate family (the Plagiotropidaceae) has been erected for *Plagiotropis* (Reimer in Patrick and Reimer, 1975), for the purposes of this account these genera are retained in the family Naviculaceae.

Plagiotropis with about 30 species is the largest of these genera, the others accounting for 5 species between them. *Plagiotropis* has world-wide distribution, but *Banquisia*, *Membraneis* and *Manguinea* are known only from coldwater or polar regions. These and allied genera are dealt with more fully in Paddock (1988).

Plagiotropis, *Banquisia*, *Membraneis* and *Manguinea* were formerly included in the genus *Tropidoneis sensu* Cleve, a large and diffuse concatenation of naviculoid species that has now been split into several genera.

Shape of the valve is an important initial feature in the recognition of these genera and in the distinction of the species. Valve shape largely determines the way in which specimens lie in the LM, and hence the views which are presented to the observer.

Two forms of valve can be distinguished, one 'vaulted' (Plate 19.1 Figs 10,11), the other 'ridged' (Plate 19.1 Figs 7,8). Vaulted valves are tall in the parapical axis, narrow in the transapical axis, with the valve face predominantly flat i.e. without a sudden change of contour. Ridged valves are relatively short in the parapical axis, relatively wide in the transapical axis, with the valves face contoured to form a distinct midline ridge. In the LM, ridged valves are particularly liable to lie at a variety of angles. The valves of *Banquisia* (Plate 19.1 Fig. 10) and *Membraneis* (Plate 19.1 Fig. 11) are very highly vaulted and usually lie in girdle view; valves of *Plagiotropis* (Plate 19.1 Figs 7,8) are ridged and may lie in girdle or in valve view, or at an intermediate angle.

Valves of similar shape (Paddock & Sims 1977, 1981, 1990) are found in the genus *Amphiprora sensu* Cleve (1894), a large shape-genus formerly considered closely related to *Tropidoneis*, but now recognised as separate. *Amphiprora* is currently being revised, but a full account is not yet available. Species of *Amphiprora* can be distinguished by details of the internal structure of the keel of the valve, by the different structure of their girdle bands, and by the absence of the very large helictoglossa which is always present in *Plagiotropis*, *Banquisia*, *Membraneis* and *Manguinea*.

In *Plagiotropis*, *Banquisia*, *Membraneis*, and *Manguinea* the raphe occupies the ridge-line of the valve. The raphe is never strongly sigmoid, a point of distinction from most species of *Amphiprora* and from all species of *Pleurosigma* Wm. Smith, especially those few planktonic species of *Pleurosigma* which have delicate, slightly vaulted valves. The raphe lacks fibulae i.e. the serially repeating structures subtending the raphe system and termed 'keel puncta' in older literature, which are seen in *Nitzschia* Hassall and are present in a modified or derived form in most species of *Amphiprora*.

There is a very large helictoglossa (a funnel-shaped structure) at each valve pole (Plate 19.1 Fig. 11). This is easily visible in the LM, especially in valves lying in girdle view. The lack of a large helictoglossa indicates that the species does not belong to *Plagiotropis*, *Banquisia*, *Membraneis* or *Manguinea*; if the overall shape of the valve is similar to species of *Plagiotropis*, but the large helictoglossa is lacking, the specimen may well belong within *Amphiprora*. If so, the valve will be keeled rather than ridged, and the keel will have more complex structure probably with numerous fibulae visible as bright spots within it in the phase contrast LM.

Some species of *Plagiotropis* have a scutum; this is a flap-like structure of hyaline silica which overlies part of the outer face of the valve. In the LM, the presence of a scutum has the effect of partly obscuring the pattern of the valve areolation (Plate 19.1 Fig. 4).

Very small fin-like structures (raphe fins) are present at about one quarter of the way along the raphe in *Banquisia*, *Manguinea*, and *Membraneis*, but these are absent in *Plagiotropis*. Once they have been seen and recognised (Plate 19.1 Fig. 10), raphe fins provide a very easily-used feature, but they are difficult to photograph and so have only been used as confirmatory characters in the keys.

The girdle bands of *Plagiotropis*, *Banquisia*, *Membraneis* and *Manguinea* lack obvious coarse areolation; they are smooth and hyaline. In contrast the girdle bands of species of *Amphiprora* are strongly areolate and have a longitudinal midrib.

There is a number of other species of uncertain taxonomic position but probably related to *Plagiotropis* or *Membraneis* which have not been investigated because of the lack of study material. These species – *Tropidoneis candida* Mann, *T. charcotii* Peragallo, *T. decussata* var. *sigmoidea* Heiden in Heiden & Kolbe, *T. proteus* Karsten, *T. adeliae* Manguin – continue, for the present, to be catalogued as species of *Tropidoneis sensu* Cleve (1894), even though the generic name *Tropidoneis* is nomenclaturally invalid (Reimer in Patrick & Reimer 1975). A summary and illustrations are given in Paddock (1988). All these species have been recorded from polar waters; a special watch should be kept for them so that their morphology and taxonomy can be fully investigated.

Table 19.1. Morphometric and distributional data on *Plagiotropis*, *Banquisia*, *Membraneis*, and *Manguinea* spp.

Taxa	*Apical axis, in μm*	*Striae in 10 μm*	*Features*	*Polar distribution*[1]
Plagiotropis scaligera Grun. in Cleve & Grun.	100–130	24–45	striae interrupted scutum	North Norway
Plagiotropis australis (M.Peragallo) Paddock	250	14	fascia scutum	Bransfield Strait (rare)
Plagiotropis gaussii (Heiden in Heiden & Kolbe) Paddock	102–159	15–18	valve delicate	Antarctic (with ice)
Plagiotropis longa (Cleve) Kuntze	220–300	10	expanded central nodule scutum	Spitzbergen, Greenland, Labrador
Banquisia belgicae (van Heurck) Paddock	70–125	18	ridge biarcuate raphe fins	South Orkney Islands (bipolar?)
Membraneis challengeri (Grun. in Cleve & Grunow) Paddock	85–270	18–24	central striae thickened raphe fins absent	Antarctic Ocean
Membraneis imposter Paddock	79–125	15–16(18)	raphe fins present	S. Atlantic
Manguinea fusiformis (Manguin) Paddock	49–135	28	frustule fusiform diagonal punctation	Antarctic Ocean
Manguinea rigida (M.Peragallo) Paddock	60–80(120)	24(18?)	frustule bacilliform	Wandel Land

[1] taken from published literature

How to identify to species:
Identifications may be based on acid cleaned material studied in the LM. A microscope fitted with phase contrast optics will be especially useful if the sample alsocontains species of *Amphiprora*, because phase contrast will reveal some of the structures within the keel. SEM observations will be helpful to confirm identifications by examination of details of structure, particularly if pictures can be compared with those published in Paddock (1988).

Careful note should be kept of cytoplasmic features since few modern observations have been published.

Characters to observe:

Is the valve lying in girdle view or valve view?
Is the valve vaulted or raised into a ridge?
Is the raphe simple i.e. lacking fibulae ('keel puncta')?
Is there a large funnel-shaped helictoglossa present at each valve pole?
When the valve is seen in girdle view is the outline of the valve ridge bi-lobed or semicircular?
Are the two faces (sides) of the valve equal, subequal or unequal in area?
Are the valve faces predominantly flat, or is each divided by a prominent contour line?
Is the striation predominantly transverse?
Is the valve face partly covered by a scutum?
Are small raphe fins present?
Are the girdle bands hyaline i.e. lacking areolation?

Key to genera:

1a Diatoms with a raphe on a structurally complex, usually bi-lobed raised keel, without an enlarged helictoglossa, with areolate girdle bands .... *Amphiprora* (not considered here).
1b Diatom with a (simple) naviculoid raphe on a raised ridge or along a vaulted valve, a large helictoglossa, and hyaline (non-areolate) girdle bands 2
2a Valve vaulted 3
2b Valve ridged 4
3a Valve vaulted with equal faces and conspicuous raphe fins .... *Banquisia*
3b Valve vaulted with unequal or subequal faces, more or less lens-shaped in girdle view .... *Membraneis*
4a Ridge lobed, raphe fins lacking .... *Plagiotropis*
4b Ridge low and not lobed, bearing raphe fins, frustule bacilliform or shuttle-shaped .... *Manguinea*

GENUS PLAGIOTROPIS Pfitzer

Valves lying in valve or girdle view, with a ridge more or less bilobed in girdle view, with valve sides unequal or subequal, usually contoured rather than flat. Raphe fins absent. Some species with a scutum.

Key to species:

1a Valve delicate, with narrow transapical axis, (therefore lying in girdle view), helictoglossa very large, solid; valve faces not strongly contoured .... *P. gaussii*
1b Valve robust, with wide transapical axis, lanceolate in valve view 2
2a Striae discontinuous, in a ladder-like arrangement, with hyaline areas at regular intervals ...... *P. scaligera*
2b Striae continuous (valve without hyaline areas) 3
3a Valve with a fascia and two extensive scuti .... *P. australis*
3b Valve without a fascia, but with clearly expanded central area formed by irregularly shortened striae ... . *P. longa*

GENUS BANQUISIA Paddock

Valves lying in girdle view, vaulted to a high ridge which is biarcuate in girdle view; the valve has flat, equal faces. Raphe fins present. Scutum absent.

Only one species is known .... *B. belgicae*

GENUS MEMBRANEIS Paddock

Valves lying in girdle view, vaulted to a high ridge with flat unequal faces. Raphe fins present or absent. Scutum absent.

Key to species:

1a Valve ridge with an elliptical profile in girdle view, reinforced striae at the central nodule, and raphe fins .... *Membraneis challengeri*
1b Valve ridge with biarcuate profile in girdle view, without reinforced striae at the central area, without raphe fins .... *Membraneis imposter*

GENUS MANGUINEA Paddock

Valves lying in girdle or valve view, formed into a low ridge with unequal valve sides; puncta separate, appearing to lie in longitudinal spiral lines. Raphe fins present. Scutum absent.

Key to species:

1a Frustule fusiform in girdle view .... *M. fusiformis*
1b Frustule bacilliform in girdle view .... *M. rigida*

Plate 19.1. Photomicrographs

Figs 1, 2 *Plagiotropis scaligera*

Fig. 1 Valve in oblique valve view; note biarcuate raphe ridge, and ladder-like interruptions of valve striation. BM (Deby) 23071 (Cleve & Möller slide 312), Maaso, Finmark Specimen 116 μm long.

Fig. 2 Central part of valve, enlarged to show striae with hyaline spaces between them. Striae 18 in 10 μm.

Figs 3, 4 *Plagiotropis australis*

Fig. 3 Valve in valve view. Note strong contour lines along the valve at the base of the raphe ridge, the prominent central nodule, and the lines marking the edge of the scutum. Type slide BM 33965 Bransfield Strait Specimen 250 μm long.

Fig. 4 Central part of valve of another specimen (Smithsonian Mann 1519), showing valve striation, strong hyaline central area and the prominent internal longitudinal crescentic thickenings surrounding the central raphe endings. Arrow marks the approximate edge of one of the two valve scuta.

Figs 5, 6 *Plagiotropis gaussii*

Fig. 5 Girdle view of part of frustule, showing hyaline girdle band g and striation of valve faces. The outline of the frustule is formed by the top of the valve ridge; note the highly refringent enlarged helictoglossae (arrowed), and the absence of raphe fins (see raphe fins in Fig. 10).

Fig. 6 Frustule lying in girdle view; the frustule is very delicate and has a distinctive outline, BRM 283.95 Gauss Expedition Specimen 109 μm long.

Figs 7, 8, 9 *Plagiotropis longa*

Fig. 7 Valve lying in valve view displays strong contour lines near the base of the raised raphe ridge. Central area is strongly thickened and laterally expanded. BM 59617 Bottom mud from the East coast of Greenland. Specimen 250 μm long.

Fig. 8 Frustule lying in girdle view; the valves have a low raphe ridge; the central nodule is only slightly depressed below the highest point of the ridge. Refringent helictoglossae are visible at the valve ends. BM 27788, Spitzbergen. Specimen 270 μm long.

Fig. 9 Enlarged view of striae and expanded central area of another specimen (from Torres Straits BM 32090). Striae 15 in 10 μm.

Fig. 10 *Banquisia belgicae*. Frustule in girdle view; bright field microscopy. Note characteristic profile, and presence of raphe fins (arrowheads) in each of the four 'shoulders' of the frustule. Enlarged helictoglossae are clearly visible at both ends of both valves. The girdle bands are hyaline, (see right-hand end of specimen). BRM 283.96 Gauss Expedition. Specimen 82 μm long, striae 18 in 10 μm.

Fig. 11 *Membraneis challengeri*. Frustule in girdle view. The valves are highly vaulted; the valve face lacks strong contours. Raphe fins are visible in two places on the raphe ridge (arrows). Note thickened transverse striae at the central area, the very refringent elaborate helictoglossae at the poles of each valve, and the hyaline girdle bands (g). BM 81290 Brategg Expedition, 63°S, 120°W. Specimen 100 μm long, striae 22-24 in 10 μm.

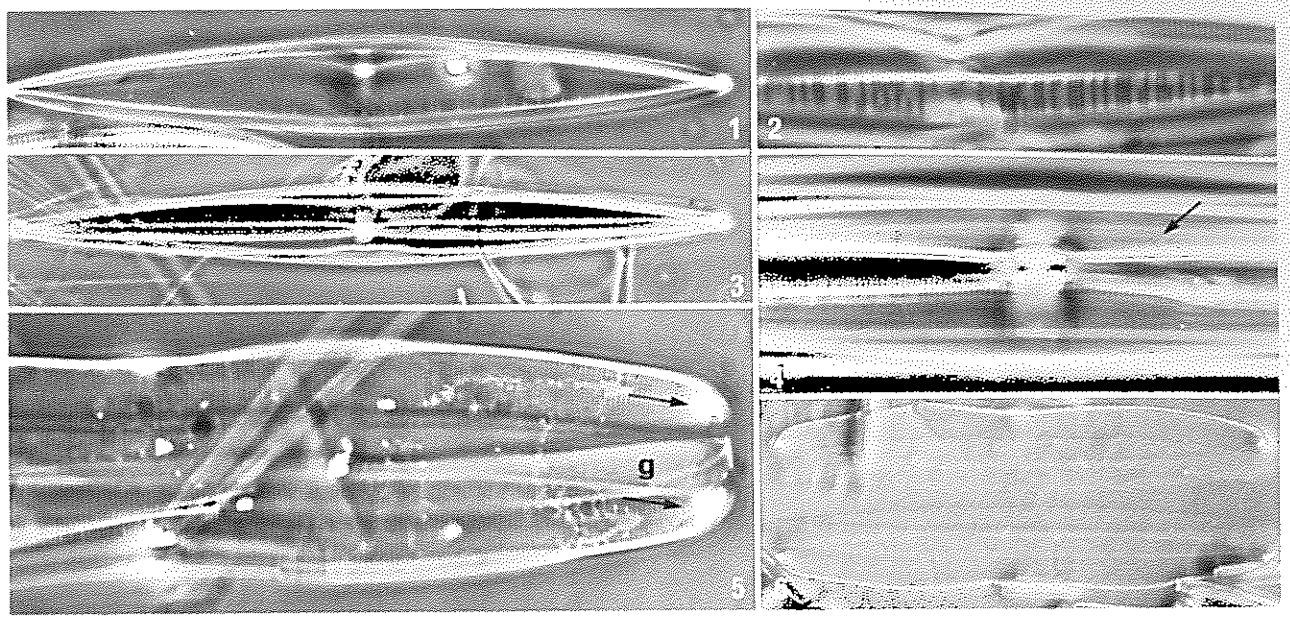
Fig. 12, 13 *Membraneis imposter*

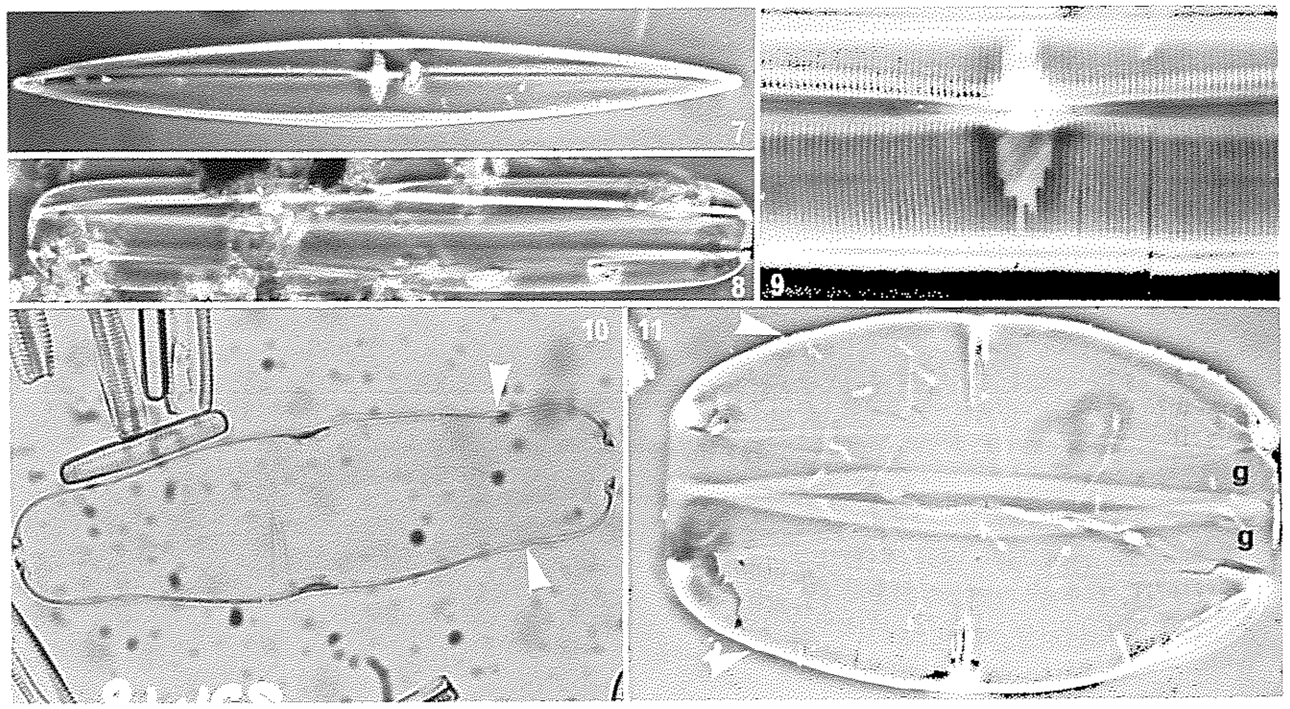
Fig. 12 Part of a valve lying in girdle view; the valve is vaulted and the outline has a slight shoulder from which raphe fins are absent (compare with Figs 10 & 11). Striae 22-24 in 10 μm.

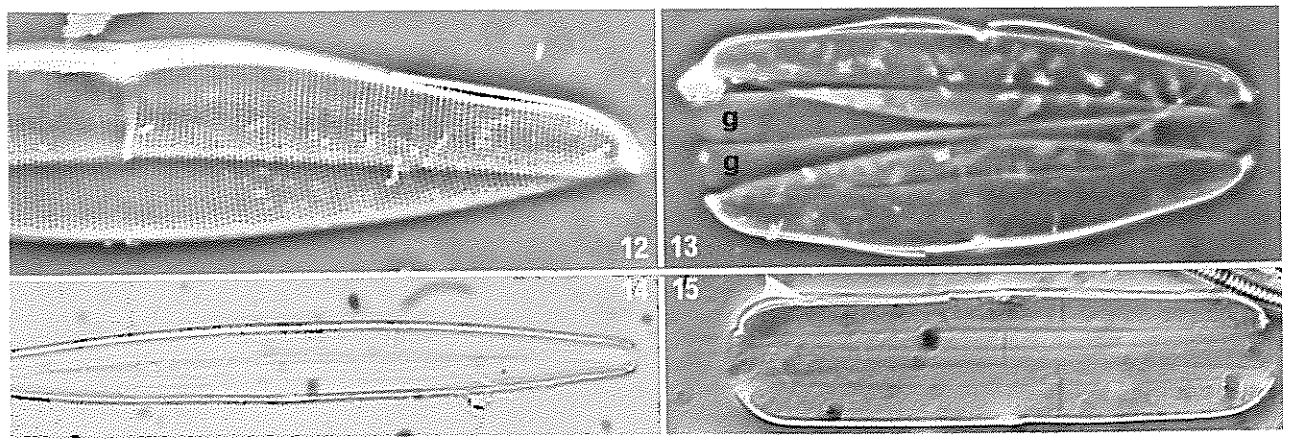
Fig. 13 Frustule lying in girdle view. Note inequality in area of the two sides of each valve. Raphe fins are not present in the slight 'shoulders' of the outline (see Fig. 12). The girdle bands (g) are hyaline. BM 81291 Brategg Expedition, 67°S, 87°W. Specimen 112 μm long.

Fig. 14 *Manguinea fusiformis*. Bright field micrograph. Frustule lying in girdle view; note the shuttle shape, and the presence of raphe fins detectable as slight irregularities in the outline (arrows). (The absence of fibulae from the raphe system confirms that this diatom does not belong to *Nitzschia*). Puncta are arranged in spiral lines along the length of the valves but are hard to see. Enlarged helictoglossae are visible at the ends of the valves. BM 81292 Discovery Expedition. Specimen 118 μm long.

Fig. 15 *Manguinea rigida*. Bright field micrograph. Note the characteristic bacilliform shape, the unequal extent of the two faces of each valve and the presence of raphe fins visible as irregularities (arrowhead) in the outline. Large helictoglossae can be seen at the ends of both valves. A longitudinal crescentic thickening is just visible at the central nodule (centre, bottom edge of picture). Areolae, visible with difficulty, lie in spiralling longitudinal lines. BM 81294 Discovery Expedition Specimen 60 μm long.







CHAPTER 20

FAMILY NAVICULACEAE:

THE GENUS PSEUDOGOMPHONEMA

Linda K. Medlin

GENUS PSEUDOGOMPHONEMA Medlin

Cells solitary or in a cluster attached by a short pad or stalk to macroalgae or other diatoms or to the underside of sea ice. Valves linear to linear-lanceolate with broadly rounded or slightly rostrate head poles and more acutely rounded foot poles. Striae lineolate. Pseudoseptum present as a bridge across the valve usually at the foot pole (but at the head pole in some species), leaving the appearance of a small chamber or hole. Raphe-sternum central, more strongly developed on the primary side of the raphe. Striae closely abut the primary side of the raphe but on the opposite side fall short of the raphe leaving an asymmetrical axial area. Striae usually less dense on the primary side of the raphe. Length of raphe system slightly shorter from central nodule to head pole than from central nodule to foot pole.

How to identify to genus/species:
The genus may be identified in water mounts by its cuneate shape cell with a raphe present on both valves, but positive species identification must rely on cleaned material in permanent mounts.

Characters to look for in valve view:
1. Shape of valve and apices
2. Number of striae in 10 μm on both sides of the raphe
3. Shape of central area

Key to species:
1a Valves linear .... *P. groenlandicum*
1b Valves lanceolate 2
2a Rostrate apices, striae 16-18 in 10 μm .... *P. arcticum*
2b Rounded apices, striae 10-14 in 10 μm 3
3a Indistinct central area formed by 2 shorter striae .... *P. septentrionale* & var. *angustatum*
3b Distinct central area formed by four or more shorter striae .... *P. kamtschaticum* & var.?

Ecology:
Marine epiphytic and ice associated diatoms in cold temperate and polar waters. The varieties of *P. kamtschaticum* will probably be described as separate species.

Table 20.1. Morphometric and distributional data on *Pseudogomphonema*

	Apical Axis in μm	*Transapical Axis in μm*	*Striae in 10 μm*		*Polar Distribution*
			Primary Side	*Secondary Side*	
P. kamtschaticum Grun.	18–70	4–11	10–14	11–14	epiphyte Arctic
var. ?	35–40	5–6	10	11	epiphyte Antarctic
P. groenlandicum Østr.	42–108	12	7–8	10–12	ice Arctic
P. septentrionale Østr.	22–30	5–7	10	12	ice Arctic
var. *angustatum* Østr.	35–50	6–7	10	12–13	ice Arctic
P. arcticum Grun.	20–45	8–10	16–18		epiphyte Arctic

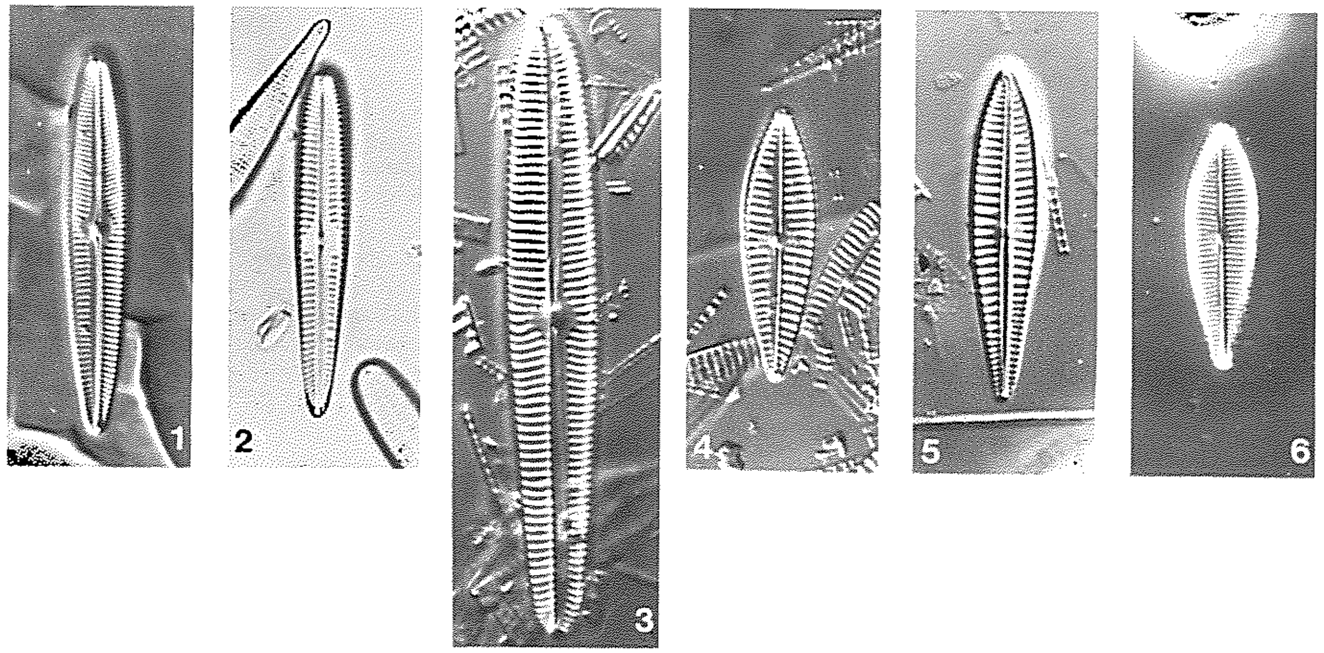


Plate 20.1. Nomarski Interference Contrast photomicrographs X1000.

Fig. 1 *P. kamtschaticum*

Fig. 2 *P. kamtschaticum* var. ?

Fig. 3 *P. groenlandicum*

Fig. 4 *P. septentrionale*

Fig. 5 *P. septentrionale* var. *angustatum*

Fig. 6 *P. arcticum*

CHAPTER 21

FAMILY AURICULACEAE AND FAMILY BACILLARIACEAE

Linda K. Medlin and Grethe R. Hasle

Key to members of the family Bacillariaceae and the family Auriculaceae in polar waters

1a Raphe diagonally or nearly centrally positioned on opposing valves of a frustule 3
1b Raphe otherwise 2
2a Raphe positioned along same margin of opposing valves of a frustule ....*Hantzschia*
2b Raphe traversing the valve face from one apex to the centre of one valve margin on the same side of opposing valves of a frustule ....*Auricula*
3a Colonies formed by overlapping cell apices ("stepped" colony formation) ....*Nitzschia* section *Pseudonitzschia*
3b No colony formation or colonies otherwise 4
4a Ribbon colony formation with cells attached along *entire* valve face ....*Nitzschia* section *Fragilariopsis*
4b No colony formation or colonies otherwise 5
5a No colonies, cells with protracted apices usually forming rostra ....*Nitzschia* section *Nitzschiella*
5b No colonies or with a different type of colony formation ....*Nitzschia* – all other species

FAMILY AURICULACEAE

GENUS AURICULA Castracane

Cells solitary. Frustules rectangular to elliptical. Valves auricular to reniform with a strongly ridged keel that is not differentiated from the valve surface as in *Amphiprora* but divides the valve into a broad and narrow face. Raphe lies atop the keel and is subtended by fibulae. Raphe biarcuate, traversing the valve from one apex to valve centre at one valve margin where the central nodule occurs, and depressed at the central nodule. Numerous girdle bands arranged into a broad and narrow view to accommodate the two valve faces. The frustule asymmetry is destroyed with cleaning and it is not surprising that *Auricula compacta*, the single species known from polar regions, was first described as a species of *Nitzschia*. For this reason it has been included in the key to *Nitzschia* spp.

FAMILY BACILLARIACEAE

GENUS HANTZSCHIA Grunow

Cells solitary. Frustules linear. Valves asymmetrical with respect to the apical axis with a convex dorsal margin and a straighter ventral margin. The raphe, associated with the ventral margin, is subtended by fibulae and is positioned on the same side of opposing valves of a cell. The single species illustrated here, *H. weyprechtii*, is included in the key to *Nitzschia* spp.

GENUS NITZSCHIA Hassall

Cells solitary or in colonies (arborescent, stellate, ribbon, "stepped"). Frustules linear or sigmoid. Valves usually symmetrical. The raphe is diagonally positioned on opposing valves of a cell. The fibulae, which subtend the raphe system, appear as distinct bars or dots on the inside of the valve surface with LM. The raphe position may be central to extremely eccentric. Those species in *Nitzschia* with a central or nearly central raphe system cannot be placed in the genus *Bacillaria* Gmel., which has central raphe systems on opposing valves. These species lack the characteristic colony formation and cell movement of *Bacillaria* and many of these also have a conopeum that places them in *Nitzschia*.

The species of this genus can be very difficult to identify because of the paucity of valve characters that can be used to distinguish taxa with LM. Three sections (*Fragilariopsis*, *Pseudonitzschia*, and *Nitzschiella*) have characteristic colony formation or valve shape and each of these sections has been dealt with separately. The remaining members of the genus *Nitzschia* that are associated with the ice or are in polar waters represent a heterogenic group. Although we can place some of them in a section, many of them cannot be assigned to any section as they are presently defined. We have included in this handbook only those species of whose identification we can be positive, and certain other unidentified species that might be confused with other known taxa.

How to identify to species:
Colony formation can be helpful in some instances, but cells must be cleaned of organic matter for reliable species identification. Some species, i.e. *Nitzschia frigida*, *Nitzschia neofrigida*, and *Nitzschia polaris*, may look similar in cleaned material, yet only one of these, *Nitzschia polaris*, does not form colonies. The other two species form similar arborescent colonies and can only be separated by their size. *Nitzschia neofrigida* and *Stenoneis inconspicua* var. *baculus* form similar arborescent shaped colonies but with fewer than ten cells per colony. These two taxa have probably been included in the distribution of *Nitzschia frigida* when only water mounts have been examined.

In all instances, water mounts should be made from cleaned preparations so that the valves may be turned to ensure that the position of the raphe is accurately determined. If the raphe is central, the valves may often rest with part of the valve folded beneath the raphe, i.e. in girdle view, thus giving the appearance that the raphe is eccentric. Often the valves do not lie flat in permanent mounts, and the appearance of the valve may be mis-

Table 21.1. Morphometric and distributional data on *Nitzschia* spp.

	Apical Axis in μm	*Transapical Axis in μm*	*Fibulae in 10 μm*	*Striae in 10 μm*	*Central Nodule*	*Polar Distribution*
Nitzschia frigida Grun.	45–75	4.5–7.5	7–9	45–50 N	+	Arctic, ice
Nitzschia neofrigida Medlin	60–109	6–7	6–8	40 R	+	Arctic, ice
Nitzschia polaris Grun.	50–169	5–7	5–8	40 P	+	Arctic, ice
Nitzschia stellata Mang.	60–134	6.5–10	4–8	40 R	+	Antarctic, ice
Nitzschia taeniiformis Sim.	110–150	5	6–10	24	+	Antarctic, ice
Nitzschia promare Medlin	31–45	4–5.5	8–12	45–50 N	+	Arctic, ice, ?plankton
Nitzschia scabra Cleve	108–220	7–10	2–3	mottled	–	Arctic, ice
Nitzschia arctica Cleve	90–155	7–8	8–10	24–26	+	Arctic, ice
Nitzschia brebissonii var. *borealis* Cleve	120–170	6–8	7–8	12–18	–	Arctic, ice
Nitzschia laevissima Grun.	115–170	6–6.5	6–8	40 V	+	Arctic, ice
Hantzschia weyprechtii Grun.	55–75	6–7	9–11	33–35	+	Arctic, ice
Auricula compacta (Hust.) Medl.	85–134	12	6–9	22–24	+	Antarctic, ice

N = not resolvable with LM
R = barely resolvable with LM, ~ 40 in 10 μm
P = not present on valve face, face appears hyaline
V = striae appearance varies from hyaline to isolated areolae to 40 in 10 μm

leading. The appearance of the striae on the valve can also be a problem. If the striae are incompletely perforated, then the valve will appear hyaline with LM. If they are partially but randomly perforated, then isolated areolae will appear scattered over the valve surface. In some cases the striae will be fully perforated throughout the valve and these may be resolved with LM. All three cases may be present in the same species.

Characters to look for in valve view:

1. Length of apical and transapical axes
2. Number of fibulae in 10 μm
3. Number of striae in 10 μm, usually about 30-35 striae in 10 μm can be resolved with LM
4. Shape of the valve, how does the valve change in curvature from the valve centre
5. Presence or absence of a central nodule (termed pseudonodulus in older literature and indicated by a greater distance between the middle two fibulae)
6. Position of the raphe(s) on the valve (cell)

Key to species based on colony formation:

1a Arborescent colonies 2
1b Ribbon colonies, *free* at cell apices 4
2a Lanceolate valve, Antarctic species .... *Nitzschia stellata*
2b Linear to linear-lanceolate valve, Arctic species ...3
3a Cells heavily silicified, greater than 80 μm in length, frustule in girdle view greater than 15 μm wide .... *Nitzschia neofrigida*
3b Cells weakly silicified, less than 80 μm in length, frustule in girdle view less than 10 μm wide .... *Nitzschia frigida*
4a Cells greater than 45 μm in length, colonies in short ribbons 5
4b Cells less than 45 μm in length, colonies in long ribbons .... *Nitzschia promare**
5a Central nodule present 6
5b Central nodule absent, fibulae 3-4 in 10 μm, Arctic species .... *Nitzschia distans* var ?
6a Fibulae 6-10 in 10 μm, Antarctic species .... *Nitzschia taeniiformis*
6b Fibulae 12-18 in 10 μm, Arctic species .... *Nitzschia pellucida****

Key to species based on cleaned material:

1a Valves very asymmetrical with respect to the apical axis, having one straight margin, one curved margin 2
1b Valves symmetrical with respect to the apical axis or slightly asymmetrical if the raphe is central and the valve lies in girdle view 3
2a Raphe on straight margin ..*Hantzschia weyprechtii*
2b Raphe on curved margin, valve ear-shaped .... *Auricula compacta***
3a Valves sigmoid .... *Nitzschia laevissima*
3b Valves linear to linear-lanceolate to lanceolate ...4
4a Striae less than 30 in 10 μm 5
4b Striae more than 30 in 10 μm, often not resolvable 7
5a Central nodule present 6
5b Central nodule absent .... *Nitzschia brebissonii* var. *borealis*
6a Valves bracket-shaped, obtuse apices .... *Nitzschia taeniiformis*
6b Valves lanceolate, acute apices ....*Nitzschia arctica*
7a Central nodule present 8
7b Central nodule absent 12
8a Valves less than 45 μm in length, waisted at central nodule .... *Nitzschia promare*
8b Valves greater than 45 μm in length 9
9a Valves lanceolate 6.5-10 μm wide ..*Nitzschia stellata*
9b Valves linear to linear-lanceolate 4-7 μm wide ..10
10a Fibulae robust, raphe central, valves heavily silicified and more linear 11
10b Fibulae delicate appearing as straight bars, raphe slightly eccentric, valves lightly silicified and more lanceolate .... *Nitzschia frigida*
11a Striae not resolvable with LM, apices sub-rostrate .... *Nitzschia polaris*
11b Striae resolvable with LM using oiled condenser, NA = 1.4, apices obtuse or broadly rounded .... *Nitzschia neofrigida*
12a Striae not resolvable with LM, raphe nearly central .... *Nitzschia distans* var ? ***
12b Striae irregularly perforated giving a "mottled" appearance to valve, raphe eccentric .... *Nitzschia scabra*

**N.hybrida*, Section *Bilobatae*, was reported by Gran 1897, to be present under the ice forming ribbon colonies. The species we have found forming these ribbon colonies is not *N.hybrida*, and has been described as a new species (Medlin and Hasle, 1990). *Nitzschia promare* may be most easily confused with *Achnanthes taeniata* and smaller colonies of *Nitzschia grunowii*, section *Fragilariopsis*, which also form ribbon colonies, although these species are attached along their entire valve length.

**originally described as *Nitzschia compacta* Hust.

***specimens not illustrated from cleaned material or in keys because of insufficient information

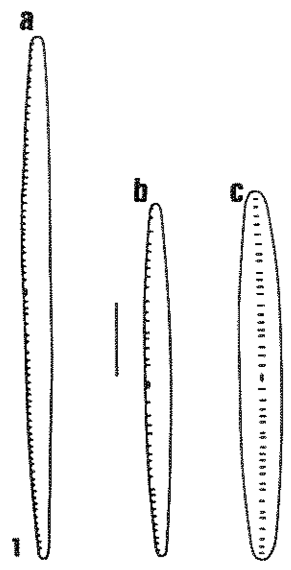
Plate 21.1. Line drawings. X1000. Striae, when resolvable with LM, are drawn in only at valve centre.

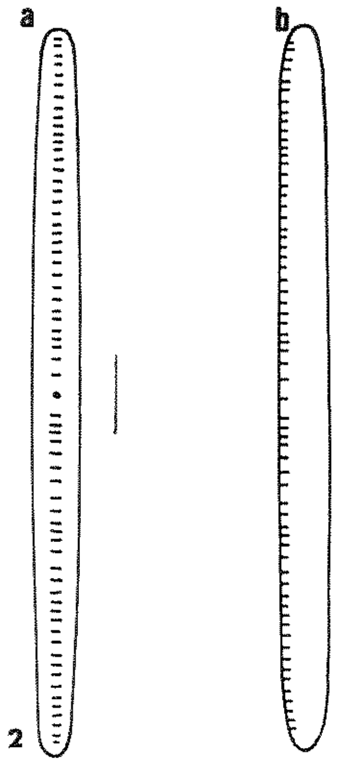
Fig. 1 *Nitzschia frigida* a,b. Valve view with eccentric raphe c. Valve with collapsed mantle so that raphe appears central.

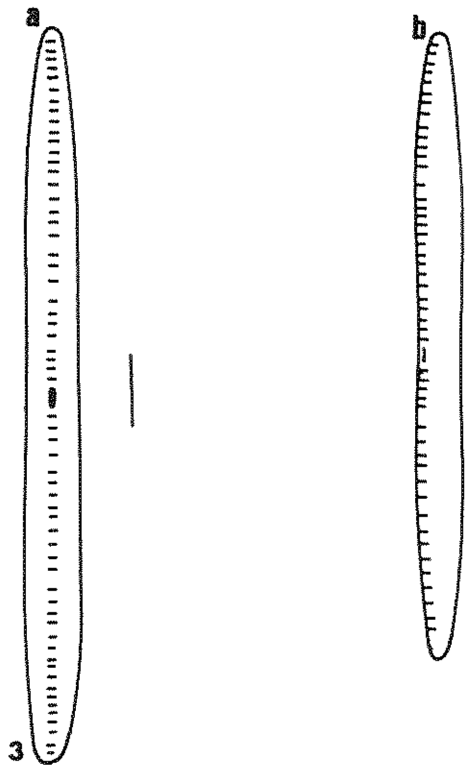
Fig. 2 *Nitzschia neofrigida* a. Valve view with central raphe. b. Valve folded back on itself so that raphe appears eccentric.

Fig. 3 *Nitzschia polaris* a. Valve view with central raphe. b. Valve folded back on itself so that raphe appears eccentric.

Fig. 4 *Nitzschia stellata* Valve view with eccentric raphe.







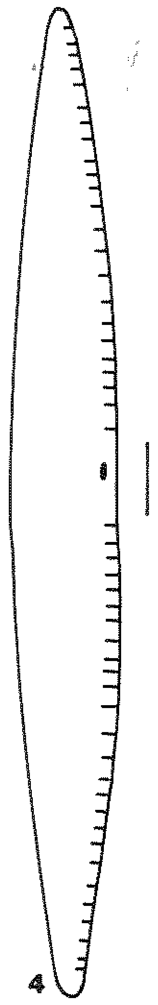


Fig. 5 *Nitzschia taeniiformis* Valve folded back on itself so that raphe appears eccentric, note distinct pinching in of raphe at central nodule.

Fig. 6 *Nitzschia promare* Valve view with eccentric raphe, note valve waisted at central nodule.

Fig. 7 *Nitzschia scabra* Valve view with slightly eccentric raphe.

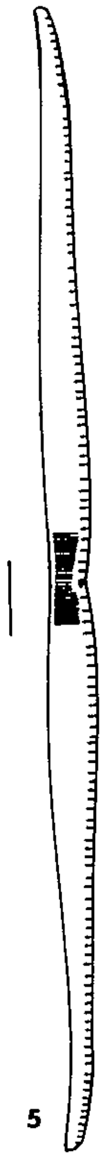
Fig. 8 *Nitzschia arctica* Valve view with eccentric raphe.

Fig. 9 *Nitzschia laevissima* Valve view with isolated puncta visible, valve may also appear hyaline.

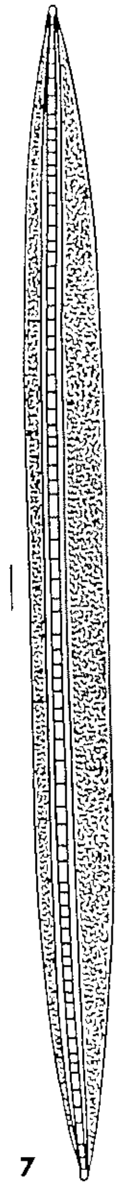
Fig. 10 *Nitzschia brebissonii* var. *borealis* Valve view with central raphe.

Fig. 11 *Auricula compacta* Narrow valve face folded beneath broad valve face, raphe appears eccentric.

Fig. 12 *Hantzschia weyprechtii* Valve view, eccentric raphe.

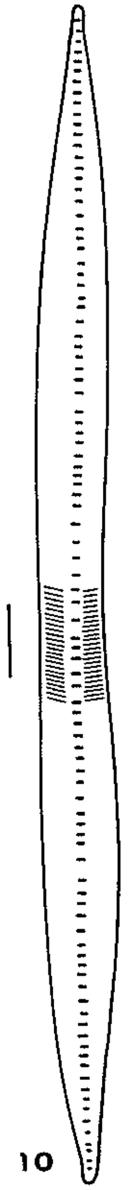

5

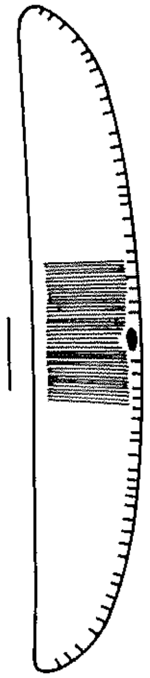

6


7


8


9


10


11


12

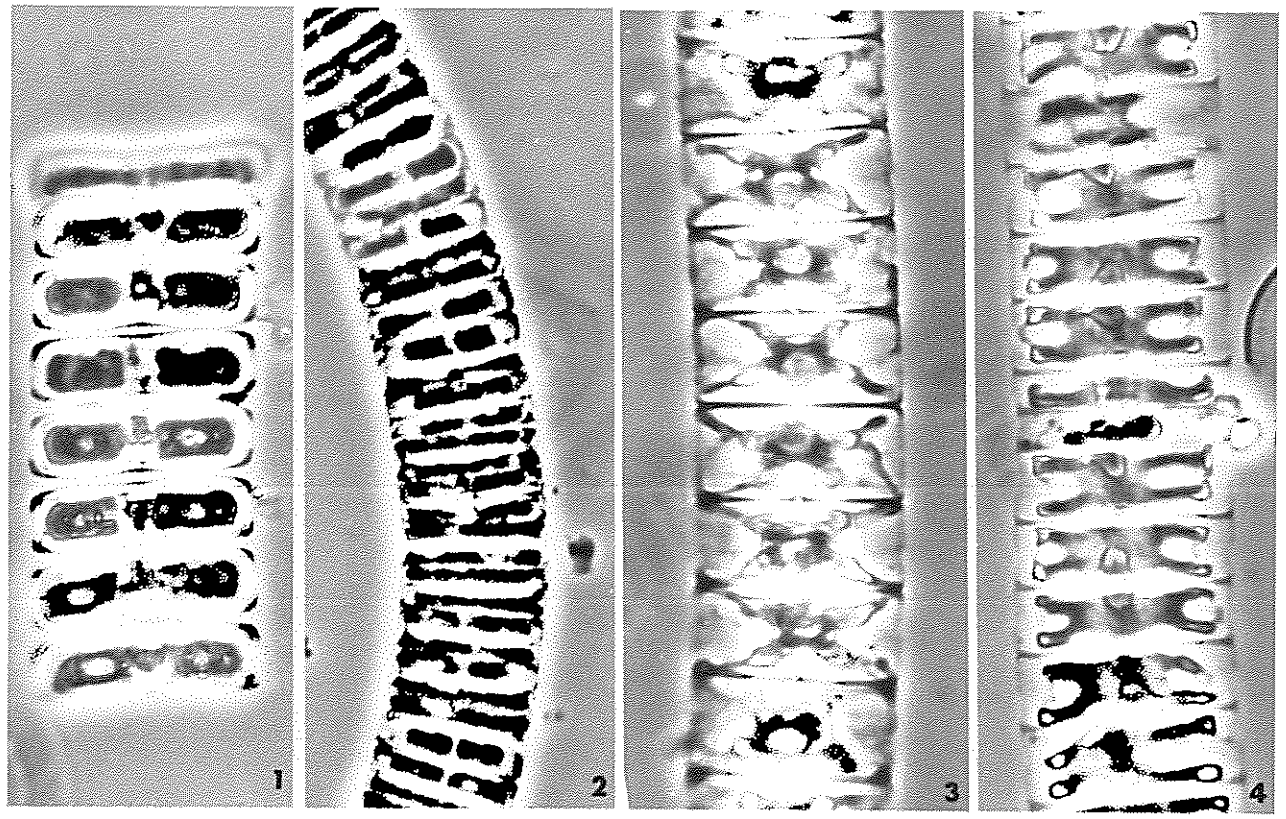


Plate 21.2. Ribbon colonies X1000.

Fig. 1 *Navicula vanhoeffenii*

Fig. 2 *Nitzschia cylindrus*

Fig. 3 *Navicula septentrionalis*

Fig. 4 *Achnanthes taeniata*

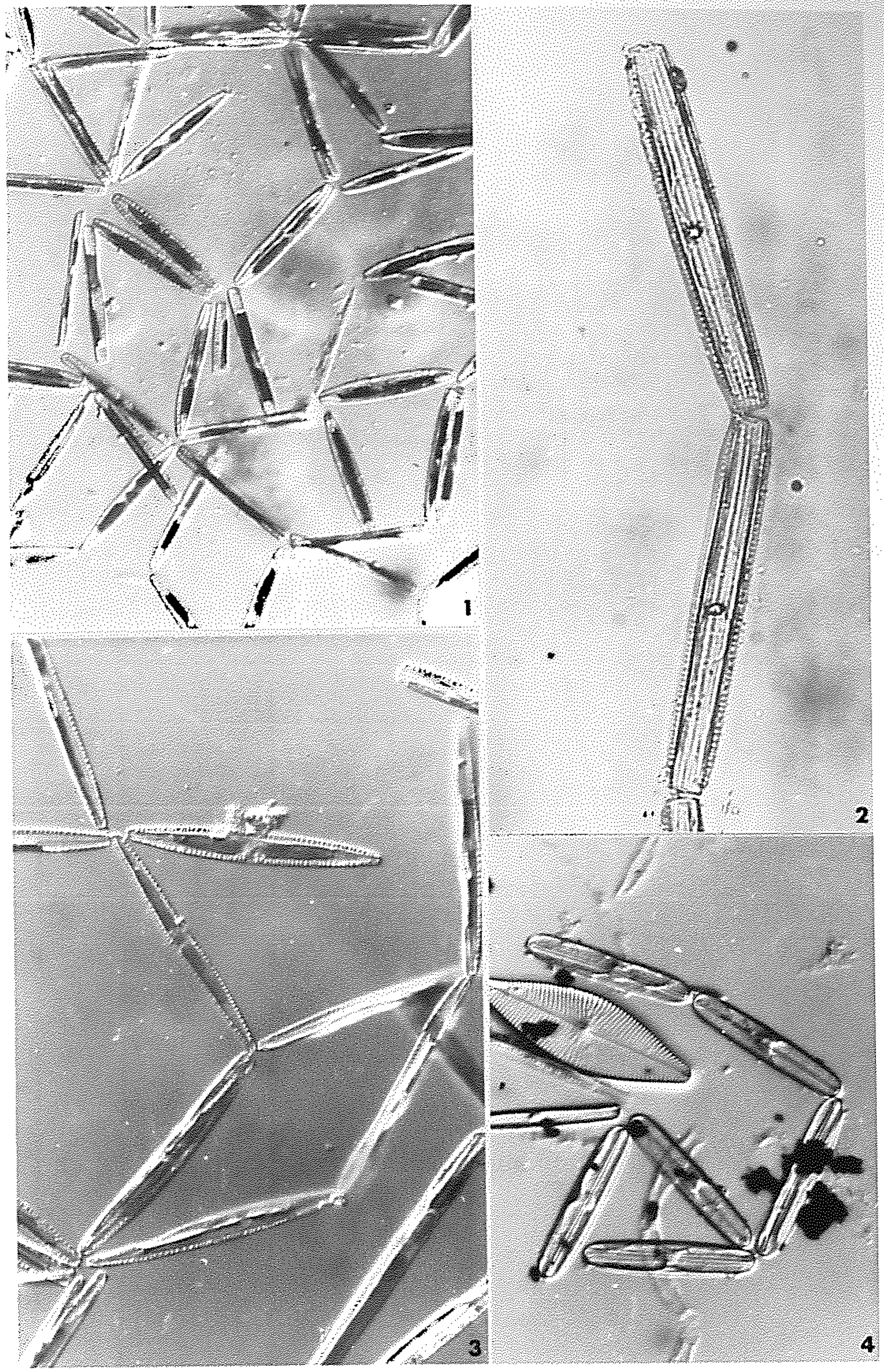


Plate 21.3. Arborescent colonies X500.

Fig. 1 *Nitzschia frigida*

Fig. 2 *Nitzschia neofrigida*

Fig. 3 *Nitzschia stellata*

Fig. 4 *Stenoneis inconspicua* v. *baculus*

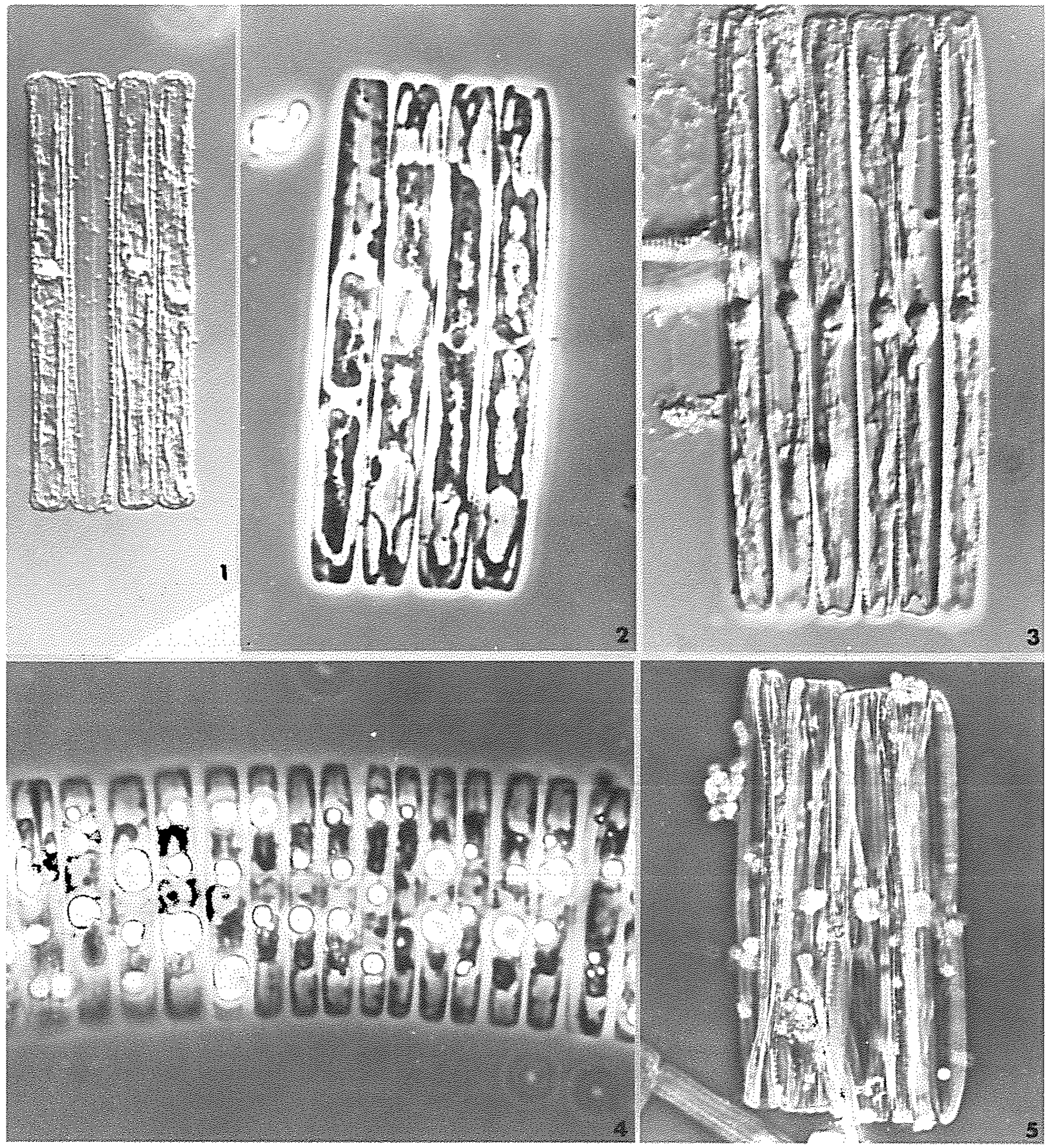


Plate 21.4. Ribbon colonies X500 except for Fig. 4 X1000.

Fig. 1 *Nitzschia distans* var.?

Fig. 2 *Nitzschia taeniiformis*

Fig. 3 *Nitzschia arctica*

Fig. 4 *Nitzschia promare*

Fig. 5 *Nitzschia pellucida*

CHAPTER 22

FAMILY BACILLARIACEAE:

GENUS NITZSCHIA
SECTION PSEUDONITZSCHIA

Grethe R. Hasle and Linda K. Medlin

Cells united into chains by overlapping of cell ends, i.e. "stepped" colony. Colonies motile. Frustules strongly elongated, linear to lanceolate in girdle view, mostly linear to lanceolate in valve view. Some species asymmetrical with respect to the apical axis, e.g. one valve margin straight, the other curved. Transapical ribs (interstriae) one or two to each fibula. Canal raphe markedly eccentric. Outer canal wall without areolae.

How to identify to species:
Frustules are most often seen in girdle view. With the exception of *N. turgidula* and *N. delicatissima*, diatoms with the *Pseudonitzschia* colony type can be identified only to section when seen in girdle view (see Table 22.1). Frustules must be cleaned of organic matter and mounted in a medium of a high refractive index to identify cells in valve view.

Characters to look for in valve view:

1. Valve outline - symmetry with respect to apical axis, linear or lanceolate outline, shape of the apices, shape of the middle part of the valve.
2. Central nodule (pseudonodulus in older literature) - indicated by a greater distance between the middle two fibulae (keel puncta in older literature) = greater middle interspace.
3. Number of fibulae, striae in 10 µm.

Key to species:

1a Apical axis asymmetrical, transapical axis about 4 µm or more 2
1b Apical axis symmetrical, transapical axis about 3 µm or less 4
2a Central nodule absent 3
2b Central nodule present .... *N. heimii*
3a Cells usually greater than 90 µm .... *N. seriata* f. *seriata*
3b Cells usually less than 90 µm with rounded apices .... *N. seriata* f. *obtusa*
4a Valves inflated in the middle part 5
4b Valves otherwise 8
5a Valves pointed, cuneate .... *N. inflatula*
5b Valves obtuse 6
6a Valves rostrate .... *N. prolongatoides*
6b Valves otherwise 7
7a Valves coarsely structured, 10-13 fibulae in 10 µm .... *N. turgiduloides*
7b Fibulae 13-18 in 10 µm .... *N. turgidula*
8a Valves lanceolate, with rounded apices .... *N. delicatissima*
8b Valves linear, with pointed apices 9
9a Valve coarse, striae 22-28 in 10 µm .... *N. lineola*
9b Valve fine, striae 30 to 46 in 10 µm .... *N. pseudodelicatissima*

Ecology: Marine, planktonic species. *N. prolongatoides* and *N. turgiduloides* are the only ones reported from ice and may be the only ones endemic to the Antarctic. *N. seriata* f. *obtusa* may be the only one endemic to the Arctic.

Photographic plates taken from Hasle 1965a.

Table 22.1. Morphometric and distributional data on *Pseudonitzschia*

	Apical axis, μm	*Transapical axis, μm*	*Central nodule*	*Fibulae in 10 μm*	*Striae in 10 μm*	*Special features in valve view*	*Polar distribution*
N.seriata f. *seriata* Cleve	91–160	5.5–8	—	14–18	14–18	one margin straight	Arctic-subarctic
N. seriata f. *obtusa* Hasle	61–100	4.5–5.3	—	15–20	15–20	as above, rounded apices	Arctic
N. heimii Manguin	67–120	4–6	+	11–16	19–26	one margin straight	Antarctic-subantarctic (doubtful reports from subarctic)
N. turgidula Hust.	30–80	2.5–3.5	+	13–18	23–28	rounded apices, middle part inflated	ca 62°S–62°N
N .prolongatoides[1] Hasle	20–70	0.5–2.5	+	15–18	30–35	rostrate, rounded, slightly inflated apices	Antarctic
N. turgiduloides Hasle	63–126	1.2–2.7	+	10–13	17–21	rounded apices	Antarctic
N. lineola (*barkleyi*) Cleve	56-112	1.8–2.7	+	11–16	22-28	pointed apices	Antarctic-subantarctic-subarctic
N. inflatula Hasle	60–100	1.5–2.5	+	18–21	32–35	middle part and next to apices inflated	Subarctic (doubtful reports from subantarctic)
N. delicatissima Cleve	40–76	ca.2	+	19–25	36–40	lanceolate, rounded apices	Arctic-subarctic
N. pseudodelicatissima Hasle	59–140	1.5–2.5	+	16–26	30–46(?)	linear, pointed apices	Subarctic

– : absent + : present Girdle view: *N.turgidula*, truncate cell ends; *N.delicatissima* partly cut cell ends; the others pointed cell ends

[1] Also appears in "star-shaped" colonies.

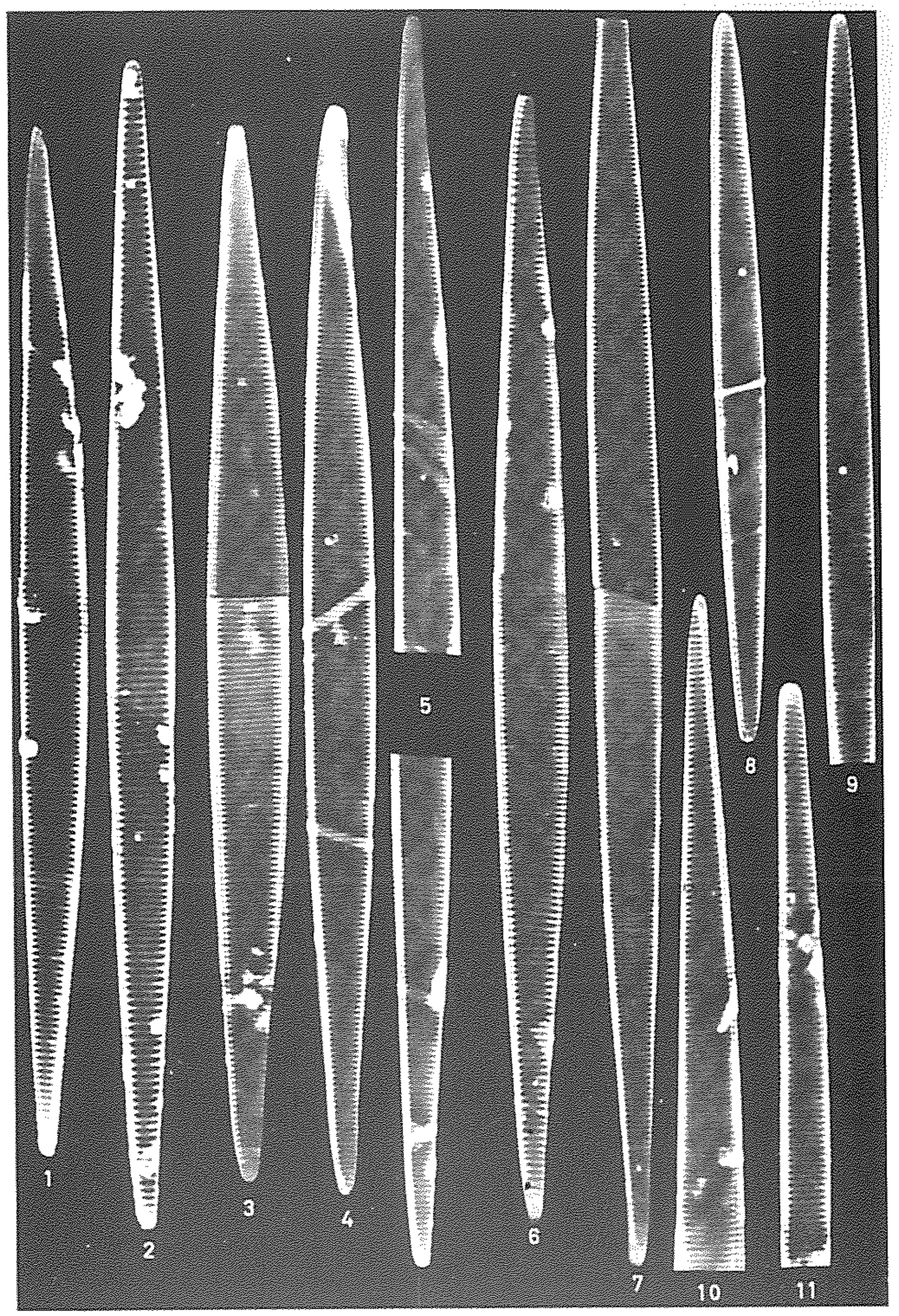


Plate 22.1. Dark field photomicrographs X1500.

Figs 1–7, 10 *Nitzschia seriata* f. *seriata*

Figs 8, 9, 11 *Nitzschia seriata* f. *obtusa*

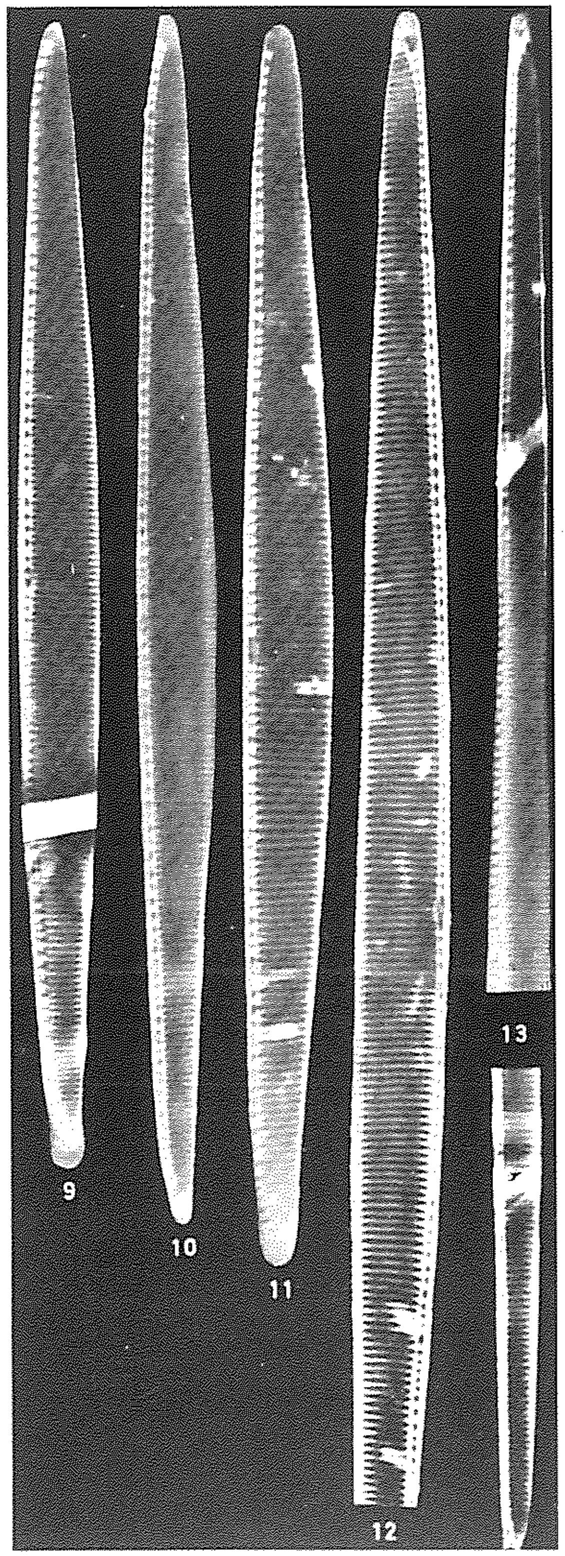


Plate 22.2. Dark field photomicrographs X2000.

Figs. 9–13 *Nitzschia heimii*

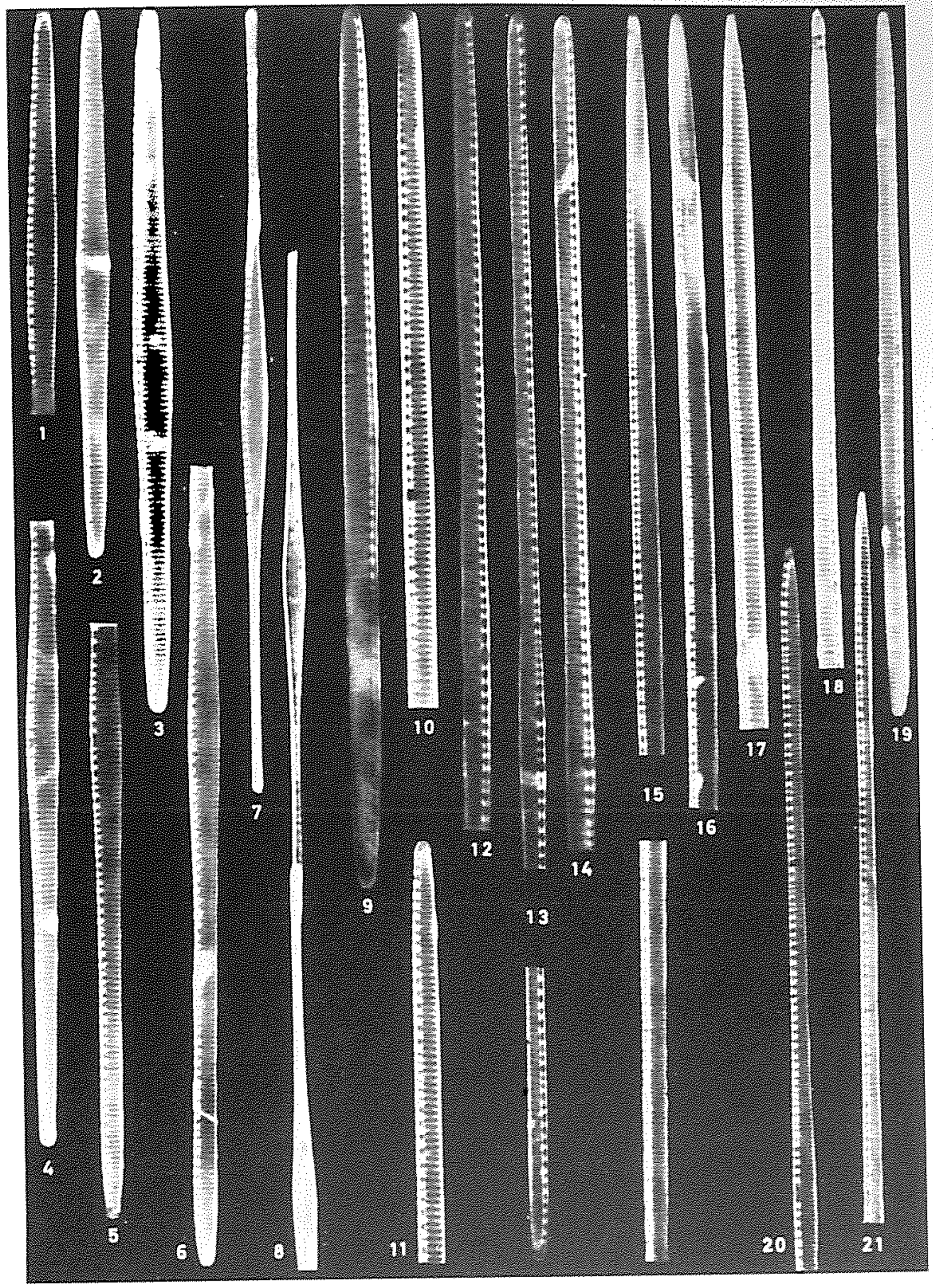


Plate 22.3. Dark field photomicrographs X2000.

Figs 1–6 *Nitzschia turgidula*

Figs 7–8 *Nitzschia prolongatoides*

Figs 9–14 *Nitzschia turgiduloides*

Figs 15–21 *Nitzschia lineola*

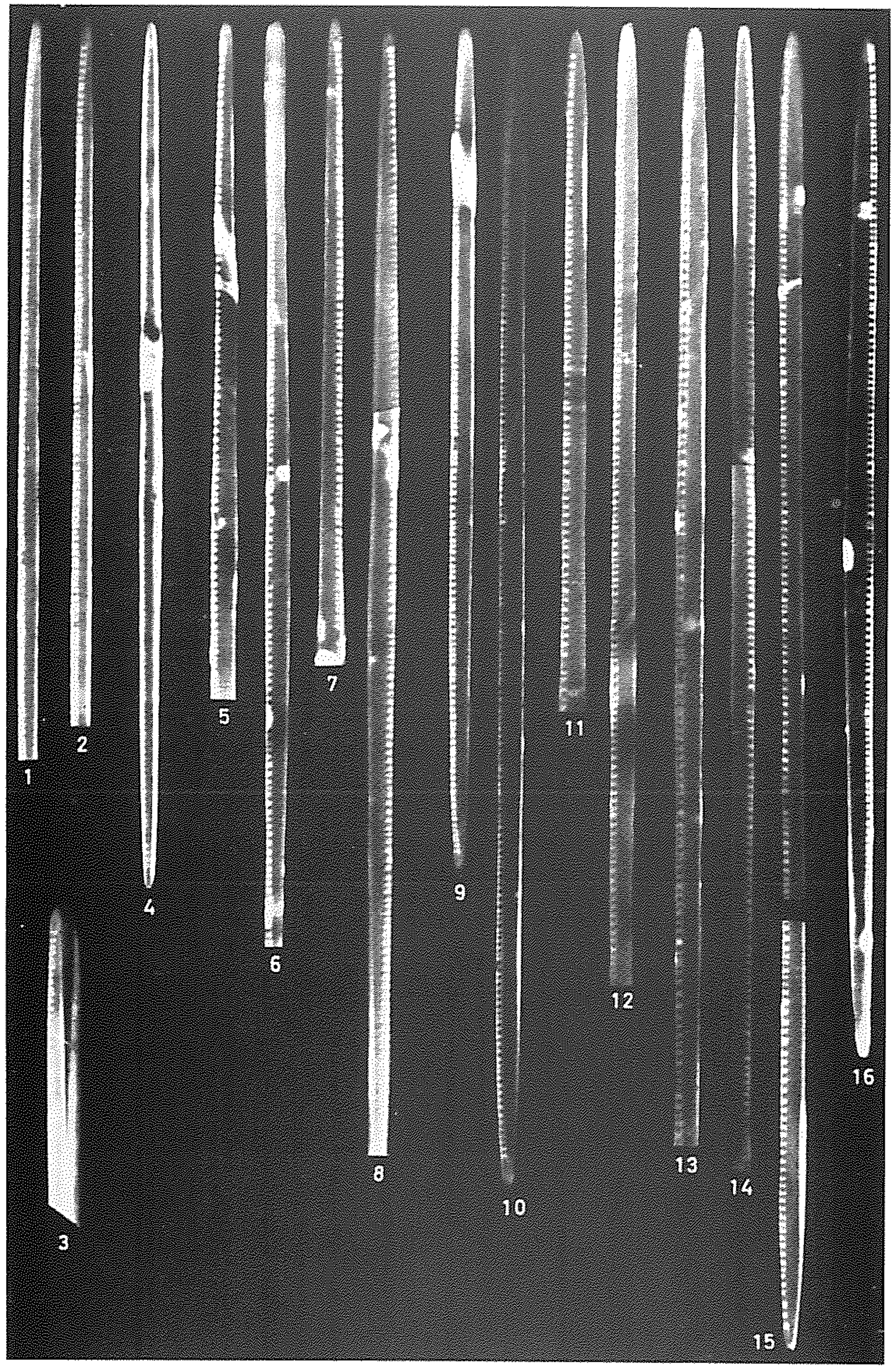


Plate 22.4. Dark field photomicrographs X2000.

Figs 1–16 *Nitzschia pseudodelicatissima*

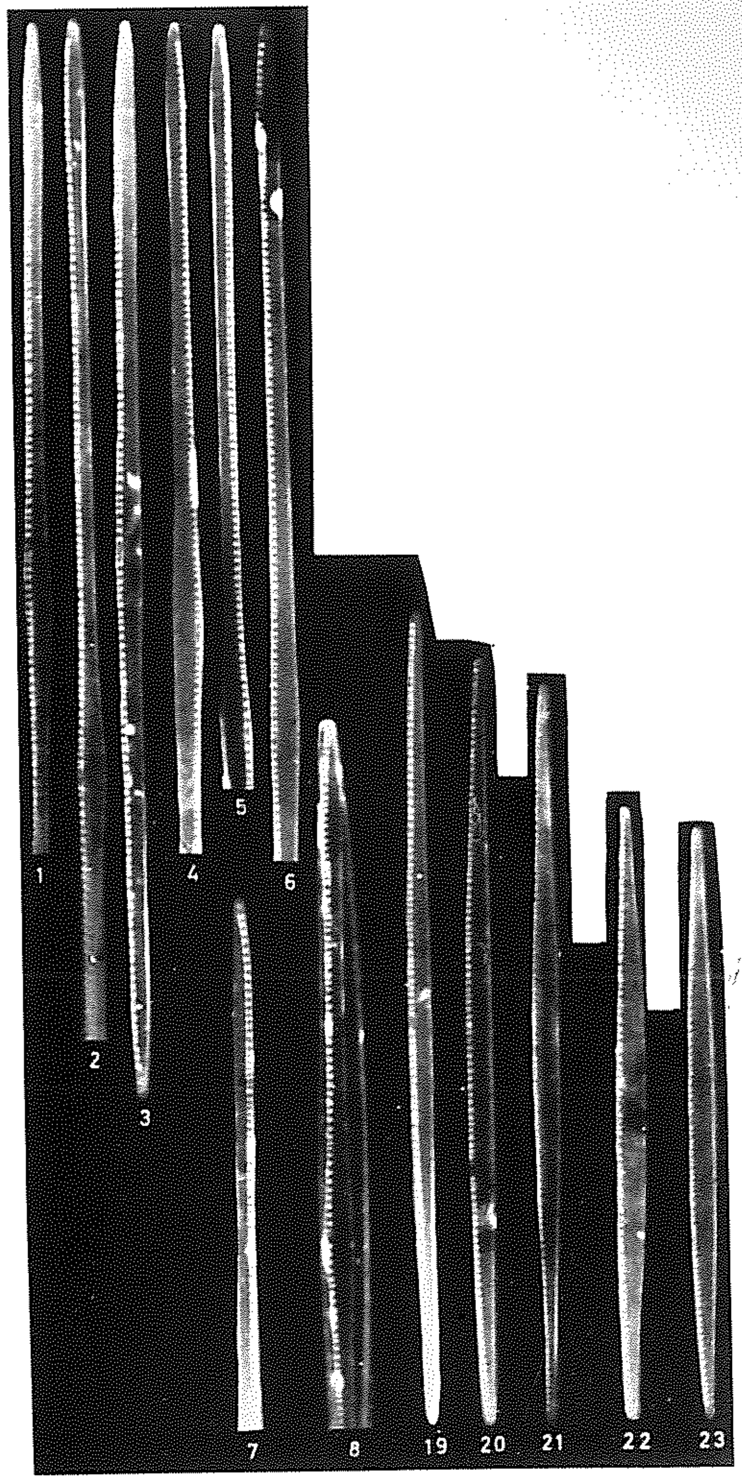


Plate 22.5. Dark field photomicrographs X2000.

Figs 1–8 *Nitzschia inflatula*

Figs 19–23 *Nitzschia delicatissima*

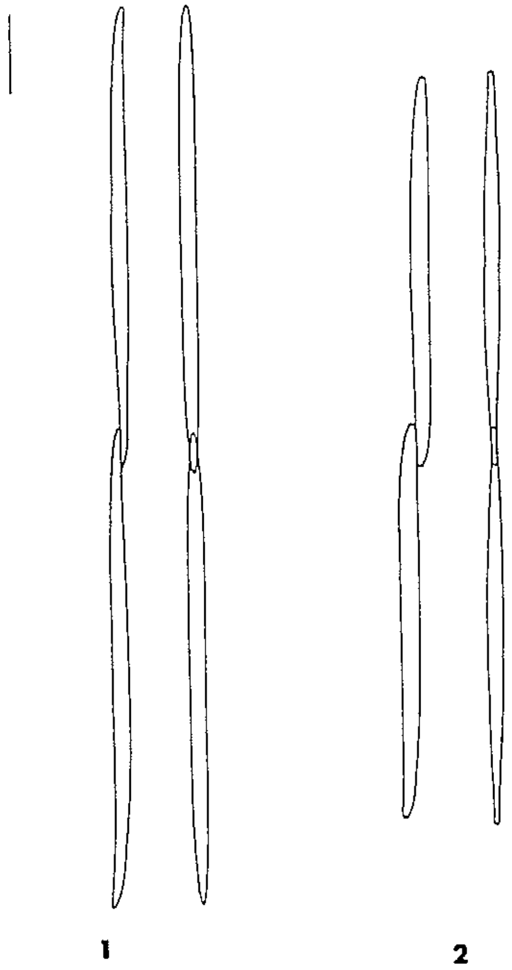


Plate 22.6. Line Drawings Scale bar = 10 µm.

Fig. 1 *Nitzschia pseudodelicatissima*

Fig. 2 *Nitzschia delicatissima*

CHAPTER 23

FAMILY BACILLARIACEAE:

GENUS NITZSCHIA SECTION NITZSCHIELLA

Grethe R. Hasle and Linda K. Medlin

This section comprises *Nitzschia* species with a more or less lanceolate central part of the frustule and rostrate ends (rostrum, pl. rostra). Some species with less distinct rostra may resemble species of the section *Lanceolatae*.

How to identify to species:
In most cases positive identification relies on cleaned material, although cells of typical appearance may be identified in water mounts, especially *N.closterium* and *N.subcurvata*.

Characters to look for in valve view:

1. Relationship between length of the median part of the frustule and the length of the rostra. How quickly does the lanceolate central portion of the frustule attenuate into the rostra?
2. Heteropolar or isopolar transapical axis
3. Presence or absence of a central nodule (pseudonodulus) indicated by a greater distance between the middle two fibulae (keel puncta).

Key to species:

1a Rostra long, slender, cell body mostly less than one half of total length 2
1b Rostra straight, comparatively shorter 3
2a Cell body lanceolate, rostra hairlike .... *N. closterium**
2b Cell body asymmetrical with one convex side, apical axis slightly curved .... *N. subcurvata*
3a Central nodule present, median part of the valve rhomboid to lanceolate, smaller cells with short or almost no rostra, larger cells with long rostra .... *N. lecointei*
3b Central nodule absent .... *N. decipiens*

* = *Cylindrotheca closterium*

Ecology:
Marine, planktonic and benthic (ice-associated) species.

Photographic plates taken from Hasle (1964).

Table 23.1. Morphometric and distributional data on *Nitzschiella*

	Apical axis, µm	*Transapical axis, µm*	*Central nodule*	*Fibulae in 10 µm*	*Striae in 10 µm*	*Special Features in Valve View*	*Polar distribution*
N. closterium (Ehrenb.) W. Smith (= *Cylindrotheca closterium*)	30–400	2.5–8	+	12–16	70–100	many narrow bands, seen in cleaned material	cosmopolitan
N.lecointei V.H.	21–112	2.5–5	+	5–14	51–55	stadial variation	Antarctic
N.decipiens Hust.	32–36	2.7	–	7–9	44		Antarctic
N.subcurvata Hasle	47–90	1.5–2	–	12–18	44–49	one margin straight, the other convex	Antarctic

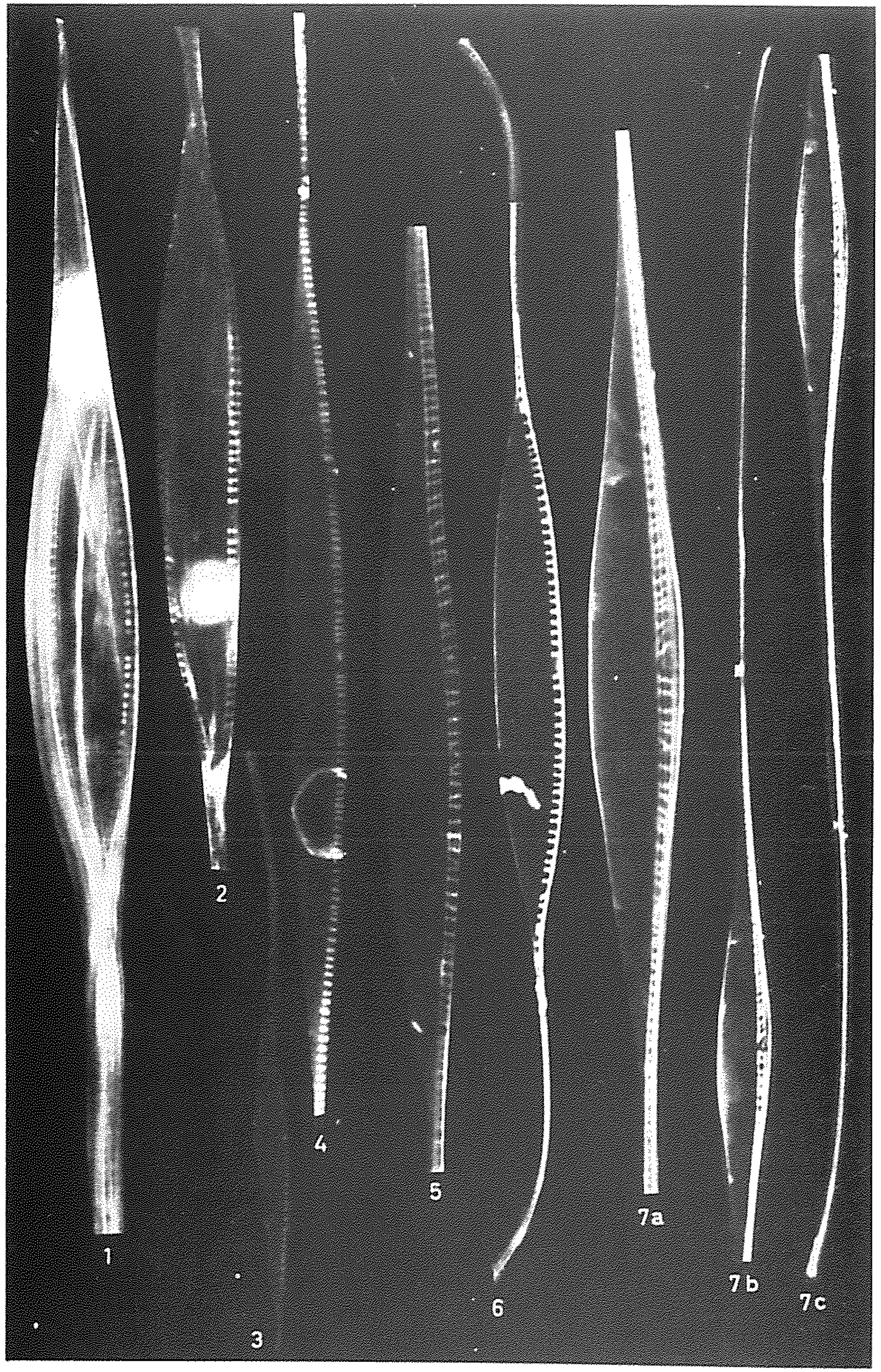


Plate 23.1. Dark field photomicrographs X2000.

Figs 1–4 *Nitzschia* (*Cylindrotheca*) *closterium*

Figs 5–7 *Nitzschia longissima* Fig. 7bc X1000.

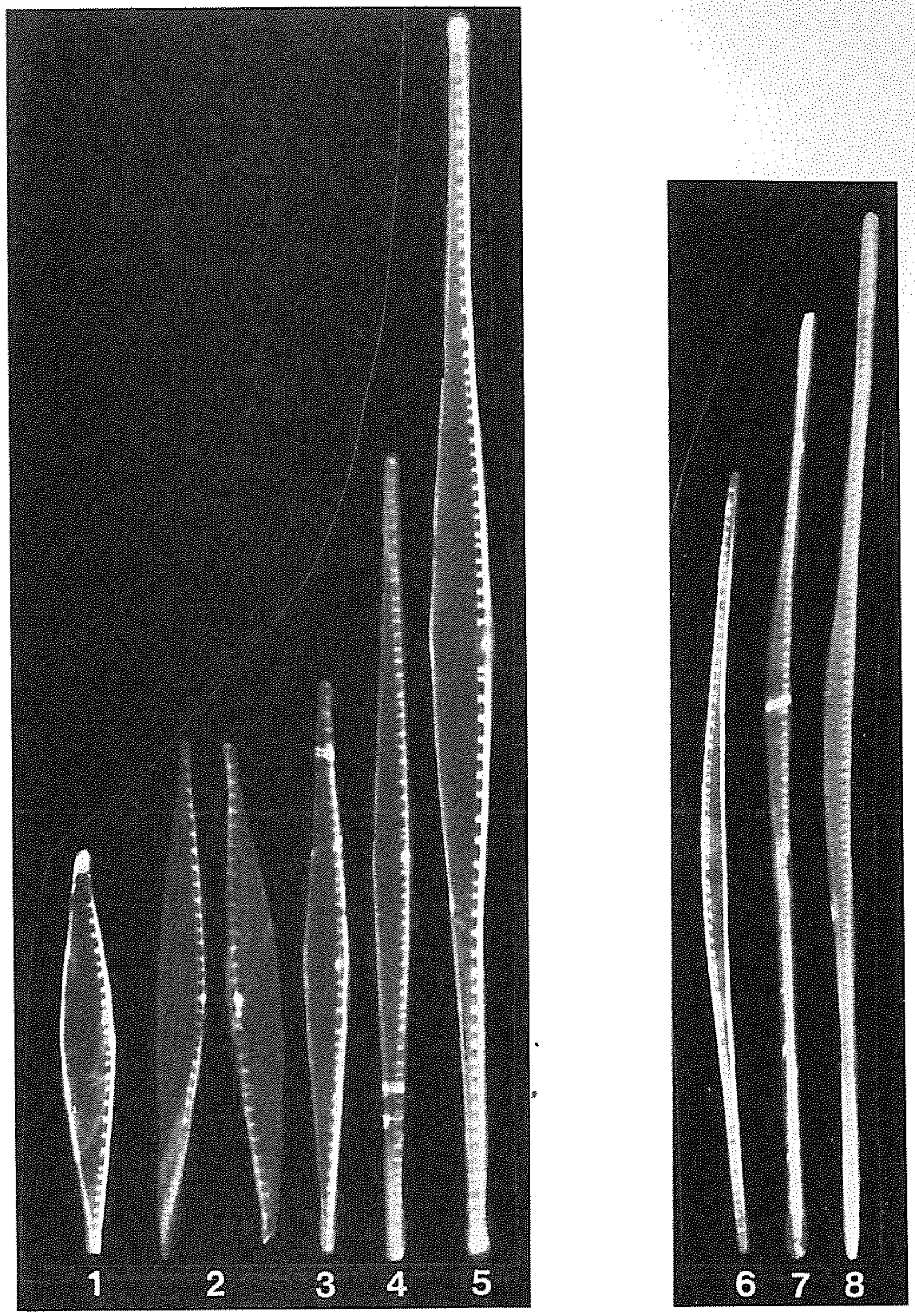


Plate 23.2. Dark field photomicrographs X2000.

Figs 1–5 *Nitzschia lecointei*

Figs 6–8 *Nitzschia subcurvata*

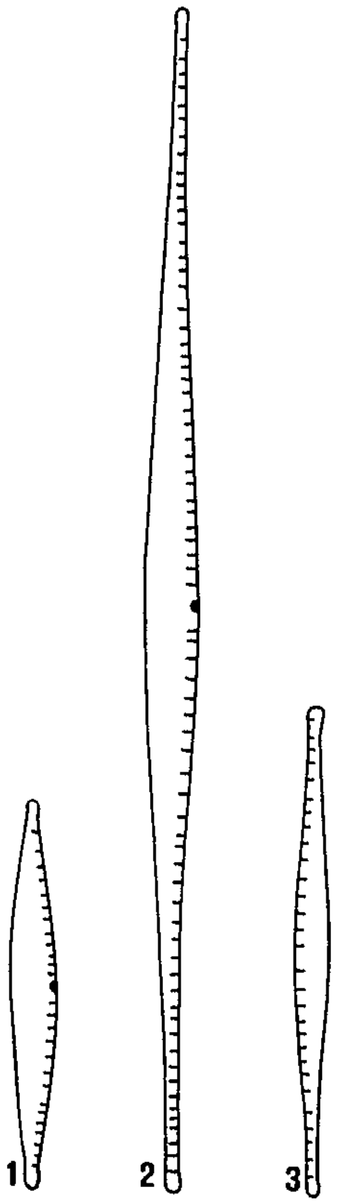


Plate 23.3. Line drawings X2000.

Figs 1–2 *Nitzschia lecointei*

Fig. 3 *Nitzschia decipiens*, redrawn from Hustedt (1958)

CHAPTER 24

FAMILY BACILLARIACEAE:

GENUS NITZSCHIA
SECTION FRAGILARIOPSIS

Grethe R. Hasle and Linda K. Medlin

Cells united into ribbon-shaped colonies. Colonies non-motile. Frustules linear in girdle view, elliptical-linear-lanceolate in valve view. Some species may be heteropolar in valve view, i.e. one apex is narrower than the other. This character often disappears with smaller specimens and therefore must be used with caution. Transapical ribs (interstriae) usually one to each fibula. Striae usually with two rows of areolae, which may be resolved in LM in some species. Canal raphe markedly eccentric. Outer canal wall without areolae. This section will be restored to generic level in Round, Crawford and Mann (1990).

How to identify to species:
Uncleaned material is difficult to identify beyond the section level because all species have the same linear shape in girdle view and form the same shape colonies. *N. kerguelensis* has a coarser structure than the other species and might be identified in water mounts. Frustules must be cleaned of organic matter and mounted in a medium of a high refractive index so that characters seen in valve view may be identified.

Characters to look for in valve view:

1. Valve outline: broad/narrow (ratio of apical to transapical axes may be helpful), shape of apices (heteropolar?), if the outline is not entirely linear, then how soon after the middle does the outline of the valve begin to change.
2. Striae: can the areolae by resolved with LM, how many rows of areolae are present? Are the interstriae (transapical costa) straight or curved?
3. Central nodule (pseudonodulus): usually indicated by a greater distance between the middle two fibulae (keel puncta).

Key to species:

1a Valves subcircular, elliptical, lanceolate 2
1b Valves sublinear, linear 10
2a Central nodule present 3
2b Central nodule absent 4
3a Valve elliptical, middle part almost straight, tapering part short, larger specimens slightly heteropolar, 18-21 fibulae in 10 μm .... *N. paaschei*
3b Valves broadly to narrowly elliptical, specimens of all sizes isopolar, 12-15 fibulae in 10 μm .... *N. grunowii*
4a Valve structure fine, ca. 20 striae in 10 μm, apical axis always isopolar 5
4b Valve structure coarser 6
5a IValves lanceolate to narrowly elliptical, transapical axis 3.5–5 μm .... *N. pseudonana*
5b Valves subcircular to narrowly elliptical, transapical axis ca. 2 μm .... *N. cylindroformis* (in part)
6a Valves broadly lanceolate, larger specimens with straight middle part, striae usually more than 10 in 10 μm, apical axis always isopolar 7
6b Valves narrowly or broadly elliptical or lanceolate, striae ca. 10 or less in 10 μm, apical axis often heteropolar 8
7a Striae with two rows of areolae .... *N. angulata*
7b Striae with one row of areolae .... *N. separanda*
8a Valves lanceolate with rounded apices, larger specimens slightly heteropolar, areolae easily resolved in LM, ca. 10 in 10 μm .... *N. kerguelensis*
8b Valves elliptical, larger specimens slightly heteropolar 9
9a Valves narrowly elliptical, interstriae oblique .... *N. obliquecostata*
9b Valves broadly elliptical, middle part almost straight, tapering part short .... *N. ritscheri*
10a Valves sublinear, tapering towards narrowly rounded apices 11
10b Valves linear 12
11a Valves greater than 20 μm long, less than 10 striae in 10 μm .... *N. sublineata*
11b Valves less than 20 μm long, 16–20 striae in 10 μm .... *N. cylindroformis* (in part)
12a Central nodule present .... *N. vanheurckii*
12b Central nodule absent 13
13a Valves heteropolar .... *N. curta*
13b Valves isopolar 14
14a Valves with pointed apices 15
14b Valves with rounded apices 16
15a Striae with two rows of areolae .... *N. peragallii*
15b Striae with one row of areolae .... *N. barbieri*
16a Valve structure coarse, less than 10 striae in 10 μm, transapical axis 7-9 μm .... *N. lineata*
16b Valve structure finer, more than 10 striae in 10 μm, transapical axis 2–4 μm .... *N. cylindrus*

Ecology: Marine, planktonic and ice-associated species which are better represented in the Antarctic than in the Arctic.

Photographic plates taken from Hasle (1965b).

Table 24.1. Morphometric and distributional data on *Fragilariopsis*

	Apical axis, μm	*Transapical axis, μm*	*Central nodule*	*Fibulae in 10 μm*	*Striae in 10 μm*	*Rows of areolae*	*Polar distribution*
N. paaschei Hasle (*F. atlantica*)	20–43	7–8	+	18–21	18–21	2–3	plankton, Arctic
N. grunowii Hasle (*F.oceanica*)	10–41	ca.6	+	12–15	12–15	2?	plankton/ice, Arctic
N. kerguelensis (O'Meara) Hasle	10–76	5–11	–	4–7	4–7	2	plankton, Antarctic
N. obliquecostata (Van Heurck) Hasle	57–110	8–10	–	6.5–8	6.5–8	2–3	ice, Antarctic
N. ritscheri (Hust.) Hasle	22–57	8–9	–	6–11	6–11	2–3	plankton, Antarctic
N. pseudonana Hasle	4–20	3.5–5	–	18–22	18–22	2	plankton, cosmopolitan
N. angulata Hasle (*F. rhombica*)	8–53	7–13	–	8–16	8–16	1–2	plankton, Antarctic
N. separanda (Hust.) Hasle	10–33	8–13	–	10–14	10–14	1	plankton, Antarctic
N. sublineata Hasle (*F.sublinearis*)	30–92	5.5–6.5	–	7.5–9	7.5–9	2	ice, Antarctic
N. vanheurckii (M.Per.) Hasle	35–77	ca.5	+	7–9	10–11	2	ice, Antarctic
N.curta (Van Heurck) Hasle	10–42	3.5–6	–	9–12	9–12	2	plankton/ice, Antarctic
N. cylindrus (Grun?) Hasle	3–48	2–4	–	13–17	13–17	2–4	plankton/ice, bipolar
N. cylindroformis Hasle	3–13	ca.2	–	16–20	16–20	2	plankton, Arctic
N. lineata (Castr.) Hasle (*F.linearis*)	40–72	7–9	–	7.5–9	7.5–9	2	ice, Antarctic
N. barbieri M. Per.	49–118	8–14	–	8–11	8–11	1–(2)	ice, Antarctic
N. peragallii Hasle	32–90	7–8	–	7–9	7–9	2	ice, Antarctic

Names in () = synonyms of species originally in the genus *Fragilariopsis*.

Plate 24.1. Dark field photomicrographs ×3000.

Figs 1–5 *Nitzschia paaschei*

Fig. 6 *Nitzschia angulata*

Figs 7–14 *Nitzschia pseudonana*

Figs 15–19 *Nitzschia grunowii*

Fig. 20 *Nitzschia ritscheri*

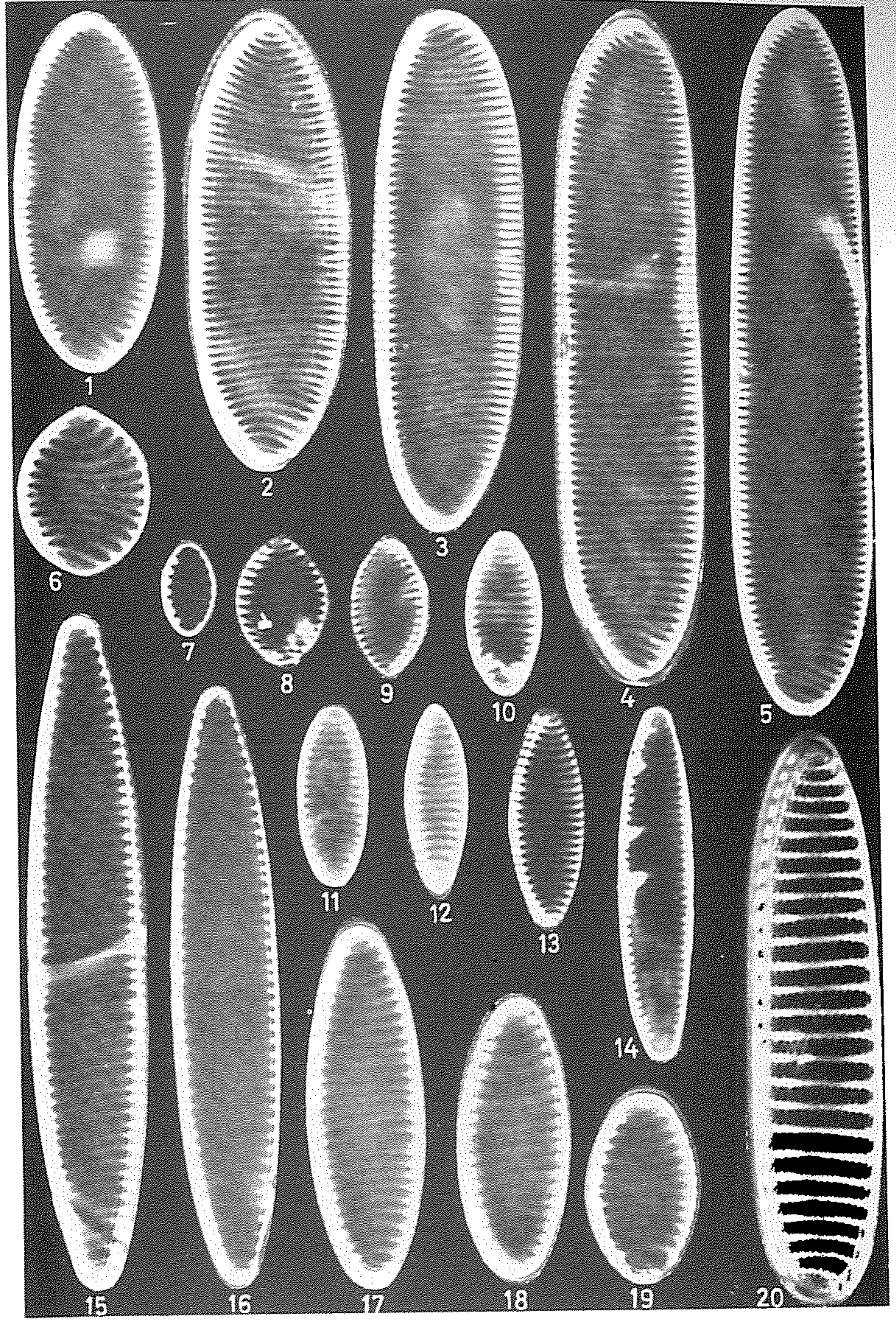


Plate 24.2. Bright field photomicrographs = Figs 1–7, 11–21 ×2000, Electron micrographs = Figs 8 (×2300), 9 (×2800), 10 (×4800).

Figs 1–10 *Nitzschia ritscheri* (Fig. 10 also includes *N. cylindrus*)

Figs 11–18 *Nitzschia kerguelensis*

Fig. 19 *Nitzschia angulata*

Figs 20–21 *Nitzschia pseudonana*

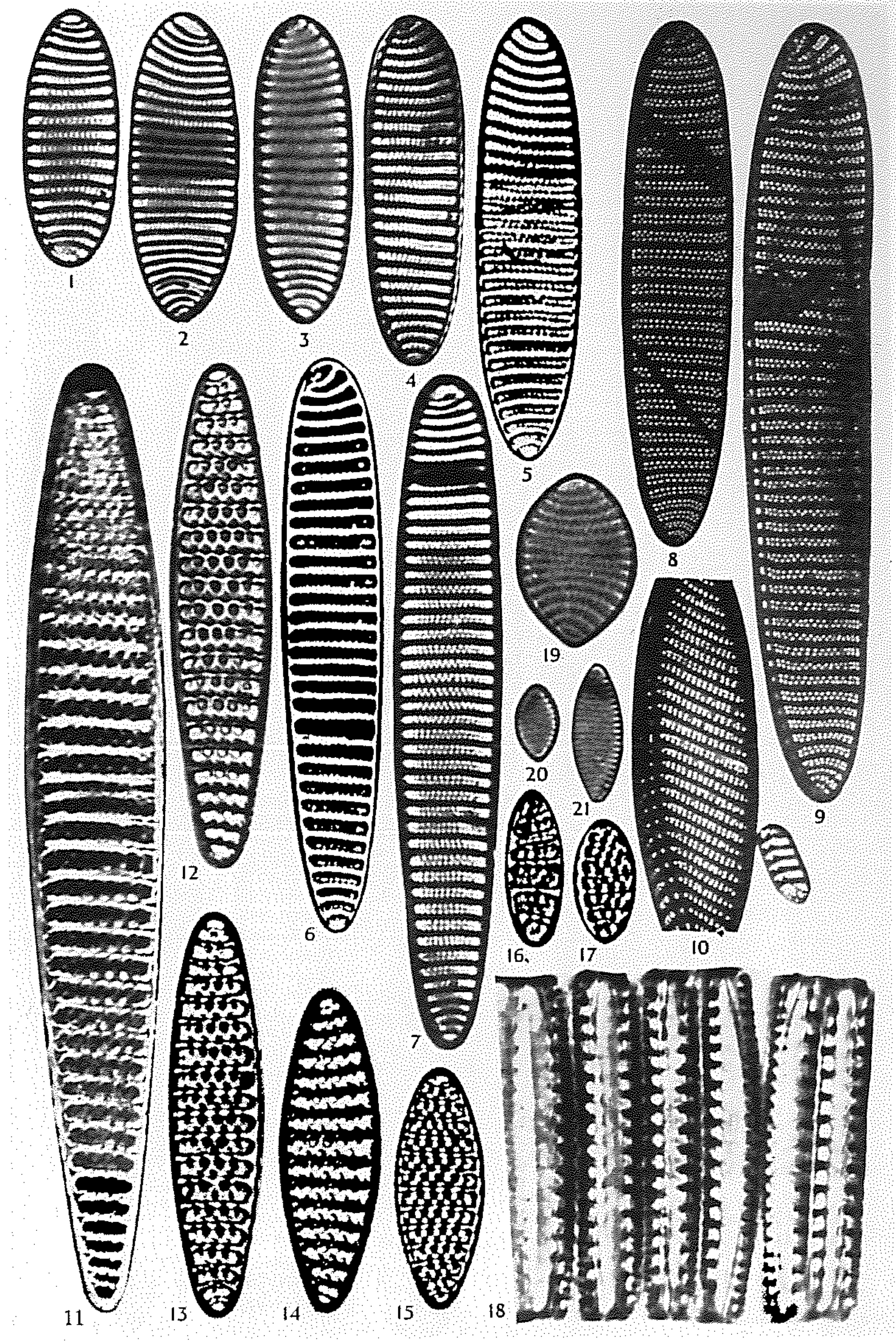


Plate 24.3. Bright field photomicrographs ×2000.

Fig. 1 *Nitzschia sublineata*

Figs 2–7 *Nitzschia obliquecostata*

Fig. 8 *Nitzschia ritscheri*

Fig. 9 *Nitzschia kerguelensis*

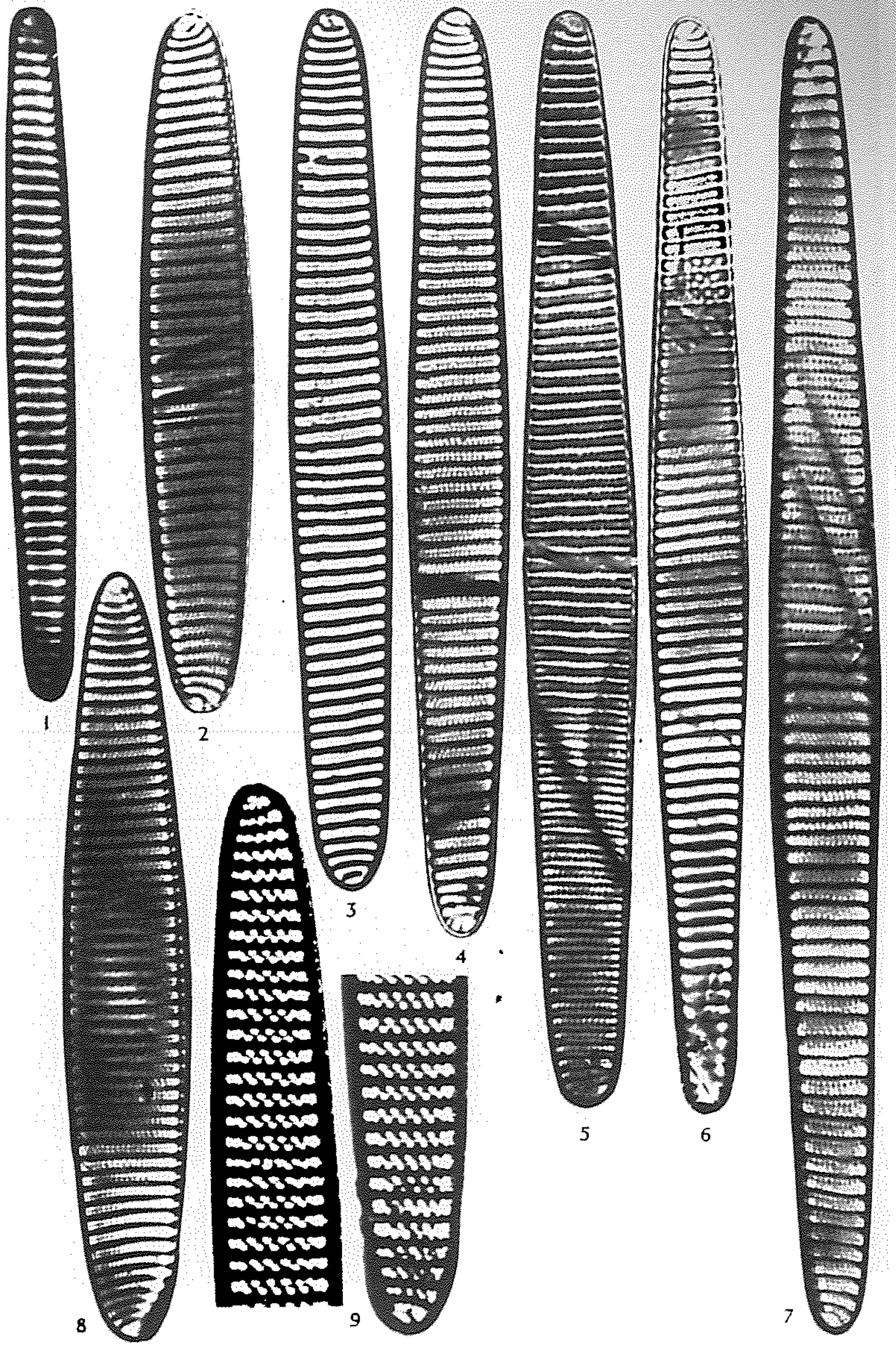


Plate 24.4. Dark field photomicrographs ×3000 except Figs 6, 10 = ×6000.

Figs 1–6 *Nitzschia angulata*

Figs 7–10 *Nitzschia separanda*

Figs 11–12 *Nitzschia peragallii*

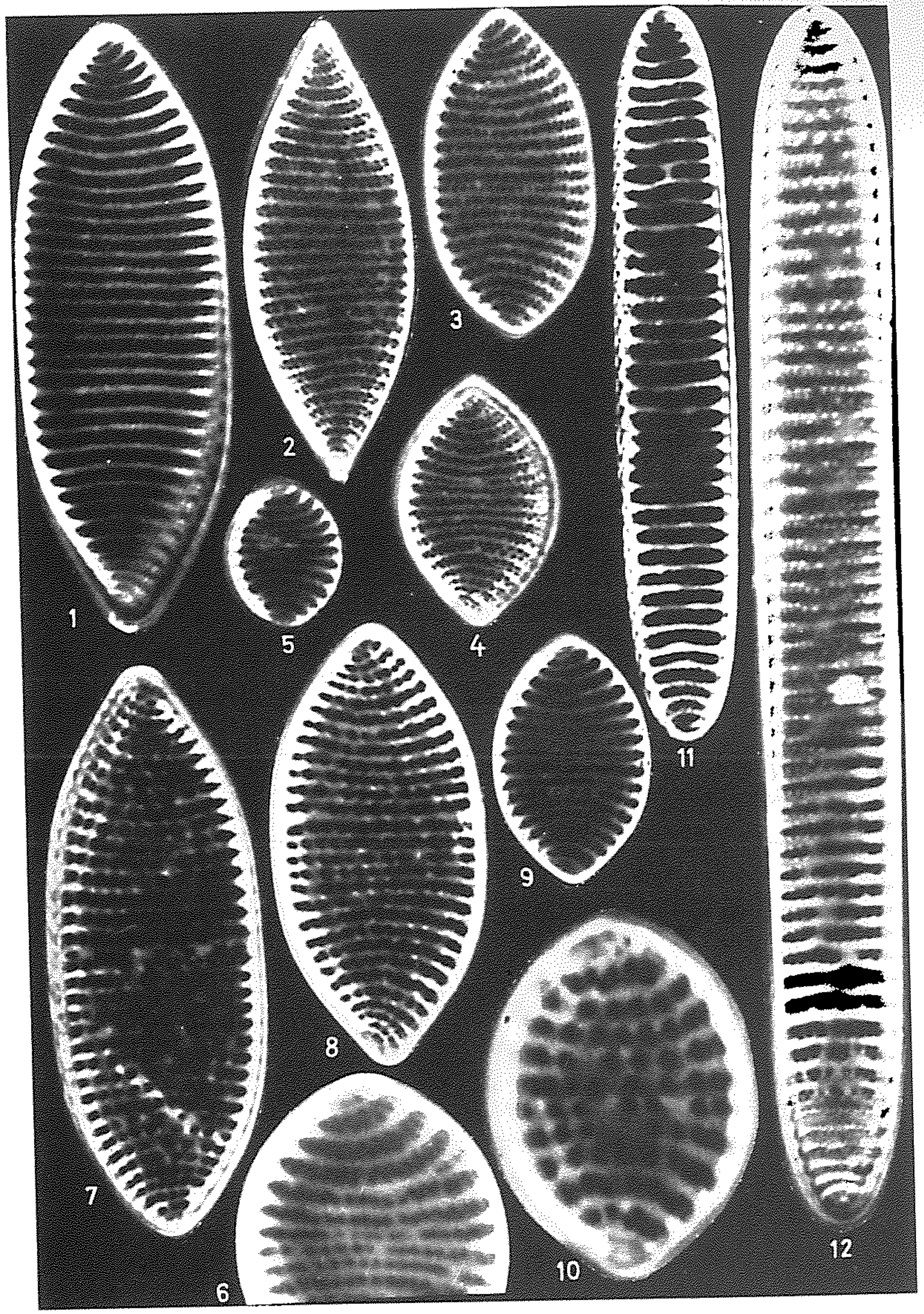


Plate 24.5. Bright field photomicrographs = Figs 1-7 ×2000, Electron micrographs = Fig. 8 (×4600), 9 (×10,400), 10 (×24,600)

Figs 1–10 *Nitzschia sublineata*

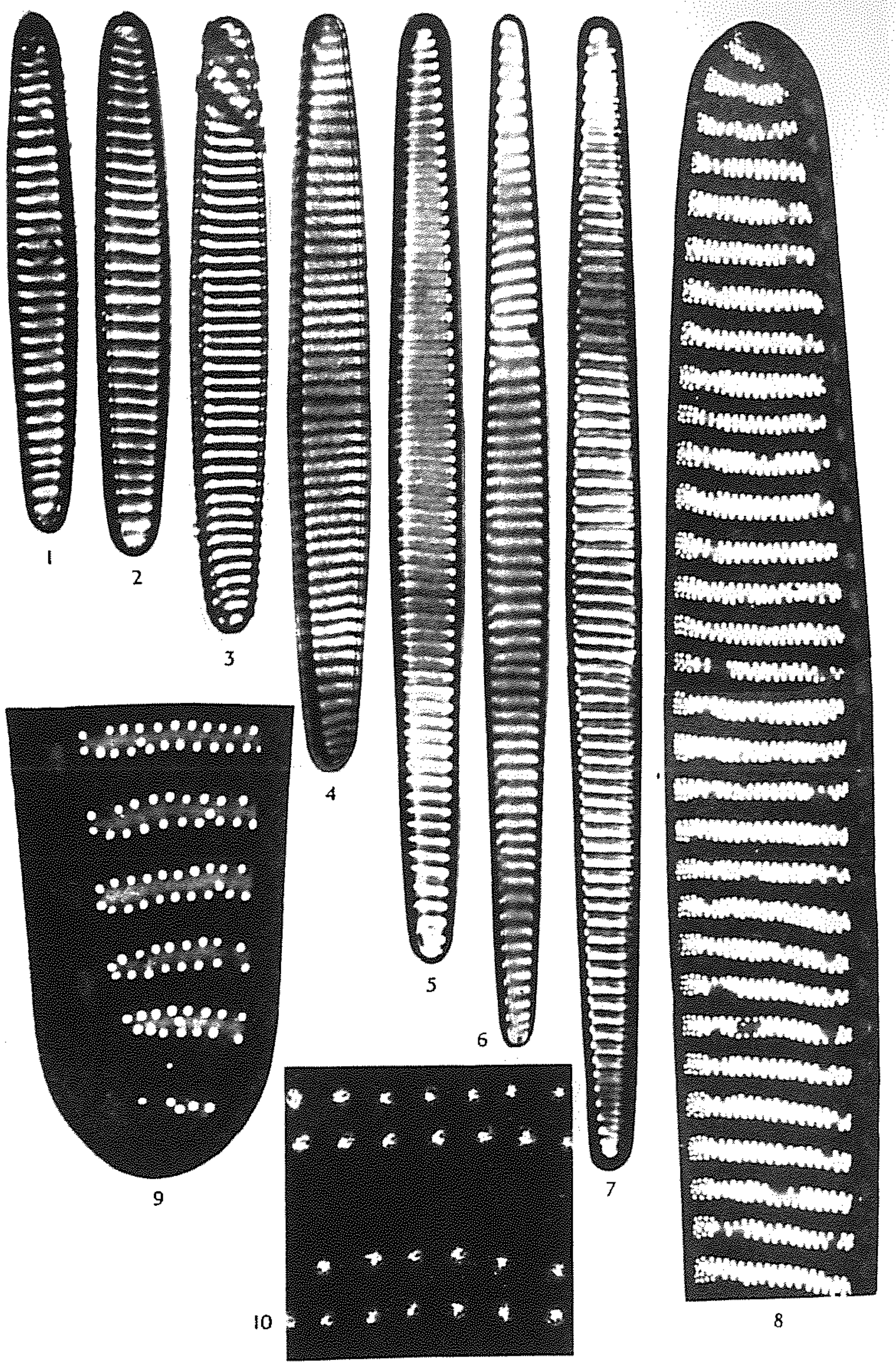


Plate 24.6. Dark field photomicrographs ×3000.

Fig. 1 *Nitzschia sublineata*

Figs 2–5 *Nitzschia curta*

Figs 6–12 *Nitzschia cylindrus*

Figs 13-16 *Nitzschia vanheurckii*

Fig. 17 *Nitzschia lineata*

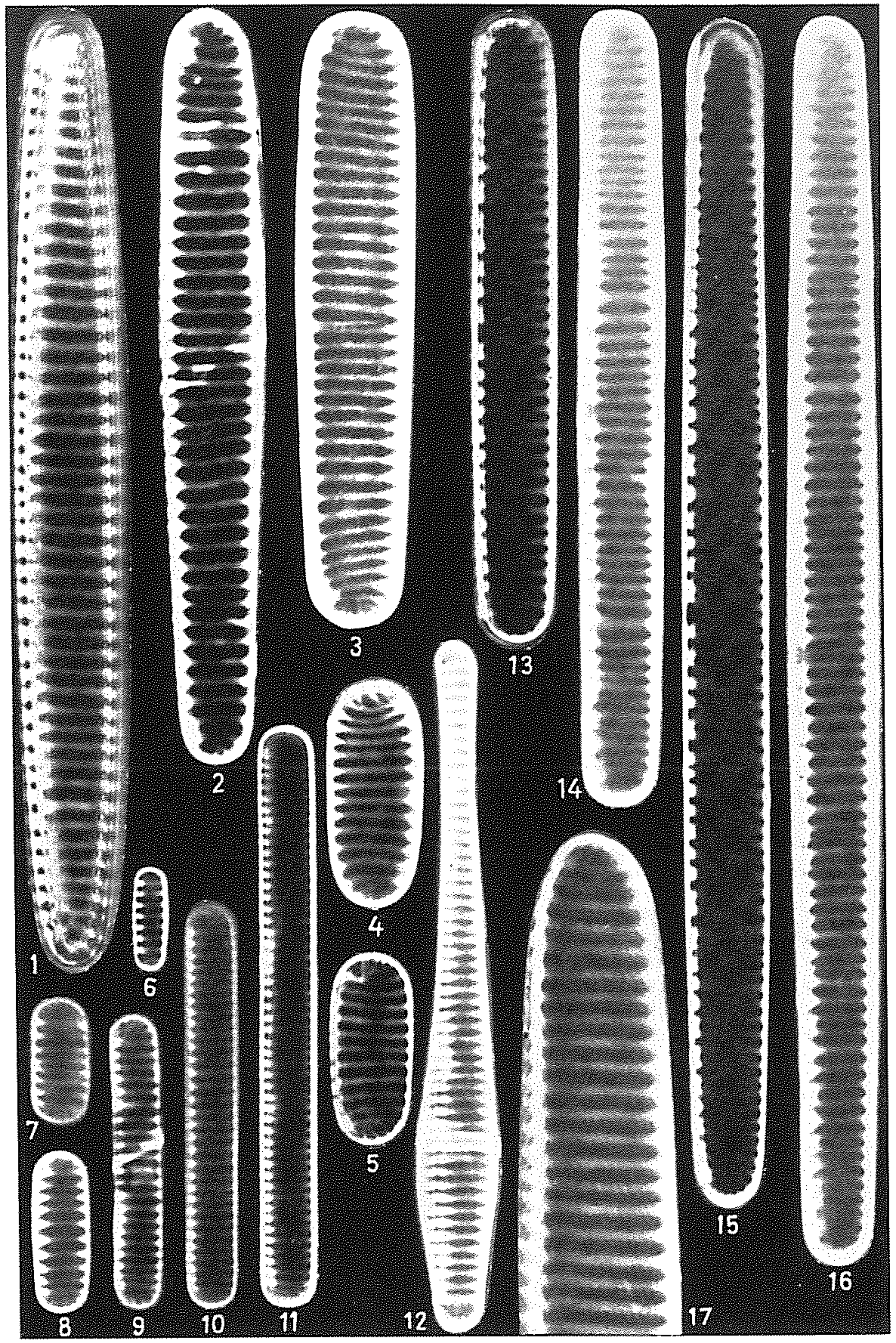


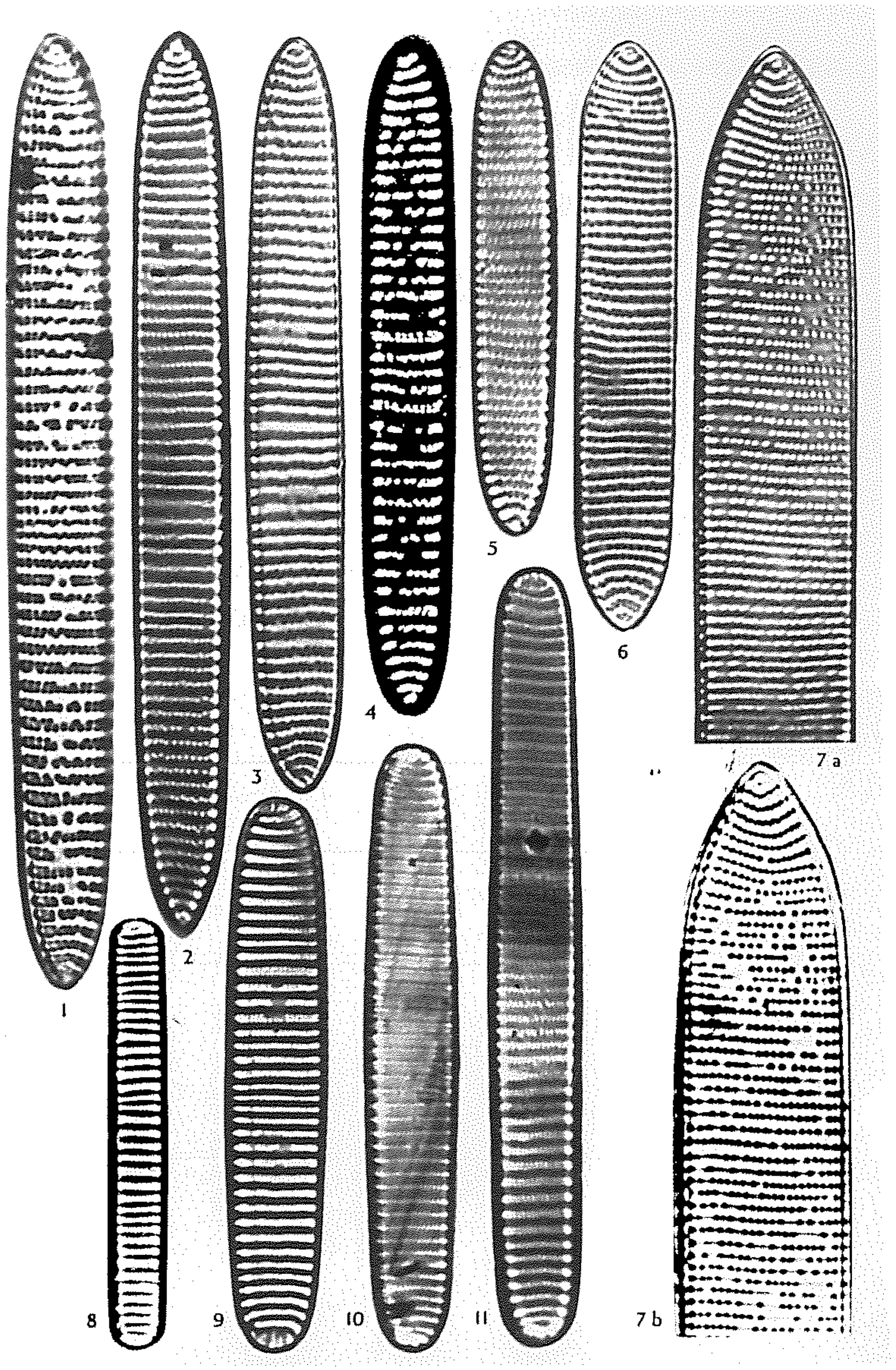
Plate 24.7. Bright field photomicrographs ×2000.

Figs 1–5 *Nitzschia peragallii*

Figs 6–7 *Nitzschia barbieri*

Fig. 8 *Nitzschia vanheurckii*

Figs 9–11 *Nitzschia lineata*



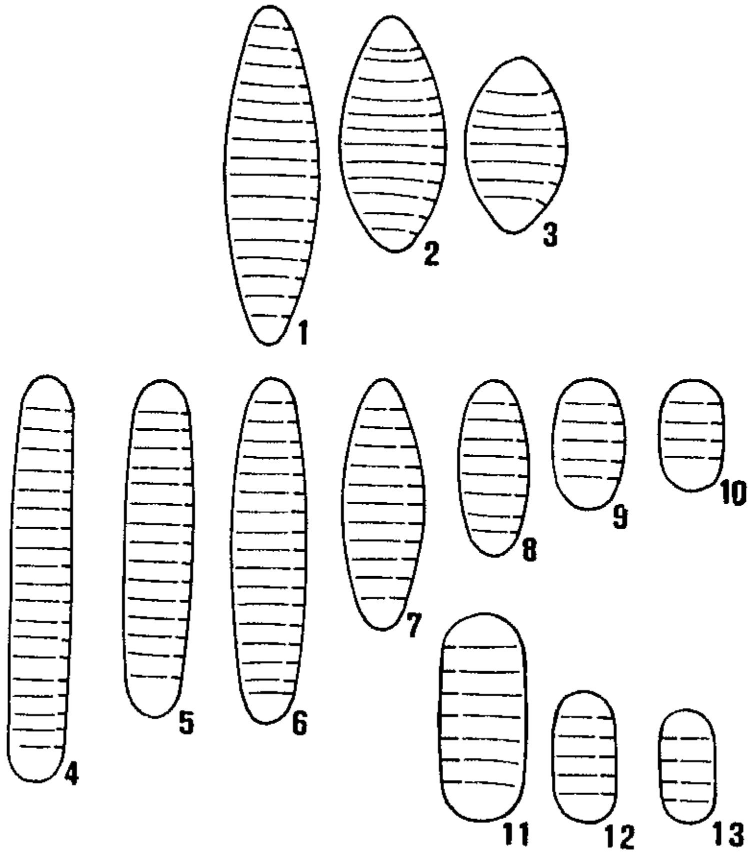


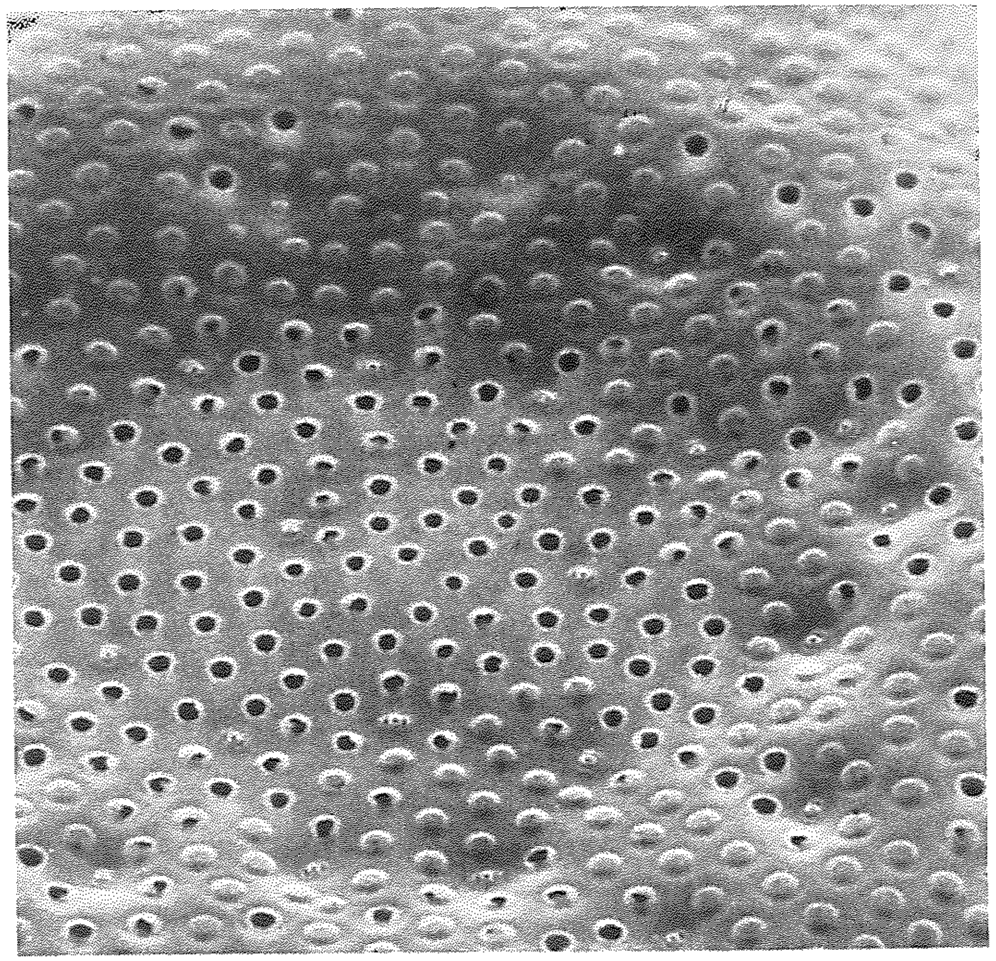
Plate 24.8. Line drawings X4500. Redrawn from Hasle and Booth (1984).

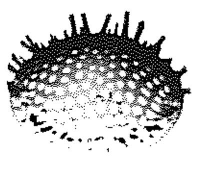
Figs 1–3 *Nitzschia pseudonana*

Figs 4–10 *Nitzschia cylindroformis*

Figs 11–13 *Nitzschia cylindrus*

Bibliography





BIBLIOGRAPHY

AAGAARD, K. 1981. On the deep circulation in the Arctic Ocean. *Deep-Sea Research*, **28**, 251-68.

AAGAARD, K. 1982. Inflow from the Atlantic Ocean to the Polar Basin. (*In* RAY, L., *ed. The Arctic Ocean, the Hydrographic Environment and the Fate of Pollutants.*, Comité Arctique International, Monaco, 69-82).

AAGAARD, K. 1984. The Beaufort undercurrent. (*In* BARNES, P.W., SCHELL, D.M. *and* REIMNITZ, E., *eds The Alaskan Beaufort Sea, Ecosystems and Environments*, Academic Press, Orlando, Fla., 47-71).

AAGAARD, K. 1989. A synthesis of the Arctic Ocean circulation. *Rapportes et Proces-Verbaux, Conseil Permanent International d'Exploration de la Mer*, **188**, 11-22.

AAGAARD, K. *and* COACHMAN, L.K. 1968a. The East Greenland Current north of Denmark Strait, Part I. *Arctic*, **21**, 181-200.

AAGAARD, K. *and* COACHMAN, L.K. 1968b. The East Greenland Current north of Denmark Strait, Part II. *Arctic*, **21**, 267-90.

AAGAARD, K. *and* COACHMAN, L.K. 1975. Toward an ice-free Arctic Ocean. *EOS*, **56**, 484-6.

AAGAARD, K. *and* GRIESMAN, P. 1975. Towards new mass and heat budgets for the Arctic Ocean. *Journal of Geophysical Research*, **90**, 3821-7.

AAGAARD, K., COACHMAN, L.K. *and* CARMACK, E.C. 1981a. On the halocline of the Arctic Ocean. *Deep-Sea Research*, **28**, 529-45.

AAGAARD, K., FOLDVIK, A. *and* HILLMAN, S.R. 1987. The West Spitzbergen Current: disposition and water mass. *Journal of Geophysical Research*, **92**, 3778-84.

AAGAARD, K., FOLDVIK, A. *and* RUDELS, B. 1981b. *Fysiskoceanografi Jmer*, **101**, 110-21.

AAGAARD, K., ROACH, A.T. *and* SCHUMACHER, J.D. 1985a. On the wind-driven variability of the flow through Bering Strait. *Journal of Geophysical Research*, **90**, 7213-21.

AAGAARD, K., SWIFT, J.H. *and* CARMACK, E.C. 1985b. Thermohaline circulation in the Arctic Mediterranean Seas. *Journal of Geophysical Research*, **90**, 4833-46.

ABBOTT, W.H. 1974. Temporal and spatial distribution of Pleistocene diatoms from the southeast Indian Ocean. *Nova Hedwigia*, **25**, 291-348.

ABELMANN, A., GERSONDE, R. *and* SPIEß, V. 1990. Pliocene-Pleistocene paleoceanography in the Weddell Sea - Siliceous microfossil evidence. (*In* BLEIL, U. *and* THIEDE, J., *eds Proceedings NATO Workshop "Geological History of the Polar Oceans: Arctic versus Antarctic"*. Kluwer, 729-59).

ABELMANN, A. *and* GERSONDE, R. 1991. Biosiliceous particle flux in Antarctic waters. (*In* QUEGUINER, B. *ed. Proceedings of the symposium on the biogeochemistry and the circulation of water masses in the Southern Ocean*. In press).

ACKLEY, S.F. 1982. Ice scavenging and nucleation: two mechanisms for incorporation of algae into newly-formed sea ice. *EOS*, **63**, 54.

ACKLEY, S.F., BUCK, K.R. *and* TAGUCHI, S. 1979. Standing crop of algae in the sea ice of the Weddell Sea region. *Deep-Sea Research*, **26**, 269-81.

AKIBA, F. 1982. Late Quaternary diatom biostratigraphy of the Bellingshausen Sea, Antarctic Ocean. *Rept. Techn. Res. Center, J.N.O.C.*, **16**, 31-74.

ALEXANDER, V. 1974. Primary productivity regimes of the nearshore Beaufort Sea, with reference to the potential role of ice biota. (*In* REED, J.C. and SATER, J.E. *eds The coast and shelf of the Beaufort Sea*, Arlington, The Arctic Institute of North America, 609-32).

ALEXANDER, V. 1980. Interrelationships between the seasonal sea ice and biological regimes. *Cold Regions Science and Technology*, **2**, 157-78.

ALEXANDER, V., HORNER, R. *and* CLASBY, R.C. 1974. *Metabolism of Arctic sea ice organisms*. Report R74-4, Institute of Marine Science, University of Alaska, Fairbanks, 1-120.

ALLDREGE, A.L. *and* SILVER, M.W. 1982. Abundance and production rates of floating diatom mats (*Rhizosolenia castracanei* and *R. imbricata* var. *shrubsolei*) in the eastern Pacific Ocean. *Marine Biology*, **66**, 83-8.

ANDERSEN, O.G.N. 1977. Primary production associated with sea ice at Godhavn Disko, West Greenland. *Ophelia*, **16**, 205-20.

ANDERSEN, R.A., MEDLIN, L.K. *and* CRAWFORD, R.M. 1986. An investigation of the cell wall components of *Actinocyclus subtilis* (Bacillariophyceae). *Journal of Phycology*, **22**, 455-79.

ANDERSON, J.T., ROFF, J.C. *and* GERRATH, J. 1983. The diatoms and dinoflagellates of Hudson Bay. *Canadian Journal of Botany*, **59**, 1793-810.

ANDRIASHEV, A.P. 1968. The problem of the life community associated with the Antarctic fast ice. (*In* CURRIE, R.I., *ed. Symposium on Antarctic oceanography*, Cambridge, W. Heffer & Sons Ltd., 147-55).

ANONYMOUS. 1975. Proposals for a standardization of diatom terminology and diagnoses. *Beihefte zur Nova Hedwigia*, **53**, 323-54.

APOLLONIO, S. 1961. The chlorophyll content of Arctic sea-ice. *Arctic*, **14**, 197-200.

APOLLONIO, S. 1965. Chlorophyll in Arctic sea ice. *Arctic*, **18**, 118-22.

APOLLONIO, S. 1980. Primary production in Dumbell Bay in the Arctic Ocean. *Marine Biology*, **61**, 41-51.

ATKINSON, A. 1989. Distribution of six major copepod species around South Georgia in early summer. *Polar Biology*, **9**, 353-63.

ATKINSON, A. *and* PECK, J. 1988. A summer-winter comparison of zoooplankton in the oceanic area around South Georgia. *Polar Biology*, **8**, 463-73.

BAKER, D.J., NOWLIN, W.D., PILLSBURY, R.D *and* BRYDEN, H.L. 1977. Antarctic Circumpolar Current: space and time fluctuations in the Drake Passage. *Nature*, **268**, 696-99.

BALDAUF, J.G. 1984. Cenozoic diatom biostratigraphy and paleoceanography of the Rockall Plateau region, North Atlantic Deep Sea Drilling Project Leg 81. (*In* ROBERTS D.G., SCHNITKER, D. *and others. Initial reports of the Deep Sea Drilling Project. Volume 81*. Washington, United States Government Printing Office, 439-78).

BALDAUF, J.G. *and* BARRON, J.A. 1987. Oligocene marine diatoms recovered in dredge samples from the Navarine Basin Province, Bering Sea. *United States Geological Survey Bulletin*, **1765**, 17 pp.

BALDAUF, J.G. *and* BARRON, J.A. 1991. Diatom Biostratigraphy: Kerguelen-Plateau and Prydz Bay regions of the Southern Ocean. (*In* BARRON, J.A., LARSEN, B.L. *and others. Proceedings of the ODP, Scientific Results, Leg 119*. College Station, Tx, ODP, in press).

BALECH, E. 1973. Segunda contribucion al conocimiento del microplancton del Mar del Bellingshausen. *Contribuciones del Instituto Antártico Argentino*, **107**, 1-63.

BALECH, E. 1975. Clave illustrada de dinoflagelados antarticos. *Publicaciones de Instituto Antártico Argentino*, **11**, 99 pp.

BALECH, E. *and* EL-SAYED, S.Z. 1965. Microplankton of the Weddell Sea. (*In* LLANO, G.A. *ed. Biology of the Antarctic seas, II*. Washington, American Geophysical Union, 107-24).

BALECH, E., EL-SAYED, S.Z., HASLE, G., NEUSHAL, M. *and* ZANEFELD, J.S. 1968. Primary productivity and benthic marine algae of the Antarctic and Subantarctic. *Antarctic Map Folio Series*, **10**, 1-12.

BARBER, H.G. *and* HAWORTH, E.Y. 1981. A guide to the morphology of the diatom frustule. *Freshwater Biological Association Scientific Publication*, **44**, 112 pp.

BARD, E., LABEYRIE, L.D., PICHON, J.-J., LABRACHERIE, M., ARNOLD, M., DUPRAT, J., MOYES, J., *and* DUPLESSY, J.-C. 1990. The last deglaciation in the southern and northern hemispheres based on oxygen isotope, sea surface temperature estimates, and accelerator ^{14}C dating from deep-sea sediments. (*In* BLEIL, U. *and* THIEDE, J. *eds Geological history of the Polar Oceans: Arctic versus Antarctic*, Kluwer, 405-15).

BARKER, P.F. *and* BURRELL, J. 1977. The opening of Drake Passage. *Marine Geology*, **25**, 15-34.

BARKER, P.F., KENNETT, J.P. *and* SCIENTIFIC PARTY. 1988a. Weddell Sea palaeoceanography: Preliminary results of ODP Leg 113. *Paleogeography, Paleoclimatology, Paleoecology*, **67**, 75-102.

BARKER, P.F., KENNETT, J.P. *and* SCIENTIFIC PARTY 1988b. *Proceedings of the ODP, Initial Reports, 113*. College Station, TX, Ocean Drilling Program.

BARRON, J.A. 1980. Miocene to Quaternary diatom biostratigraphy of DSDP Leg 57, off northeast Japan (*In Scientific party, Initial Reports of the Deep Sea Drilling Project* Volume 56, 57(2). Washington, United States Government Printing Office, 641-85).

BARRON, J.A. 1985a. Miocene to Holocene planktonic diatoms. (*In* BOLLI, H.M., SAUNDERS, J.B. *and* PERCH-NIELSEN, K. *eds Plankton stratigraphy*. Cambridge, Cambridge University Press, 763-809).

BARRON, J.A. 1985b. Diatom biostratigraphy of the CESAR 6 Core, Alpha Ridge. (*In* JACKSON, H.R., MUDIE, P.J. *and* BLASCO, S.M. *eds Initial geological report on CESAR: The Canadian Expedition to Study the Alpha Ridge, Arctic Ocean. Paper 84-22.* Geological Survey of Canada, 137-47).

BERGER, W.H. 1970. Biogenous deep-sea sediments: fractionation by deep-sea circulation. *Bulletin of the Geological Society of America*, **81**, 1385-402.

BERGER, W.H. 1974. Deep-sea sedimentation. (*In* BURK, C.A. *and* DRAKE, C.L. *eds The geology of continental margins.* Berlin, Springer Verlag, 213-41).

BILLEN, G., LANCELOT, C. *and* MATHOT, S. 1988. Ecophysiology of phyto- and bacterioplankton growth in the Prydz Bay area during the austral summer 1987. *Proceedings of the Belgian National Colloquium on Antarctic Research, October 20, 1987*, 134-46.

BJOEKLUND, K.R., THIESE, J. *and* HOLTEDAHL, H. 1979. Deglaciation of the southeastern Norwegian Sea towards the end of the last glacial age. *Boreas*, **8**, 133-5.

BLINDHEIM, J. 1989. Ecological features of the Norwegian Sea. (*In* REY, L. *and* ALEXANDER, V. *eds Proceedings of the 6th conference of the Comité Arctique International*, Leiden, The Netherlands, E .J. Brill, 366-401).

BODEN, B.P. 1949. The diatoms collected by the U.S.S. *Cacopan* in the Antarctic in 1947. *Journal of Marine Research*, **8**, 6-13.

BODEN, B.P. 1985. The South African SIBEX I cruise to the Prydz Bay region, 1984: VIII. The plankton encountered during the survey. *South African Journal of Antarctic Research*, **15**, 28-32.

BODEN, B.P., DUNCOMBE RAE, C.M. *and* LUTJEHARMS, J.R.E. 1988. The distribution of the diatoms of the south-west Indian Ocean surface waters between Cape Town and the Prince Edward Islands archipelago. *South African Journal of Science*, **84**, 811-8.

BOOTH, J.A. 1984. The epontic algal community of the ice edge zone and its significance to the Davis Strait ecosystem. *Arctic*, **37**, 234-43.

BOOTH, J.D. *and* BURCKLE, L.H. 1976. Displaced Antarctic diatoms in the southwestern and central Pacific. *Pacific Geology*, **11**, 99-108.

BOURKE, R.H., NEWTON, J.L., PAQUETTE, R.G. *and* TUNNICLIFFE, M.D. 1987. Circulation and water masses of the East Greenland Shelf. *Journal of Geophysical Research*, **92**, 6729-40.

BRAARUD, T. 1935. The "0st" expedition to the Denmark Strait 1929. II. Phytoplankton and its conditions of growth. *Hvalrådets Skrifter*, **10**, 1-173.

BRADSTREET, M.S.W. *and* CROSS, W.E. 1982. Trophic relationships at high Arctic ice edges. *Arctic*, **35**, 1-12.

BREWSTER, N.A. 1980. Cenozoic biogenic silica sedimentation in the Antarctic Ocean, based on two Deep Sea Drilling Project Sites. *Bulletin of the Geological Society of America*, **91**, 337-47.

BRÖCKEL, K. von. 1981. The importance of nanoplankton within the pelagic Antarctic ecosystem. *Kieler Meeresforschungen*, **5**, 61-7.

BRÖCKEL, K von. 1985. Primary production data from the southeastern Weddell Sea. *Polar Biology*, **4**, 75-80.

BRODIE, P.F., SAMEOTO, D.D. *and* SHELDON, R.W. 1978. Population densities of euphausiids off Nova Scotia as indicated by net samples, whale stomach contents, and sonar. *Limnology and Oceanography*, **23**, 1264-7.

BROOKS, M. 1975. Studies of the genus *Coscinodiscus*. II. Light, transmission and scanning electron microscopy of *C. asteromphalus* Ehr. *Botanica Marina*, **18**, 15-27.

BROWN, N.E. 1920. New and old diatoms from the Antarctic Region. *English Mechanic and World of Science*, **111**, 210-11, 219-20, 232-3.

BRYDEN, H.L. 1983. The Southern Ocean. (*In* ROBINSON, A.R. *ed. Eddies in marine science*. Berlin, Springer, 265-277).

BUCK, K.R. 1981. A study of choanoflagellates (Acanthoecidae) from the Weddell Sea, including a description of *Diaphanoeca multiannulata* n. sp. *Journal of Protozoology*, **28**, 47-54.

BUCK, K.R. *and* GARRISON, D.L. 1983. Protists from the ice-edge region of the Weddell Sea. *Deep-Sea Research*, **30**, 1261-77.

BUCKLEY, J.R., GAMMELSRÚD, T., JOHANNESEN, O.M *and* RÚEDM, L.P. 1979. Upwelling: oceanic structure at the ice edge of the Arctic ice pack in winter. *Science*, **203**, 165-7.

BUCKLEY, R.G. *and* TRODAHL, A.J. 1987. Scattering and absorption of visible light by sea ice. *Nature*, **326**, 867-9.

BUINITSKY, V. KH. 1968. The influence of microalgae on the structure and strength of Antarctic sea ice. *Oceanology*, **8**, 771-6.

BUINITSKY, V. KH. 1977. Organic life in sea ice. (*In* DUNBAR, M.J. *ed. Polar oceans*, Calgary, The Arctic Institute of North America, 301-6).

BUMA, A., ESTRADA, M., LARSEN, J., RIEBESELL, U., SCHLOSS, I. *and* THOMSEN, H.A. 1989. Unicellular organisms studied alive using photographic and video techniques. *Berichte zur Polarforschung*, **65**, 102-10.

BUNT, J.S. 1963. Diatoms of Antarctic sea-ice as agents of primary production. *Nature*, **199**, 1255-7.

BUNT, J.S. 1968. Some characteristics of microalgae isolated from Antarctic sea ice. (*In* LLANO, G.A. *and* SCHMITT, W.L. *eds Biology of the Antarctic seas, III.* Washington DC, American Geophysical Union, 1-14).

BUNT, J.S. *and* LEE, C.C. 1969. Observations within and beneath Antarctic sea ice in McMurdo Sound and the Weddell Sea, 1967-1968. *Methods and data. Institute of Marine Sciences, University of Miami, Report 69-1.* 32 pp.

BUNT, J.S. *and* LEE, C.C. 1970. Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. *Journal of Marine Research*, **28**, 304-20.

BUNT, J.S. *and* LEE, C.C. 1972. Data on the composition and dark survival of four sea-ice microalgae. *Limnology and Oceanography*, **17**, 458-61.

BUNT, J.S. *and* WOOD, E.J.F. 1963. Microalgae and Antarctic sea-ice. *Nature*, **199**, 1254-5.

BURCHETT, M.S. 1983. The life-cycle of *Notothenia rossii* from South Georgia. *British Antarctic Survey Bulletin*, **61**, 71-3.

BURCKLE, L.H. 1972. Diatom evidence bearing on the Holocene in the South Atlantic. *Quaternary Research*, **2**, 323-6.

BURCKLE, L.H. 1981. Displaced Antarctic diatoms in the Almirante Passage. *Marine Geology*, **39**, 39-43.

BURCKLE, L.H. 1984a. Diatom distribution and paleoceanographic reconstruction in the Southern Ocean - present and last glacial maximum. *Marine Micropaleontology*, **9**, 241-61.

BURCKLE, L.H. 1984b. Ecology and paleoecology of the marine diatom *Eucampia antarctica* (Castr.) Mangin. *Marine Micropaleontology*, **9**, 77-86.

BURCKLE, L.H. *and* ABRAMS, A. 1986. Diatom species diachrony in the late Neogene sediments of the Southern Ocean. *South African Journal of Science*, **82**, 505-6.

BURCKLE, L.H. *and* ABRAMS, N. 1987. Regional late Pliocene-early Pleistocene hiatuses of the Southern Ocean - diatom evidence. *Marine Geology*, **77**, 207-18.

BURCKLE, L.H. *and* BURAK, R.W. 1988. Fluctuations in late Quaternary diatom abundances: stratigraphic and paleoclimatic implications from subantarctic deep sea cores. *Paleogeography, Paleoclimatology, Paleoecology*, **67**, 147-56.

BURCKLE, L.H. *and* CIRILLI, J. 1987. Origin of diatom ooze belt in the Southern Ocean: implications for late Quaternary paleoceanography. *Micropaleontology*, **33**, 82-6.

BURCKLE, L.H. *and* COOKE, D.W. 1983. Late Pleistocene *Eucampia antarctica* abundance stratigraphy in the Atlantic sector of the Southern Ocean. *Micropaleontology*, **29**, 6-10.

BURCKLE, L.H. *and* OPDYKE, N.D. 1977. Late Neogene diatom correlations in the circum-Pacific. (*In* SAITO, T. *and* TAKAYANAGI, Y. *eds Proceedings of the first international congress on Pacific Neogene stratigraphy*. Tokyo, Geological Society of Japan, 255-84).

BURCKLE, L.H. *and* STANTON, D. 1975. Distribution of displaced Antarctic diatoms in the Argentine Basin. *Nova Hedwigia*, **55**, 283-91.

BURCKLE, L.H., CLARKE, D.B. *and* SHACKLETON, N.J. 1978. Isochronous last-abundant-appearance datuum (LAAD) of the diatom *Hemidiscus karstenii* in the Sub-Antarctic. *Geology*, **6**, 243-6.

BURCKLE, L.H., GERSONDE, R. *and* ABRAMS, J. 1990. Late Pliocene-Pleistocene paleoceanography in the Jane Basin. (*In* BARKER, P.F., KENNETT, J.P. *and others. Proceedings of the ODP, Scientific Results, Leg 113*. College Station, Texas, ODP, 803-12).

BURCKLE, L.H., JACOBS, S.S. *and* McLAUGHLIN, R.B. 1987. Late austral spring diatom distribution between New Zealand and the Ross Ice Shelf, Antarctica: hydrographic and sediment correlations. *Micropaleontology*, **33**, 74-81.

BURCKLE, L.H., ROBINSON, D. *and* COOKE, D. 1982. Reappraisal of sea-ice distribution in the Atlantic and Pacific sectors of the Southern Ocean at 18,000 yr BP. *Nature*, **299**, 435-7.

BURKHOLDER, P.R. *and* MANDELLI, E.F. 1965. Productivity of microalgae in Antarctic sea ice. *Science*, **149**, 872-4.

BURKHOLDER, P.R. *and* SIEBURTH, J.McN. 1961. Phytoplankton and chlorophyll in the Gerlache and Bransfield Straits of Antarctica. *Limnology and Oceanography*, **6**, 45-52.

BURSA, A. 1961. The annual oceanography cycle at Igloolik in the Canadian Arctic. II. The phytoplankton. *Journal of the Fisheries Research Board of Canada*, **18**, 563-615.

CALVERT, S.E. 1974. Deposition and diagenesis of silica in marine sediments. (*In* HSÜ, K.J. *and* JENKYNS, H.C. *eds Pelagic sediments on land and under the sea.* Special Publication Number 1 of the International Association of Sedimentologists, Oxford, Blackwell Scientific Publications, 273-99).

CAREY, A.G. 1985. Marine ice fauna: Arctic. (*In* HORNER, R.A. *ed. Sea ice biota*, Boca Raton, CRC Press, 173-90).

CAREY, A.G. 1987. Particle flux beneath fast ice in the shallow southwestern Beaufort Sea, Arctic Ocean. *Marine Ecology - Progress Series*, **40**, 247-57.

CAREY, A.G. *and* BOUDRIAS, M.A. 1987. Feeding ecology of *Pseudalibrotus* (= *Onisimus*) *litoralis* Kröyer (Crustacea: Amphipoda) on the Beaufort Sea inner continental shelf. *Polar Biology*, **8**, 29-33.

CAREY, A.G. *and* MONTAGNA, P.A. 1982. Arctic sea ice faunal assemblages: first approach to description and source of the under-ice meiofauna. *Marine Ecology - Progress Series*, **8**, 1-8.

CAREY, A.G., BOUDRIAS, M.A., KERN, J.C. *and* RUFF, R.E. 1984. Selected ecological studies on continental shelf benthos and sea ice fauna in the southwestern Beaufort Sea. *Outer Continental Shelf Environmental Assessment Program, Final Reports of Principal Investigators*, **23**, 1-164.

CARMACK, E.C. 1986. Circulation and mixing in ice-covered waters. (*In* UNTERSTEINER, N. *ed. The geophysics of sea ice*, New York, Plenum, 641-712).

CARMACK, E.C. 1990. Large-scale physical oceanography of Polar Oceans. (*In* SMITH, W.O., *ed. Polar Oceanography*. Academic Press, 171-22).

CARMACK, E.C. *and* FOSTER, T.D. 1975. On the flow of water out of the Weddell Sea. *Deep-Sea Research*, **22**, 722-4.

CARSEY, F.D. 1982. Arctic sea-ice distribution at the end of summer 1973-1976 from satellite microwave data. *Journal of Geophysical Research*, **87**, 5809-35.

CASSIE, V. 1963. Distribution of surface phytoplankton between New Zealand and Antarctica, December 1957. *Trans-Antarctic Expedition 1955-1958. Scientific Reports*, **7**, 11 pp.

CASTRACANE, A.F.A. 1886. Report of the Diatomaceae collected by HMS *Challenger* during the years 1873-76. *Report of the Scientific Results of the Voyage of HMS Challenger, 1873-76 - Botany* **2**, 178 pp.

CENTRAL INTELLIGENCE AGENCY. 1978. *Polar regions atlas.* GC 78 - 10040, Washington DC, US Government Printing Office.

CIESIELSKI, P.F. 1983. The Neogene and Quarternary diatom biostratigraphy of Subantarctic sediments, Deep Sea Drilling Project Leg 71. (*In* LUDWIG, W.J., KRASHENINNIKOV, V.A. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 71.* Washington, United States Government Printing Office, 635-65).

CLARKE, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanography and Marine Biology Annual Review*, **21**, 342-453.

CLARKE, A., HOLMES, L.J. *and* WHITE, M.G. 1988. The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands, 1969-82. *British Antarctic Survey Bulletin*, **80**, 65-86.

CLARKE, A., QUETIN, L.B. *and* ROSS, R.M. 1988. Laboratory and field estimates of the rate of faecal pellet production by Antarctic krill, *Euphausia superba. Marine Biology*, **98**, 557-63.

CLARKE, D.B. *and* ACKLEY, S.F. 1984. Sea ice structure and biological activity in the Antarctic marginal ice zone. *Journal of Geophysical Research*, **89**, 2087-95.

CLARKE, D.B., ACKLEY, S.F. *and* KUMAI, M. 1984. Morphology and ecology of diatoms in sea ice from the Weddell Sea. *Cold Regions Engineering Laboratory Report*, **84-5**, 41 pp.

CLARKE, M.R. 1985. Marine habitats - Antarctic cephalopods. (*In* BONNER, W.N. *and* WALTON, D.W.H. *eds Key environments - Antarctica*, Oxford, Pergamon, pp. 193-200).

CLARKE, M.R. 1987. Cephalopod biomass - estimation from predation. (*In* BOYLE, P.R. *ed. Cephalopod life cycles, volume 2*, London, Academic Press, 221-237).

CLASBY, R.C., HORNER, R. *and* ALEXANDER, V. 1973. An *in situ* method for measuring primary productivity of Arctic sea ice algae. *Journal of the Fisheries Research Board of Canada*, **30**, 835-8.

CLASBY, R.C., ALEXANDER, V. *and* HORNER, R. 1976. Primary productivity of sea-ice algae. (*In* HOOD, D.W. and BURRELL, D.C. *eds Assessment of the Arctic marine environment: Selected Topics*, Fairbanks, Unviversity of Alaska, 289-304).

CLEMONS, M.J. *and* MILLER, C.B. 1984. Blooms of larger diatoms in the oceanic, subarctic Pacific. *Deep-Sea Research*, **31**, 85-99.

CLEVE, P.T. 1873. On diatoms from the Arctic Sea. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **1**(13), 1-28.

CLEVE, P.T. 1883. Diatoms collected during the Expedition of the Vega. (*In* NORDENSKIOLD, A.E. *ed. Vega-Expeditionens Vetenskapliga Iakttagelser*. **3**, 455-517.

CLEVE, P.T. 1894-1895. Synopsis of the naviculoid diatoms. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **26**, 1-194; **27**, 1-219.

CLEVE, P.T. 1896. Diatoms from Baffins Bay and Davis Strait, collected by M.E. Nilsson. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **22**, Afd. III(4), 3-22.

CLEVE, P.T. 1898. Diatoms from Franz-Joseph Land collected by the Harmsworth-Jackson Expedition. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **24**, Afd. III(2), 3-26.

CLEVE, P.T. 1899. Mikroskopisk undersökning af stoft, funnet pa drifis i Ishafvet. *Öfversigt af Kongliga Vetenskaps - Akademiens Förhandlingar*, **1899**, 123-30.

CLEVE, P.T. 1900. Microscopical examination of dust from drift-ice north of Jan Mayen. *Öfversigt af Kongliga Vetenskaps - Akademiens Förhandlingar*, **1900**, 393-7.

CLEVE, P.T. *and* GRUNOW, A. 1880. Beiträge zur Kenntniss der arctischen Diatomeen. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **17**(2), 1-121.

CLOWES, A.J. 1934. Hydrology of the Bransfield Strait. *Discovery Reports*, **9**, 1-64.

COACHMAN, L.K. 1986a. Circulation, water masses, and fluxes on the Southeastern Bering Sea Shelf. *Continental Shelf Research*. **5**, 23-108.

COACHMAN, L.K. 1986b. Observations of fine structure formed in a continental shelf front, Southeastern Bering Sea. (*In* NIHOUL, J.C.J. *ed. Marine interfaces ecohydrodynamics*, Amsterdam, Elsevier, 215-255).

COACHMAN, L.K. *and* AAGAARD, K. 1966. On the water exchange through Bering Strait. *Limnology and Oceanography*, **11**, 44-59.

COACHMAN, L.K. *and* AAGAARD, K. 1974. Physical oceanography of Arctic and subarctic seas. (*In* HERMAN, Y. *ed. Marine geology and oceanography of the Arctic seas*. Berlin, Springer-Verlag, pp. 1-72).

COACHMAN, L.K. *and* AAGAARD, K. 1981. Reevaluation of water transports in the vicinity of Bering Strait. (*In* HOOD, D.W. *and* CALDER, J.A. *eds The eastern Bering Sea shelf: oceanography and resources*, Seattle, University of Washington Press, 95-110).

COACHMAN, L.K. *and* AAGAARD, K. 1988. Transports through Bering Strait: Annual and Interannual Variability. *Journal of Geophysical Research*, **93**, 15535-9.

COACHMAN, L.K. *and* BARNES,C.A. 1961. The contribution of Bering Sea water to the Arctic Ocean. *Arctic*, **14**, 147-61.

COACHMAN, L.K. *and* BARNES,C.A. 1962. Surface water in the Eurasian basin of the Arctic Ocean. *Arctic*. **15**, 251-77.

COACHMAN, L.K., AAGAARD, K. *and* TRIPP, R.B. 1975. *Bering Strait: the regional physical oceanogranhy*. Seattle, University of Washington Press.

CODISPOTI, L. 1979. Arctic ocean processes in relation to the dissolved silicon content of the Atlantic. *Marine Science Communications*, **5**, 361-81.

CODISPOTI, L. 1983. On nutrient variability and sediments in upwelling regions. (*In* SUESS, E. *and* THIEDE, J. *eds Coastal upwelling*. New York, Plenum, 125-45).

CODISPOTI, L.A. *and* RICHARDS, F.A. 1968. Micronutrient distribution in the East Siberian and Laptev Seas during summer 1963. *Arctic*, **21**, 67-83.

CODISPOTI, L.A. *and* RICHARDS, F.A. 1971. Oxygen supersaturation in the Chukchi and East Siberian seas. *Deep-Sea Research*, **18**, 341-51.

COLONY, R. *and* THORNDIKE, A.S. 1980. The horizontal coherency of the motion of summer Arctic sea ice. *Journal of Physical*

Oceanography, **10**, 1281-9.

COLONY, R. *and* THORNDIKE, A.S. 1984. An estimate of the mean field of Arctic sea ice. *Journal of Geophysical Research*, **89**, 10623-9.

COLONY, R. *and* THORNDIKE, A.S. 1985. Sea ice motion as a drunkard's walk. *Journal of Geophysical Research*, **90**, 965-74.

COLTON, M.T. *and* CHASE, R.R.P. 1983. Interaction of the Antarctic Circumpolar Current with bottom topography: an investigation using satellite altimetry. *Journal of Geophysical Research*, **88**, 1825-43.

COTA, G.F. 1985. Photoadaptation of high Arctic ice algae. *Nature*, **315**, 219-22.

COTA, G.F., PRINSENBERG, S.J., BENNETT, E.B., LODER, J.W., LEWIS, M.R., ANNING, J.L., WATSON, N.H.F. *and* HARRIS, L.R. 1987. Nutrient fluxes during extended blooms of Arctic ice algae. *Journal of Geophysical Research*, **92**, 1951-62.

CRIPPS, G.C. 1989. Problems in the identification of anthropogenic hydrocarbons against natural background levels in the Antarctic. *Antarctic Science*, **1**, 307-12.

CROSS, W.E. 1982. Under-ice biota at the Pond Inlet ice edge and in adjacent fast ice areas during spring. *Arctic*, **35**, 13-27.

CUPP, E.E. 1943. Marine plankton diatoms of the west coast of North America. *Bulletin of the Scripps Institution of Oceanography*, **5**, 1-237.

DALY, K.L. *and* MACAULAY, M.C. 1987. Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. *Deep-Sea Research*, **35**, 21-41.

DAYTON, P.K., ROBILLIARD, G.A. *and* DEVRIES, A.L. 1969. Anchor ice formation in McMurdo Sound, Antarctica, and its biological effects. *Science*, **163**, 273-4.

DEFELICE, D.R. 1979. Morphological comparision of *Coscinodiscus lentiginosus* Janisch and *Coscinodiscus obovatus* Castracane. *Antarctic Journal of the United States*, **14**, 127-9.

DEFELICE, D.R. *and* WISE, S.W. 1981. Surface lithofacies, biofacies, and diatom diversity patterns as models for delineation of climatic change in the southeast Atlantic Ocean. *Marine Micropaleontology*, **6**, 29-70.

DEIBEL, D. *and* POWELL, C.V.L. 1987. Ultrastructure of the pharyngeal filter of the appendicularian *Oikopleura vanhoeffeni*: implications for particle size selection and fluid mechanics. *Marine Ecology - Progress Series*, **35**, 243-50.

DEMASTER, D.J. 1979. *The marine budgets of silica and* ^{32}*Si.* Unpublished Ph.D. dissertation, Yale University.

DEMERS, S., LEGENDRE, L., THERRIAULT, J.-C. and INGRAM, R.G. 1986. Biological production at the ice-water ergocline. (*In* NIHOUL, J.C.J. *ed. Marine interfaces ecohydrodynamics*, Amsterdam, Elsevier, 31-54).

DEMERS, S., THERRIAULT, J.-C. *and* DESCOLAS-GROS, C. 1984. Biomasse et composition spécifique de la microflore des glaces saisonnières: influences de la lumière et de la vitesse de congélation. *Marine Biology*, **78**, 185-91.

DIECKMANN, G., ROHARDT, G., HELLMER, H., *and* KIPFSTUHL, J. 1986. The occurrence of ice platelets at 250 m depth near the Filchner Ice Shelf and its significance for sea ice biology. *Deep-Sea Research*, **33**, 141-8.

DIGBY, D.S.P. 1953. Plankton production in Scoresby Sound, East Greenland. *Journal of Animal Ecology*, **22**, 289-322.

DODGE, J.D. *and* PRIDDLE, J. 1987. Species composition and ecology of dinoflagellates from the Southern Ocean near South Georgia. *Journal of Plankton Research*, **9**, 685-97.

DONAHUE, J.G. 1970a. *Diatoms as Quaternary bistratigraphic and paleoclimatic indicators in high latitudes of the Pacific Ocean.* Unpublished Ph.D. dissertation, Columbia University, NY.

DONAHUE, J.G. 1970b. Pleistocene diatoms as climatic indicators in North Pacific sediments. (*In* HAYS, J.D. *ed. Geological investigation of the north Pacific*. Memoirs of the Geological Society of America, **126**, 121-38).

DONAHUE, J.G. 1973. Distribution of planktonic diatoms in surface sediments of the southern south Pacific. *Antarctic Map Folio Series*, **17**, 1-18.

DOUCETTE, G.J. *and* FRYXELL, G.A. 1985. *Thalassiosira antarctica* (Bacillariophyceae): vegetative and resting stage ultrastructure of an ice-related marine diatom. *Polar Biology*, **4**, 107-12.

DREBES, G. 1974. *Marines Phytoplankton*. Stuttgart, Georg Thieme Verlag.

DUBINSKY, Z., FALKOWSKI, P.G *and* WYMAN, K. 1986. Light harvesting and utilization by phytoplankton. *Plant and Cell Physiology (Tokyo)*, **27**, 1335-49.

DUNBAR, M.J. *and* ACREMAN, J.C. 1980. Standing crops and species composition of diatoms in sea ice from Robeson Channel to the Gulf of St. Lawrence. *Ophelia*, **19**, 61-72.

DUNBAR, R.B. 1985. Sediment trap experiments on the Antarctic continental margin. *Antarctic Journal of the United States*, **19**(5), 70-71.

DURBIN, E.G. 1974. Studies on the autecology of the marine diatoms *Thalassiosira nordenskiöldii* and *Detonula confervacea. Marine Biology*, **45**, 31-7.

DZINORIDZE, R.N., JOUSÉ, A.P., DOROLEVA-GOLIKOVA, G.S., KOZLOVA, G.E., NAGAEVA, G.S., PETRUSHEVSKAJA, M.G. *and* STRELNIKOVA, N.I. 1978. Diatom and radiolarian Cenozoic stratigraphy, Norwegian Basin; DSDP Leg 38. (*In* TALWANI, M., UDINTSEV, G. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 38.* Published in Supplement to Volumes 38, 39, 40 and 41. Washington United States Government Printing Office, 287-427).

EHRENBERG, C.G. 1841. Einen Nachtrag zu dem Vortrage über Verbreitung und Einfluβ des mikroskopischen Lebens in Süd- und Nord-Amerika. *Deutsche Akademie der Wissenschaften zu Berlin, Monatsberichte*, **1841**, 202-7.

EHRENBERG, C.G. 1853. Über neue Anschaunungen des kleinsten nördlichen Polarlebens. *Deutsche Akademie der Wissenschaften zu Berlin, Monatsberichte*, **1853**, 522-9.

EIDE, L.I. *and* MARTIN, S. 1975. The formation of brine drainage features in young sea ice. *Journal of Glaciology*, **14**, 137-54.

ELDHOLM, O., THIEDE, J., TAYLOR, E. *and* SHIPBOARD SCIENTIFIC PARTY. 1987. Summary and preliminary conclusions, ODP Leg 104. (*In* ELDHOLM, O., THIEDE, J., TAYLOR, E. I. *and others. Proceedings, Intitial Reports (part A), Ocean Drilling Program*, 104, 751-71).

EL-SAYED, S.Z. 1971. Dynamics of trophic relations in the Southern Ocean. (*In* QUAM, L.O. *ed. Research in Antarctica*, Washington, DC, American Association for the Advancement of Science, 73-90).

EL-SAYED, S.Z. 1984. Productivity of the Antarctic waters - a reappraisal. (*In* HOLM-HANSEN, O., BOLIS, L. *and* GILLES, R. *eds Marine phytoplankton and productivity. Lecture notes on coastal and estuarine studies. Volume 8.* Berlin, Springer Verlag, 19-34).

EL-SAYED, S.Z. *and* TAGUCHI, S. 1981. Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. *Deep-Sea Research*, **28**, 1017-32.

EVENSEN, D.L. *and* HASLE, G.R. 1975. The morphology of some *Chaetoceros* (Bacillariophyceae) species as seen in the electron microscope. *Beihefte zur Nova Hedwigia*, **53**, 153-84.

EVERITT, D.A. *and* THOMAS, D.P. 1986. Observations of seasonal changes in diatoms at inshore localities near Davis Station, East Antarctica. *Hydrobiologia*, **139**, 3-12.

FALKOWSKI, P.G. *and* OWENS, T.G. 1980. Light-shade adaptation: two strategies in marine phytoplankton. *Plant Physiology*, **66**, 592-5.

FALKOWSKI, P.G. *and* WIRICK, C.D. 1981. A simulation model of the effects of vertical mixing on primary productivity. *Marine Biology*, **65**, 69-75.

FAY, F.H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. (*In* HOOD, D.W. *and* KELLEY, E.J. *eds Oceanography of the Bering Sea with emphasis on renewable resources*, Fairbanks, University of Alaska, 383-99).

FENCHEL, T. *and* LEE, C.C. 1972. Studies on ciliates associated with sea ice from Antarctica I. The nature of the fauna. *Archiv für Protistenkunde*, **114**, 231-6.

FENNER, J. 1984. Eocene-Oligocene planktic diatom stratigraphy in high and low latitudes. *Micropaleontology*, **30**, 319-42.

FENNER, J. 1985. Late Cretaceous to Oligocene planktic diatoms. (*In* BOLLI, H.M., SAUNDERS, J.B. *and* PERCH-NIELSEN, K. *eds Plankton stratigraphy*. Cambridge, Cambridge University Press, 713-62).

FENNER, J., SCHRADER, H.J. *and* WEINIGE, H. 1976. Diatom phytoplankton studies in the southern Pacific Ocean, composition and correlation to the Antarctic Convergence and its palaeoecological significance. (*In* HOLLISTER, C.D., CRADDOCK, C. *and others. Initial reports of the Deep Sea Drilling Project. Volume 35.* Washington, United States Government Printing Office, 757-813).

FERGUSON WOOD, E.J. 1959. An unusual diatom from the Antarctic. *Nature*, **184**, 1962-3.

FERRARIO, M.E. *and* FERREYRA, G. 1983. Casos teratológicos y de polimorfismo observados en diatomeas antárticas y otros ambientes continentales y marinos de Argentina. 1. *Contribucíónes del Instituto Antártico Argentino*, **290**, 8 pp..

FERREYRA, G. *and* FERRARIO, M.E. 1983a. Observaciones

sistemáticas y autoecológicas sobre diatomeas antárticas. 1. *Coscinodiscus asteromphalus* Ehr. *Contribucíónes del Instituto Antártico Argentino*, **297**, 19 pp.

FERREYRA, G. *and* FERRARIO, M.E. 1983b. Varición morfológica estacional de *Rhizosolenia alata* Brightwell en Bahia Paraiso, Antartida Occidental. *Contribucíónes del Instituto Antártico Argentino*, **300**, 18 pp.

FILLON, R.H. 1979. Ross Sea diatoms: modern assemblage distribution and their relationship to ecological, oceanographic, and sedimentary conditions - discussion. *Marine Micropaleontology*, **4**, 399-400.

FISCHER, G., FÜTTERER, D., GERSONDE, R., HONJO, S., OSTERMANN, D. *and* WEFER, G. 1988. Particle flux in the Northern Weddell Sea: seasonality and its relationship to ice-cover. *Nature*, **335**, 426-8.

FISSEL, D.B., BIRCH, J.R., MELLING, H. *and* LAKE, R.A. 1988. Non-tidal flows in the Northwest Passage. *Canadian Technical Report of Hydrography and Ocean Sciences*, **98**, 143 pp.

FOGG, G.E. 1977. Aquatic primary production in the Antarctic. *Philosophical Transactions of the Royal Society*, B **279**, 27-38.

FOLDVIK, A., AAGAARD, K. *and* TORRESEN, T. 1988. On the velocity field of the East Greenland Current. *Deep-Sea Research*, **35**, 1335-54.

FOSTER, T.D. 1984. The marine environment. (*In* LAWS, R.M. *ed. Antarctic ecology, volume 2*, London, Academic Press, 345-371).

FRANKENSTEIN, G. *and* GARNER, R. 1967. Equations for determining the brine volume of sea ice from −0.5°C to −22.9°C. *Journal of Glaciology*, **6**, 943-4.

FRENGUELLI, J. 1943. Diatomeas de las Orcadas del Sur. *Revista del Museo de la Plata n.s. Botanica*, **5**, 221-65.

FRENGUELLI, J. 1960. Diatomeas y silicoflagellados recogidas en Tierra Adelia durante las Expediciones Polares Francesas de Paul-Emile Victor (1950-1952). *Revue Algologique, n.s.*, **5**, 3-48.

FRENGUELLI, J. *and* ORLANDO, H.A. 1958. Diatomeas y silicoflagellados del sector Antártico Sudamericano. *Publicacíónes del Instituto Antártico Argentino*, **5**, 1-191.

FRYXELL, G.A. 1975a. *Morphology, taxonomy, and distribution of selected diatom species of* Thalassiosira *Cleve in the Gulf of Mexico and Antarctic waters.* Unpublished PhD thesis, Texas A & M University.

FRYXELL, G.A. 1975b. Three new species of *Thalassiosira*, with observations on the occluded process, a newly observed structure of diatom valves. *Beihefte zur Nova Hedwigia*, **53**, 57-75.

FRYXELL, G.A. 1976. The position of the labiate process in the diatom genus *Skeletonema. British Phycological Journal*, **11**, 93-9.

FRYXELL, G.A. 1977. *Thalassiosira australis* Peragallo and *T. lentiginosa* (Janisch) G. Fryxell, comb. nov.: two Antarctic diatoms (Bacillariophyceae). *Phycologia*, **16**, 95-104.

FRYXELL, G.A. 1978. The diatom genus *Thalassiosira: T. licea* sp. nov. and *T. angusti* (Gran) Makarova, species with occluded processes. *Botanica Marina*, **21**, 131-42.

FRYXELL, G.A. 1989. Marine phytoplankton at the Weddell Sea ice shelf: seasonal changes at the specific level. *Polar Biology*, **10**, 1-18.

FRYXELL, G.A. *and* EL-SAYED, S.Z. 1976. Diatoms in a phytoplankton sample from the 1907-1909 British Antarctic Expedition. *Antarctic Journal of the United States*, **11**, 33-6.

FRYXELL, G.A. *and* HASLE, G.R. 1971. *Corethron criophilum* Castracane: its distribution and structure. (*In* LLANO, G.A. *and* WALLEN, I.E. *eds Biology of Antarctic seas IV, Antarctic Research Series 17*. Washington, American Geophysical Union, 335-46).

FRYXELL, G.A. *and* HASLE, G.R. 1972. *Thalassiosira eccentrica* (Ehr.) Cleve, *T. symmetrica* spec. nov. and some related centric diatoms. *Journal of Phycology*, **8**, 297-317.

FRYXELL, G.A. *and* HASLE, G.R. 1973. Coscinodiscaceae: some consistent patterns in diatom morphology. *Beihefte zur Nova Hedwigia*, **45**, 69-84.

FRYXELL, G.A. *and* HASLE, G.R. 1977. The genus *Thalassiosira*: some species with a modified ring of central strutted processes. *Beihefte zur Nova Hedwigia*, **54**, 67-98.

FRYXELL, G.A. *and* HASLE, G.R. 1979. The genus *Thalassiosira*: species with internal extensions of the strutted processes. *Phycologia*, **18**, 378-93.

FRYXELL, G.A. *and* HASLE, G.R. 1979. The genus *Thalassiosira*: *T. trifulta*, sp. nov., and other species with tricolumnar support on strutted processes. *Beihefte zur Nova Hedwigia*, **64**, 13-32.

FRYXELL, G.A. *and* HASLE, G.R. 1980. The marine diatom *Thalassiosira oestruppii*: structure, taxonomy and distribution. *American Journal of Botany*, **67**, 804-14.

FRYXELL, G.A. *and* HASLE, G.R. 1983. The Antarctic diatoms *Thalassiosira dichotomica* (Kozlova) comb. nov. and *T. ambigua* Kozlova. *Polar Biology*, **2**, 53-62.

FRYXELL, G.A. *and* MEDLIN, L.K. 1981. Chain forming diatoms: evidence of parallel evolution in *Chaetoceros. Cryptogamie: Algologie*, **2**, 3-29.

FRYXELL, G.A. *and* MILLER, W.I. 1978. Chain-forming diatoms: three araphid species. *Bacillaria*, **1**, 113-36.

FRYXELL, G.A. *and* PRASAD, A.K.S.K. 1990. *Eucampia antarctica* var. *recta* (Mangin) stat. nov. (Biddulphiaceae, Bacillariophyceae) life stages at the Weddell Sea ice edge. *Phycologia*, **29**, 27-38.

FRYXELL, G.A. *and* SEMINA, H.J. 1981. *Actinocyclus exiguus* sp. nov. from the southern parts of the Indian and Atlantic oceans. *British Phycological Journal*, **16**, 441-8.

FRYXELL, G.A., DOUCETTE, G.J., *and* HUBBARD, G.F. 1981. The genus *Thalassiosira*: the bipolar diatom *Thalassiosira antarctica. Botanica Marina*, **24**, 321-36.

FRYXELL, G.A., HUBBARD, G.F. *and* VILLAREAL, T.A. 1981. The genus *Thalassiosira*: variations of the cingulum. *Bacillaria*, **4**, 41-63.

FRYXELL, G.A., PRASAD, A.K.S.K. *and* FRYXELL, P.A. 1989. *Eucampia antarctica* (Castracane) Mangin (Bacillariophyta): complex nomeclatural and taxonomic history. *Taxon*, **38**, 638-40.

FRYXELL, G.A., SIMS, P.A. *and* WATKINS, T.P. 1986. *Azpeitia* (Bacillariophyceae): related genera and promorphology. *Systematic Botany Monographs*, **13**, 1-74.

FRYXELL, G.A., VILLAREAL, T.A. *and* DOUCETTE, G.J. 1980. Antarctic phytoplankton: fieldwork and establishment of living cultures. *Antarctic Journal of the United States*, **15**(5), 141-2.

FRYXELL, G.A., VILLAREAL, T.A. *and* DOUCETTE, G.J. 1981. Diatom resting spores and *Agulhas* collections. *Antarctic Journal of the United States*, **15**(5), 128-9.

FRYXELL, G.A., VILLAREAL, T.A. *and* HOBAN, M.A. 1979. *Thalassiosira scotia*, sp. nov.: observations on a phytoplankton increase in early austral spring north of the Scotia Ridge. *Journal of Plankton Research*, **1**, 355-70.

FUKUCHI, M. and SASAKI, H. 1981. Phytoplankton and zooplankton standing stocks and downward flux of particulate material around fast ice edge of Lützow-Holm Bay, Antarctica. *Memoirs of National Institute of Polar Research, Series E*, **34**, 13-36.

FUKUSHIMA, H. 1961. Preliminary reports of the biological studies on coloured ocean ice. *Antarctic Record*, **11**, 164.

FUKUSHIMA, H. 1965. Preliminary report on diatoms from colored ice at Point Barrow, Alaska. *Antarctic Record*, **24**, 31-5.

FURHMAN, J.A. *and* AZAM, F. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. *Applied Microbiology*, **39**, 1085-95.

GAARDER, K.R. 1938. Phytoplankton studies from the Tromsø district 1930-31. *Tromsø Museums Årshefter, Naturhistoriske Avd. nr. 11*, **55**, 1-159.

GALLEGOS, C.L. *and* PLATT, T. 1982. Phytoplankton production and water motion surface mixed layers. *Deep-Sea Research*, **29**, 65-76.

GALLEGOS, C.L., PLATT, T., HARRISON, W.G. *and* IRWIN, B. 1983. Photosynthetic parameters of arctic marine phytoplankton: vertical variation and time scales of adaptation. *Limnology and Oceanography*, **28**, 698-708.

GARDNER, W.D. 1980a. Sediment trap dynamics and calibration: a laboratory examination. *Journal of Marine Research*, **38**, 17-39.

GARDNER, W.D. 1980b. Field assessment of sediment traps. *Journal of Marine Research*, **38**, 41-52.

GARRISON, D.L. *and* BUCK, K.R. 1982. Sea-ice algae in the Weddell Sea. I. Biomass distribution and the physical environment. *EOS*, **63**, 47.

GARRISON, D.L. *and* BUCK, K.R. 1985. Sea-ice algal communities in the Weddell Sea: species composition in ice and plankton assesmblages. (*In* GRAY, J.S. and CHRISTIANSEN, M.E. *eds. Marine biology of polar regions and effects of stress on marine organisms*. Chichester, New York, John Wiley & Sons Ltd., 102-21).

GARRISON, D.L. *and* BUCK, K.R. 1986. Organism losses during ice melting: a serious bias in sea ice community studies. *Polar Biology*, **6**, 237-9.

GARRISON, D.L. *and* BUCK, K.R. 1989a. Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. *Polar Biology*, **9**, 341-51.

GARRISON, D.L. *and* BUCK, K.R. 1989b. The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula regions. *Polar Biology*, **10**, 211-9.

GARRISON, D.L., ACKLEY, S.F. *and* BUCK, K.R. 1983. A physical mechanism for establishing algal populations in frazil ice. *Nature*, **306**, 363-5.

GARRISON, D.L., SULLIVAN, C.W. *and* ACKLEY, S.F. 1986. Sea ice microbial communities in Antarctica. *BioScience*, **36**, 243-50.

GARRISON, G.R. *and* BECKER, P. 1976. The Barrow Submarine Canyon: a drain for the Chukchi Sea. *Journal of Geophysical Research*, **81**, 4445-53.

GASCARD, J.C., KERGOMARD, C., JEANNIN, P.F., *and* FILY, M. 1988. Diagnostic study of the Fram Strait marginal ice zone during summer from Marginal Ice Zone Experiment 83 and 84 Lagrangian observations. *Journal of Geophysical Research*, **93**, 3613-41.

GEORGI, D.T. 1978. Fine structure in the Antarctic Polar Front Zone: its characteristics and possible relationships to internal waves. *Journal of Geophysical Research*, **83**, 4579-88.

GERSONDE, R. 1986a. Siliceous microorganisms in sea ice and their record in sediments in the Southern Weddell Sea (Antarctica). (*In* RICARD, M. *ed. Proceedings of the Eighth International Diatom Symposium, Paris 1984*, 549-66).

GERSONDE, R. 1986b. Biogenic siliceous particle flux in Antarctic waters and its palaeoecological significance. *South African Journal of Science*, **82**, 500-1.

GERSONDE, R. 1990a. Taxonomy and morphostructure of lower Pliocene diatoms from the Maud Rise (Antarctic Ocean). *Polarforschung*, **60**, in press.

GERSONDE, R. 1990b. Taxonomy and morphostructure of Neogene diatoms from the Southern Ocean (ODP Leg 113). (*In* BARKER, P.F., KENNETT, J.P., *and others. Proceedings of the ODP, Scientific results, Leg 113.* College Station, Texas, ODP, 791-802).

GERSONDE, R. in press, a. Seasonal particle flux in the Weddell Sea. *Polar Biology*.

GERSONDE, R. in press, b. A three year monitoring (1983-1986) of diatom particle flux in the Bransfield Strait (Antarctic Ocean). *Deep-Sea Research*.

GERSONDE, R. *and* BURCKLE, L.H. 1990. Neogene diatom biostratigraphy (ODP Leg 113). (*In* BARKER, P.F., KENNETT, J.P., *and others. Proceedings of the ODP, Scientific results, Leg 113.* College Station, Texas, ODP, 761-90).

GERSONDE, R. *and* HARWOOD, D.M. 1990. Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 1. Vegetative Cells. (*In* BARKER, P.F., KENNETT, J.P., *and others. Proceedings of the ODP, Scientific results, Leg 113.* College Station, Texas, ODP, 365-402).

GERSONDE, R. *and* TREPPKE, U. in press. Pleistocene diatom species fluctuations south of the Antarctic Convergence (Weddell Sea, Antarctic Ocean). *Micropaleontology*.

GERSONDE, R. *and* WEFER, G. 1987. Sedimentation of biogenic siliceous particles in Antarctic waters from the Atlantic sector. *Marine Micropaleontology*, **11**, 311-32.

GERSONDE, R., ABELMANN, A., BURCKLE, L.H., HAMILTON, N., LAZARUS, D., McCARTNEY, K., O'BRIAN, V., SPIEß, V., *and* WISE, S.W. 1990. Biostratigraphic systhesis of Neogene siliceous microfossils from the Antarctic Ocean, ODP Leg 113 (Weddell Sea). (*In* BARKER, P.F., KENNETT, J.P., *and others. Proceedings of the ODP, Scientific results, Leg 113.* College Station, Texas, ODP, 915-36).

GIESKES, W.W.C. *and* ELBRÄCHTER, M. 1986. Abundance of nanoplankton-size chlorophyll-containing particles caused by diatom disruption in surface waters of the Southern Ocean (Antarctic Peninsula region). *Netherlands Journal of Sea Research*, **20**, 291-303.

GILSTAD, M. *and* SAKSAHUG, E. 1990. Growth rates of ten diatom species from the Barents Sea at different irradiances and day lengths. *Marine Ecology - Progress Series*, **64**, 169-73.

GLADENKOV, A.Y. 1988. The Paleogene diatom flora of the Komandorsky Islands (The Bering Sea). (*In International symposium on living and fossil diatoms.* Joensuu, Finland, Abstracts, p. 41).

GLIBERT, P.M., BIGGS, D.G. *and* McCARTHY, J.J. 1982. Utilisation of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Research*, **29**, 837-50.

GOES, J.J. *and* DEVASSY, V.P. 1983. Phytoplankton organisms collected during the First Indian Antarctic Expedition. *Scientific Reports of the First Indian Expedition to Antarctica. Technical Publication*, **1**, 198-201.

GOMBOS, A.M. Jr. 1976. Paleogene and Neogene diatoms from the Falkland Plateau and Malvinas Outer Basin: Leg 36, Deep Sea Drilling Project. (*In* BARKER, P.F., DALZIEL, I.W.D. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 36.* Washington, United States Government Printing Office, 575-687).

GOMBOS, A.M. Jr. 1983. Middle Eocene diatoms from the South Atlantic. (*In* LUDWIG, W.J., KRASHENINNIKOV, V.A. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 71.* Washington, United States Government Printing Office, 565-81).

GOMBOS, A.M. Jr. 1984. Late Paleocene diatoms in the Cap Basin. (*In* HSÜ, K.J., LABREQUE, J.L. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 23.* Washington, United States Government Printing Office, 495-511).

GOMBOS, A.M. Jr. *and* CIESIELSKI, P.F. 1983. Late Eocene to early Miocene diatoms from the Southwest Atlantic. (*In* LUDWIG, W.J., KRASHENINNIKOV, V.A. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 71.* Washington, United States Government Printing Office, 583-634).

GORDON, A.L. 1988. Spatial and temporal variability within the Southern Ocean. (*In* SAHRHAGE, D. *ed. Antarctic ocean and resources variability*, Berlin, Springer, 41-56).

GORDON, A.L. *and* NOWLIN, W.D. 1978. The basin waters of the Bransfield Strait. *Journal of Physical Oceanography*, **8**, 258-64.

GORSCHKOV, S.G. 1983. *World Ocean Atlas. Arctic Ocean, 3*, Oxford, Pergamon Press.

GOSSELIN, M., LEGENDRE, L., DEMERS, S. *and* INGRAM, R.G. 1985. Responses of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay). *Canadian Journal of Fisheries and Aquatic Science*, **42**, 999-1006.

GOSSELIN, M., LEGENDRE, C., THERRIAULT, J.-C., DEMERS, S. *and* ROCHET, M. 1986. Physical control of the horizontal patchiness of sea-ice microalgae. *Marine Ecology - Progress Series*, **29**, 289-98.

GRAINGER, E.H. *and* HSIAO, S.I.C. 1982. A study of the ice biota of Frobisher Bay, Baffin Island 1979-1981. *Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 1647*, Arctic Biological Station, Department of Fisheries and Oceans, Canada, ix + 128 pp.

GRAN, H.H., 1897. Bacillariaceen vom kleinen Karajakfjord. *Bibliotheca Botanica*, **42**, 13-24.

GRAN, H.H. 1900. Diatomaceae from the ice-floes and Plankton of the Arctic Ocean. (*In* NANSEN, F. *ed. The Norwegian North-Polar expedition 1893-1896, Scientific Results. Volume IX*, 1-74).

GRAN, H.H., 1904a. Die Diatomeen der arktischen Meere. Diatomeen des Planktons. *Fauna Arctica*, **3**, 511-54.

GRAN, H.H., 1904b. Diatomaceae from the ice-floes and plankton of the Arctic Ocean. *Scientific Results of the Norwegian North Polar Expedition*, **4**(11), 3-74.

GRAN, H.H., 1905. Diatomeen. *Nordisches Plankton, Botanischer Teil*, XIX, 1-146.

GRAN, H.H., 1931. On the conditions for the production of plankton in the sea. *Rapportes et Proces-Verbaux, Conseil Permanent International d'Exploration de la Mer*, **75**, 37-46.

GRANT, W.S. *and* HORNER, R. 1976. Growth responses to salinity variation in four arctic ice diatoms. *Journal of Phycology*, **12**, 180-5.

GRENFELL, T.C. *and* MAYKUT, G.A. 1977. The optical properties of ice and snow in the Arctic Basin. *Journal of Glaciology*, **18**, 445-463.

GRENFELL, T.C. *and* PEROVICH, D.K. 1986. Optical properties of ice and snow in the polar ocean 2: Theoretical calculations. *Proceedings of SPIE - the International Society of Optical Engineering*, **637** (Ocean Optics VIII), 242-52.

GRØNTVED, J. *and* SEIDENFADEN, G. 1938. The Godthaab Expedition 1928. The phytoplankton of the waters west of Greenland. *Meddeleser om Grønland*, **82**(5), 1-380.

GROSSI, S.M. *and* SULLIVAN, C.W. 1985. Sea ice microbial communities. V. The vertical zonation of diatoms in an Antarctic fast ice community. *Journal of Phycology*, **21**, 401-9.

GROSSI, S.M., KOTTMEIER, S.T., MOE, R.L., TAYLOR, G.T. *and* SULLIVAN, C.W. 1987. Sea ice microbial communities. VI. Growth and primary production in bottom ice under graded snow cover. *Marine Ecology-Progress Series*, **35**, 153-64.

GROSSI, S.M., KOTTMEIER, S.T. *and* SULLIVAN, C.W. 1984. Sea ice microbial communities. III. Seasonal abundance of microalgae and associated bacteria, McMurdo Sound, Antarctica. *Microbial Ecology*, **10**, 231-42.

GRUNOW, A. 1884. Die Diatomeen von Franz Josef-Land. *Denkschriften der Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse* **I**, **48**, 53-112.

GRUSOV, E.N. 1977. Seasonal alteration in coastal communities in the Davis Sea. (*In* LLANO, G.A. *ed. Adaptations within Antarctic ecosystems*, Houston, Gulf Publishing Co., 263-78).

GULLIKSEN, B. 1984. Cryopelagic fauna from Svalbard waters. *Sarsia*, **69**, 17-23.

HADA, Y. 1970. The protozoan plankton of the Antarctic and Subantarctic seas. *Japanese Antarctic Research Expedition. Scientific Reports Series E*, **31**, 1-51.

HAJOS, M. (with additional contribution from STRADNER, H.) 1974. Late Cretaceous Archaemonadaceae, Diatomaceae and Silicoflagellatae from the South Pacific Ocean, Deep Sea Drilling Project, Leg 29, Site 275. (*In* KENNETT, J.P., HOUTZ, R.E. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 29.* Washington, United States Government Printing Office, 913-1009).

HAJOS, M. 1976. Upper Eocene and Lower Oligocene Diatomaceae, Archaemonadaceae and Silicoflagellatae in Southwestern Pacific sediments, DSDP Leg 29. (*In* HOLLISTER, C.D., CRADDOCK, C. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 35.* Washington, United States Government Printing Office, 817-84).

HAMNER, W.M., HAMNER, P.P., STRAND, S.W. *and* GILMER, R.W. 1983. Behaviour of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. *Science*, **220**, 433-5.

HANSON, R.B., LOWERY, H.K., SHAFER, D., SOROCCO, R. *and* POPE, D.H. 1983. Microbes in Antarctic waters of the Drake Passage: vertical patterns of substrate uptake, productivity and biomass in January 1980. *Polar Biology*, **2**, 179-188.

HANZLICK, D.J. 1983. *The west Spitsbergen Current: transport, forcing and variability.* Ph.D. Thesis, University of Washington, Seattle, Washington.

HANZLICK, D.J *and* AAGAARD, K. 1980. Freshwater and Atlantic Water in the Kara Sea. *Journal of Geophysical Research*, **85**, 4937-42.

HARDY, A.C. *and* GUNTHER, E.R. 1935. The plankton of the South Georgia whaling grounds and adjacent waters 1926-1927. *Discovery Reports*, **11**, 1-456.

HARGRAVE, B.T. *and* PHILLIPS, G.A. 1986. Dynamics of the benthic food web in St. Georges Bay, southern Gulf of St. Lawrence. *Marine Ecology-Progress Series*, **31**, 277-94.

HARGRAVES, P.E. 1968. *Species composition and distribution of net plankton diatoms in the Pacific Sector of the Antarctic Ocean.* PhD thesis. College of William and Mary, Virginia.

HARRISON, W.G., PLATT, T. *and* IRWIN, B. 1982. Primary production and nutrient assimilation by natural phytoplankton populations of the eastern Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 335-45.

HART, T.J. 1934. On the phytoplankton of the south-west Atlantic and the Bellingshausen Sea. *Discovery Reports*, **8**, 1-268.

HART, T.J. 1937. *Rhizosolenia curvata* Zacharias, an indicator species in the Southern Ocean. *Discovery Reports*, **16**, 113-46.

HART, T.J. 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports*, **21**, 261-356.

HARWOOD, D.M. 1985. Late Neogene climatic fluctuations in the southern high-latitudes: implications of a warm Pliocene and deglaciated Antarctic continent. *South African Journal of Science*, **81**, 239-41.

HARWOOD, D.M. 1986. Diatoms. (*In* BARRETT, P.J. *ed. Antarctic Cenozoic history from the MSSTS-1 drillhole, McMurdo Sound. DSIR Bulletin*, **237**, 69-107).

HARWOOD, D.M. 1988. Upper Cretaceous and Lower Paleocene diatom and silicoflagellate biostratigraphy of Seymour Island, eastern Antarctic Peninsula. (*In* FELDMAN, R. and WOODBURNE, M.O. *eds Geology and paleontology of Seymour Island. Geological Society of America, Memoires*, **169**, 55-129).

HARWOOD, D.M. and GERSONDE, R. 1990. Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 2: Resting spores, Chrysophycean cysts, an endoskeletal dinoflagellate, and notes on the origin of diatoms. *In* BARKER, P.F., KENNETT, J.P., *and others. Proceedings of the ODP, Scientific Results, Leg 113.* College Station, Texas, ODP, 403-26).

HARWOOD, D.M. *and* MARUYAMA, T. 1991. Middle Eocene to Pleistocene diatom biostratigraphy of Southern Ocean sediments from the Kerguelen Plateau. ODP Leg 120. (*In* SCHLICH, R., WISE, S.W., *and others. Proceedings of the ODP, Scientific Results, Leg 120.* College Station, Texas, ODP, in press).

HASLE, G.R. 1964. *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. I. Some marine species of the groups Nitzschiella and Lanceolatae. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskabelig Klasse, New Series*, **16**, 1-48.

HASLE, G.R. 1965a. *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. II. The group Pseudonitzschia. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskabelig Klasse, New Series*, **18**, 1-45.

HASLE, G.R. 1965b. *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. III. The genus *Fragilariopsis*. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I. Matematisk-Naturvidenskabelig, Klasse, New Series*, **21**, 1-49.

HASLE, G.R. 1968. Observations on the marine diatom *Fragilariopsis kerguelensis* (O'Meara) Hust. in the scanning electron microscope. *Norwegian Journal of Botany*, **15**, 205-8.

HASLE, G.R. 1969. An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition, and distribution during the *Brategg* expedition, 1947-1948. *Hvalrådets Skrifter*, **52**, 169 pp.

HASLE, G.R. 1971. *Nitzschia pungiformis* (Bacillariophyceae), a new species of the *Nitzschia seriata* group. *Norwegian Journal of Botany*, **18**, 139-44.

HASLE, G.R. 1972a. *Thalassiosira subtilis* (Bacillariophyceae) and two allied species. *Norwegian Journal of Botany*, **19**, 111-39.

HASLE, G.R. 1972b. *Fragilariopsis* Hustedt as a Section of the Genus *Nitzschia* Hassall. *Beihefte zur Nova Hedwigia*, **39**, 111-19.

HASLE, G.R. 1972c. The distribution of *Nitzschia seriata* Cleve and allied species. *Beihefte zur Nova Hedwigia*, **39**, 171-90.

HASLE, G.R. 1973a. Some marine plankton genera of the diatom family Thalassiosiraceae. *Beihefte zur Nova Hedwigia*, **45**, 1-49.

HASLE, G.R. 1973b. Morphology and taxonomy of *Skeletonema costatum* (Bacillariophyceae). *Norwegian Journal of Botany*, **20**, 109-37.

HASLE, G.R. 1974. Validation of the names of some marine planktonic species of *Nitzschia* (Bacillariophyceae). *Taxon*, **23**, 425-8.

HASLE, G.R. 1975. Some living marine species of the diatom family Rhizosoleniaceae. *Beihefte zur Nova Hedwigia*, **53**, 99-140.

HASLE, G.R. 1976a. The biogeography of some marine planktonic diatoms. *Deep-Sea Research*, **23**, 319-38.

HASLE, G.R. 1976b. Examination of diatom type material: *Nitzschia delicatissima* Cleve, *Thalassiosira miniscula* Kraske, and *Cyclotella nana* Hustedt. *British Phycological Journal*, **11**, 101-10.

HASLE, G.R. 1978. Some *Thalassiosira* species with one central process (Bacillariophyceae). *Norwegian Journal of Botany*, **25**, 77-110.

HASLE, G.R. 1980. Examination of *Thalassiosira* type material: *Thalassiosira minima* and *Thalassiosira delicatula* (Bacillariophyceae). *Norwegian Journal of Botany*, **27**, 167-74.

HASLE, G.R. *and* BOOTH, B.C. 1984. *Nitzschia cylindroformis* sp. nov., a common and abundant nanoplankton diatom of the eastern subarctic Pacific. *Journal of Plankton Research*, **6**, 493-503.

HASLE, G.R. *and* FRYXELL, G.A. 1977a. The genus *Thalassiosira*: some species with a linear areola array. *Beihefte zur Nova Hedwigia*, **54**, 15-66.

HASLE, G.R. *and* FRYXELL, G.A. 1977b. *Thalassiosira conferta* and *T. binata*, two new diatom species. *Norwegian Journal of Botany*, **24**, 239-48.

HASLE, G.R. *and* LANGE, C.B. 1988. Freshwater and brackish water *Thalassiosira* (Bacillariophyceae): taxa with tangentially undulated valves. *Phycologia*, **28**, 120-35.

HASLE, G.R. *and* MENDIOLA, B.R.E. de. 1967. The fine structure of some *Thalassionema* and *Thalassiothrix* species. *Phycologia*, **6**, 107-25.

HASLE, G.R. *and* SEMINA, H.J. 1987. The marine planktonic diatoms *Thalassiothrix longissima* and *Thalassiothrix antarctica* with comments on *Thalassionema* spp. and *Synedra reinboldii*. *Diatom Research*, **2**, 175-92.

HASLE, G.R. *and* SIMS, P.A. 1986. The diatom genera *Stellarima* and *Symbolophora* with comments on the genus *Actinoptychus*. *British Phycological Journal*, **21**, 97-114.

HASLE, G.R. *and* SYVERTSEN, E.E. 1985. An Arctic ice-diatom assemblage. Second International Phycological Congress, Copenhagen, 4-10 August 1985, Book of Abstracts, p. 62.

HASLE, G.R., HEIMDAL, B.R. *and* FRYXELL, G.A. 1971. Morphologic variability in fasciculated diatoms as exemplified by *Thalassiosira tumida* (Janisch) Hasle comb. nov. (*In* LLANO, G.A. *and* WALLEN, I.E. *eds Biology of the Antarctic Seas IV*, Washington, American Geophysical Union, 313-33).

HASLE, G.R., SIMS, P.A. *and* SYVERTSEN, E.E. 1988. Two Recent *Stellarima* species: *S. microtrias* and *S. stellaris* (Bacillariophyceae). *Botanica Marina*, **31**, 195-206.

HAYES, P.K., WHITAKER, T.M. *and* FOGG, G.E. 1984. The distribution and nutrient status of phytoplankton in the Southern Ocean between 20° and 70°W. *Polar Biology*, **3**, 153-65.

HEGSETH, E.N. *and* SAKSHAUG, E. 1983. Seasonal variation in light- and temperature-dependent growth of marine planktonic diatoms in *in situ* dialysis cultures in the Trondheimsfjord, Norway (63°N). *Journal of Experimental Marine Biology and Ecology*, **67**, 199-220.

HEIDEN, H. *and* KOLBE, R.W. 1928. Die marinen Diatomeen der Deutschen Südpolar-Expedition 1901-1903. *Deutsche Südpolar Expedition 1901-1903.*, Berlin, Walter de Gruyter, **8**(5), 450-714.

HEIMDAL, B.R. 1970. Morphology and distribution of two *Navicula* species in Norwegian coastal waters. *Nytt magasin for Botanikk*, **17**, 65-75.

HEIMDAL, B.R. 1974. Composition and abundance of phytoplankton in the Ullsfjord area, North Norway. *Astarte*, **7**, 17-42.

HEIMDAL, B.R. 1983. Phytoplankton and nutrients in the waters north-west of Spitsbergen in the autumn of 1979. *Journal of Plankton Research*, **5**, 901-18.

HELLAND-HANSEN, B. *and* NANSEN, F. 1909. The Norwegian Sea. Its physical oceanography based upon the Norwegian researches 1900-1904. *Report on the Norwegian Fishery and Marine Investigations*. Mallingske, Christiania, **2**, Pt. 1, No. 2, 390 pp.

HENDEY, N.I. 1937. The plankton diatoms of the Southern Seas. *Discovery Reports*, **16**, 151-364.

HENDEY, N.I. 1964. *An introductory account of the smaller algae of British coastal waters - 5, Bacillariophyceae (Diatoms). Fishery Investigations, Series* 4. London, HMSO.

HENTSCHEL, E. 1932. Die biologischen Methoden und das biologische Beobachtungsmaterial der Meteor-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Atlantischen Expedition auf dem Vermessungs- und Forschungsschiff 'Meteor', 1925-27*, **10**, 151-364.

HEWES, C.D., HOLM-HANSEN, O. *and* SAKSHAUG, E. 1985. Alternative carbon pathways at lower trophic levels in the Antarctic food web. (*In* SIEGFRIED, W.R., CONDY, P.R. *and* LAWS, R.M. *eds Antarctic nutrient cycles and food webs.* Berlin, Springer Verlag, 277-83).

HEYWOOD, R.B. 1985. Environmental conditions in the Antarctic Peninsula area of the Southern Ocean during the Anglo-German Joint Biological Expedition, February 1982. *Meeresforschung*, **30**, 220-39.

HEYWOOD, R.B. *and* PRIDDLE, J. 1987. Retention of phytoplankton by an eddy. *Continental Shelf Research*, **7**, 937-55.

HEYWOOD, R.B. *and* WHITAKER, T.M. 1984. The Antarctic marine flora. (*In* LAWS, R.M. *ed. Antarctic ecology*. London, Academic Press, 373-419).

HEYWOOD, R.B., EVERSON, I. *and* PRIDDLE, J. 1985. The absence of krill from the South Georgia zone, winter 1983. *Deep-Sea Research*, **32**, 369-78.

HOBAN, M.A., FRYXELL, G.A. *and* BUCK, K.R. 1980. Biddulphioid diatoms: resting spores in Antarctic *Eucampia* and *Odontella. Journal of Phycology*, **16**, 591-602.

HOLLOWAY, G. 1987. Systematic forcing of large-scale geophysical flows by eddy-topography interaction. *Journal of Fluid Mechanics*, **184**, 463-476.

HOLM-HANSEN, O. 1985. Nutrient cycles in Antarctic marine ecosystems. (*In* SIEGFRIED, W.R., CONDY, P.R. *and* LAWS, R.M., *eds Antarctic nutrient cycles and food webs.* Berlin, Springer-Verlag, 6-10).

HOLM-HANSEN, O. *and* HUNTLEY, M. 1984. Feeding requirements of krill in relation to food resources. *Journal of Crustacean Biology*, **4** (Spec. no. 1), 156-73.

HOLM-HANSEN, O., EL-SAYED, S.Z., FRANCESCHINI, G.A. *and* CUHEL, D. 1977. Primary production and the factors controlling phytoplankton growth in the Antarctic seas. (*In* LLANO, G.A. *ed. Adaptations within Antarctic ecosystems: Proceedings of the third SCAR symposium on Antarctic biology*. Washington, Smithsonian Institution, 11-50).

HOPKINS, T.L. 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. (*In* LLANO, G.A. *and* WALLEN, I.E. *eds Biology of the Antarctic seas, 4*, Washington, DC, American Geophysical Union, 347-362).

HOPKINS, T.S. 1988. The GIN Sea: review of physical oceanography and literature since 1972. SACLANT Undersea Research Centre, SR-124, 190 pp.

HORNER, R. 1976. Sea ice organisms. *Oceanography and Marine Biology Annual Review*, **14**, 167-82.

HORNER, R. 1981. Ecology and productivity of Arctic sea ice diatoms. (*In* ROSS, R. *ed. Proceedings of the Sixth Symposium on Recent and Fossil Diatoms*, Koenigstein, Otto Koeltz, 359-69).

HORNER, R. 1984. Phytoplankton abundance, chlorophyll *a*, and primary productivity in the western Beaufort Sea. (*In* BARNES, P., SCHELL, D.M. *and* REIMNITZ, E. *eds The Alaskan Beaufort Sea: ecosystems and environments*, 295-310).

HORNER, R. 1985. Ecology of sea ice microalgae. (*In* HORNER, R. *ed. Sea ice biota*. Boca Raton, CRC Press, 83-103).

HORNER, R. *and* ALEXANDER, V. 1972. Algal populations in Arctic sea ice: an investigation of heterotrophy. *Limnology and Oceanography*, **17**, 454-58.

HORNER, R. *and* SCHRADER, G.C. 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic*, **35**, 485-503.

HORNER, R., SYVERTSEN, E.E., THOMAS, D.P. *and* LANGE, C. 1988. Proposed terminology and reporting units for sea ice algal assemblages. *Polar Biology*, **8**, 249-53.

HOSHIAI, T. 1969. Ecological observations of the coloured layer of the sea ice at Syowa Station. *Antarctic Record*, **34**, 60-72.

HOSHIAI, T. 1977. Seasonal change of ice communities in the sea ice near Syowa Station Antarctica. (*In* DUNBAR, M.J. *ed. Polar oceans*, Calgary, The Arctic Institute of North America, 307-17).

HOSHIAI, T. 1981. The plant pigments, chlorinity, and pH distribution in the sea ice of the Syowa Station area in 1970. *National Institute of Polar Reserach, JARE Data Reports*, **67**, 1-42.

HOSHIAI, T. *and* FUKUCHI, M. 1981. Sea ice colored by ice algae in a lagoon, Lake Saroma, Hokkaido, Japan. *Antarctic Research*, **71**, 113-30.

HSIAO, S.I.C. 1979a. Sea ice microalgal data from Eclipse Sound, 1976 and 1977. *Fisheries and Marine Science Data Report No. 131*, Arctic Biological Station, Department of Fisheries and Oceans, Canada, iv + 34 pp.

HSIAO, S.I.C. 1979b. Sea ice microalgal data from Eskimo Lakes, 1972 to 1974. *Fisheries and Marine Service Data Report No. 146*, Arctic Biological Station, Department of Fisheries and Oceans, Canada, iv + 43 pp.

HSIAO, S.I.C. 1979c. Phytoplankton and seacie microalgal data from Frobisher Bay, 1971 to 1978. *Fisheries and Marine Service Data Report No. 155*, Arctic Biological Station, Department of Fisheries and Oceans, Canada, iv + 82 pp.

HSIAO, S.I.C. 1980. Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. *Arctic*, **33**, 768-93.

HSIAO, S.I.C. 1983. A checklist of marine phytoplankton and sea ice microalgae recorded from Arctic Canada. *Nova Hedwigia*, **37**, 225-313.

HSIAO, S.I.C., FOY, M.G. *and* KITTLE, D.W. 1977. Standing stock, community structure, species composition, distribution, and primary production of natural populations of phytoplankton in the southern Beaufort Sea. *Canadian Journal of Botany*, **55**, 685-94.

HSIAO, S.I.C., PINKEWYCZ, N., MOHAMMED, A.A. *and* GRAINGER, E. H. 1984. Sea ice biota and under-ice plankton from southeastern Hudson Bay in 1983. *Canadian Data Report of Fisheries and Aquatic Sciences, No. 494*, Arctic Biological Station, Department of Fisheries and Oceans, Canada, iv + 49 pp.

HUFFORD, G.L. 1973. Warm water advection in the southern Beaufort Sea, August - September 1971. *Journal of Geophysical Research*, **78**, 274-9.

HUSTEDT, F. 1930. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. (*In* RABENHORST, L. *ed. Kryptogamen-Flora von Deutschland, Österreichs und der Schweiz*. Leipzig, Akademische Verlagsgesellschaft mbH, 920 pp.).

HUSTEDT, F. 1958. Diatomeen aus der Antarktis und dem Südatlantik. *Deutsche Antarktische Expedition 1938/39*, **2**, 103-91.

IIZUKU, HJ., TANABE, I. *and* MEGURO, H. 1966. Microorganisms in plankton-ice of the Antarctic Ocean. *Journal of General and Applied Microbiology*, **12**, 101-20.

IMBRIE, J. *and* KIPP, N.G. 1971. A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Carribean core. (*In* TUREKIAN, K.K. *ed. The late Cenozoic glacial ages*. Yale University Press, 71-181).

IORIYA, T. *and* KATA, M. 1982. Phytoplankton collection during the FIBEX cruise of the *Umitaka Maru III*, 1980-1981: a preliminary report. *Transactions of the Tokyo University of Fisheries*, **5**, 129-44.

IVERSON, R.L., WHITLEDGE, T.I. *and* GOERING, J.T. 1979. Chlorophyll and nitrate fine structure in the southeastern Bering Sea shelf break front. *Nature*, **281**, 664-6.

JACQUES, G. 1983. Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biology*, **2**, 27-33.

JACQUES, G. *and* HOEPFFNER, N. 1984. Vitesse de sedimentation du phytoplancton neritique subantarctique. *Comptes rendus hebdomadaires des Séances de l'Academies des Sciences, Serie 3*, **299**, 581-4.

JACQUES, G., DESCOLAS-GROS, C., GRALL, J.R. *and* SOURNIA, A. 1979. Distribution du phytoplancton dans la partie antarctique de l'Ocean Indien en fin d'été. *Internationale Revue der Gesamten Hydrobiologie*, **64**, 609-28.

JANSEN, E., SEJRUP, P.H., FJAERAN, T., HALD, M., HOLTEDAHL, H. *and* SKARBOE, O. 1983. Late Weichselian paleoceanography of the southeastern Norwegian Sea. *Norsk Geologisk Tidsskrift*, **63**, 117-46.

JAWORSKI, G.H.M., WISEMAN, S.W. *and* REYNOLDS, C.S. 1988. Variability in sinking rate of the freshwater diatom *Asterionella formosa*: the influence of colony morphology. *British Phycological Journal*, **23**, 167-76.

JOHANNESSEN, O.M., JOHANNESSEN, J.A., SVENDSEN, E., SHUCKMAN, R.A., CAMPBELL, W.J. *and* JOSBERGER, E. 1987a. Ice edge eddies in the Fram Strait marginal ice zone. *Science*, **236**, 427-9.

JOHANNESSEN, J.A., JOHANNESSEN, O.M., SVENDSEN, E., SCHUCKMAN, R., MANLEY, T., CAMPBELL, W.J., JOSBERGER, E.G., SANDVEN, S., GASCARD, J.C., OLAUSSEN, T., DAVIDSON, K., *and* VAN LEER, J. 1987b. Mesoscale eddies in the Fram Strait marginal ice zone during the 1983 and 1984 Marginal Ice Zone Experiments. *Journal of Geophysical Research*, **92**, 6754-772, + plates 7199-202.

JOHANSEN, J.R. *and* FRYXELL, G.A. 1985. The genus *Thalassiosira* (Bacillariophyceae): studies on species occurring south of the Antarctic Convergence Zone. *Phycologia*, **24**, 155-79.

JOHANSEN, J.R., DOUCETTE, G.J. *and* FRYXELL, G.A. 1985. The genus *Thalassiosira* (Bacillariophyceae): morphology of heterovalvate resting spores of *T. scotia*. *American Journal of Botany*, **72**, 1861-70.

JOHNSON, C.M. 1980. Wintertime Arctic sea-ice extremes and the simultaneous atmospheric circulation. *Monthly Weather Review*, **108**, 1782-91.

JOHNSON, T.O. *and* SMITH, W.O. 1985. Sinking rates of natural phytoplankton population of the western Weddell Sea. *Antarctic Journal of the United States*, **20**, 139-40.

JONES, E.P. *and* ANDERSON, L.G. 1986. On the origin of the chemical properties of the Arctic Ocean halocline. *Journal of Geophysical Research*, **91**, 10 759-67.

JONES, G.A. *and* JOHNSON, D.A. 1984. Displaced Antarctic diatoms in Vema Channel sediments: late Pleistocene/Holocene fluctuations in AABW flow. *Marine Geology*, **58**, 165-86.

JOUSÉ, A.P. 1960. Les diatomées des dépots de fond de la partie nord-ouest de l'Ocean Pacifique. *Deep-Sea Research*, **6**, 187-96.

JOUSÉ, A.P. 1962. *Stratigraphic and paleogeographic studies in the Northwest part of the Pacific Ocean*. Izdatel'stvo Akademii Nauk SSRSR, Moscow.

JOUSÉ, A.P. 1967. Diatom floras and the history of the Bering and Okhotsk Seas. (*In* HOPKINS, DM. *ed. The Bering land bridge.* California, Stanford University Press, 369-72).

JOUSÉ, A.P. 1971. Diatoms in Pleistocene sediments from the northern Pacific ocean. (*In* FUNNELL, B.M. *and* RIEDEL, W.R. *eds The micropalaeontology of oceans*. Cambridge, Cambridge University Press, 407-21).

JOUSÉ, A.P., KOROLEVA, G.S. *and* NAGAEVA, G.A. 1962. Diatoms in the surface layer of sediment in the Indian sector of the Atlantic. *Trudy Instituta Okeanologii. Akademiya Nauk, SSSR*, **61**, 20-91.

JOUSÉ, A.P., KOROLEVA, G. *and* NAGAEVA, G. 1963. Stratigraphic and paleogeographic investigations in the Indian sector of the Southern Ocean. *Oceanologial Research Articles, Section X, no.8, Academy of Science USSR*, Moscow, 147-60.

JOUSÉ, A.P., KOZLOVA, O.G. *and* MUCHINA, V.V. 1971. Distribution of diatoms in the surface layer of sediment from the Pacific Ocean. (*In* FUNNELL, B.M. *and* RIEDEL W.R. *eds The micropalaeontology of oceans*. Cambridge, Cambridge University Press, 263-9).

KANAYA, T. *and* KOIZUMI, I. 1966. Interpretation of diatom thanatocoenoses from the North Pacific applied to a study of Core V20-130 (Studies of a deep-sea Core V20-130, Part IV). *Science Reports of the Tohoku University, Second Series (Geology)*, **37**(2), 89-130.

KANEKO, T., ATLAS, R.M. *and* KRICHEVSKY, M. 1977. Diversity of bacterial populations in the Beaufort Sea. *Nature*, **270**, 596-9.

KANEKO, T., ROUBAL, G. *and* ATLAS, R.M. 1978. Bacterial populations in the Beaufort Sea. *Arctic*, **31**, 97-107.

KARSTEN, G. 1905. Das Phytoplankton des Antarktischen Meeres nach dem material der Deutschen Tiefsee-Expedition 1898-1899. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*, **2**(2), 3-136.

KELLOG, D.E. *and* KELLOG, T.B. 1986. Diatom biostratigraphy of sediment cores from beneath the Ross Ice Shelf. *Micropaleontology*, **32**, 74-94.

KELLOG, D.E. *and* KELLOG, T.B. 1987. Microfossil distribution in modern Amundsen Sea sediments. *Marine Micropaleontology*, **12**, 203-22.

KELLOG, D.E. *and* TRUESDALE, R.S. 1979. Ross Sea diatoms: modern assemblage distribution and their relationship to ecological oceanographic, and sedimentary conditions – reply. *Marine Micropaleontology*, **4**, 401-4.

KENNETT, J.P. *and* HODELL, D.A. 1986. Major events in Neogene oxygen isotopic records. *South African Journal of Science*, **82**, 497-8.

KENNETT, J.P. *and* SHACKLETON, N.J. 1976. Oxygen isotopic evidence for the development of the psychrosphere 38 Myr ago. *Nature*, **260**, 513-5.

KERN, J.C. *and* CAREY, A.G. 1983. The faunal assemblage inhabiting seasonal sea ice in the nearshore Arctic Ocean with emphasis on copepods. *Marine Ecology – Progress Series*, **10**, 159-67.

KIEFER, D.A. *and* MITCHELL, B.G. 1983. A simple, steady state description of phytoplankton growth based on absorption cross section and quantum efficiency. *Limnology and Oceanography*, **28**, 770-6.

KILLWORTH, P.D. 1983. Deep convection in the world ocean. *Reviews of Geophysics and Space Physics*, **21**, 1-26.

KILLWORTH, P.D. *and* SMITH, J.M. 1984. A one-and-a-half dimensional model for the Arctic halocline. *Deep-Sea Research*, **31**, 271-93.

KILS, U. 1982. Swimming behaviour, swimming performance and energy balance of Antarctic Krill, *Euphausia superba. BIOMASS Scientific Series*, **3**, 121 pp.

KINDER, T.H., CHAPMAN, D.C. *and* WHITEHEAD, J.A. JR. 1986. Westward intensification of the mean circulation on the Bering Sea shelf. *Journal of Physical Oceanography*, **16**, 1217-29.

KITCHELL, J.A. *and* CLARK, D.L. 1982. Late Cretaceous-Paleogene paleogeography and placocirculation: evidence of north Polar upwelling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **40**, 135-65.

KOCK, K.-H. 1985. Marine habitats.– Antarctic fish. (*In* BONNER, W.N. *and* WALTON, D.W.H. *eds Key environments – Antarctica*, Oxford, Pergamon, 173-192).

KOIKE, I., HOLM-HANSEN, O. *and* BIGGS, D.C. 1986. Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. *Marine Ecology – Progress Series*, **30**, 105-16.

KOIZUMI, I. 1973. The late Cenozoic diatoms of Sites 183-193, Leg 19, Deep Sea Drilling Project. (*In* CREAGER, J.S., SCHOLL, D.W. *and others, Initial reports of the deep sea drilling project. Volume 19*. Washington, United States Government Printing Office, 805-55).

KOIZUMI, I. 1975. Diatom events in late Cenozoic deep sea sequences in the North Pacific. *Journal of the Geological Society of Japan*, **81**, 611-27.

KOIZUMI, I. *and* BURCKLE L.H. 1984. Evaluation of diatom datum planes of the Pacific Neogene. (*In* IKEBE, N. *and* TSUCHI, R. *eds Pacific Neogene datum planes*. University of Tokyo Press, 41-6).

KOPCZYŃSKA, E.E. 1980. Small-scale vertical distribution of phytoplankton in Ezcurra Inlet (Admiralty Bay, South Shetland Islands). *Polish Polar Research*, **1**, 77-96.

KOPCZYŃSKA, E.E. *and* LIGOWSKI, R. 1982. Phytoplankton abundance and distribution in the southern Drake Passage and the Bransfield Strait in February-March 1981 (BIOMASS-FIBEX). *Polish Polar Research*, **3**, 193-202.

KOPCZYŃSKA, E. *and* LIGOWSKI, R. 1985. Phytoplankton composition and biomass distribution in the southern Drake Passage, the Bransfield Strait and the adjacent waters of the Weddell Sea in December 1983 -January 1984 (BIOMASS-SIBEX). *Polish Polar Research*, **6**, 65-77.

KOTTMEIER, S.T., GROSSI, S.M. *and* SULLIVAN, C.W. 1987. Sea ice microbial communities. VIII. Bacterial production in annual sea ice of McMurdo Sound, Antarctic. *Marine Ecology – Progress Series*, **35**, 175-86.

KOTTMEIER, S.T., MUSCAT, A.M., CRAFT, L.L., KASTENDIEK, J.E. *and* SULLIVAN, C.W. 1984. Ecology of sea-ice microalgal communities in McMurdo Sound, Antarctica, in 1983. *Antarctic Journal of the United States*, **19**, 129-31.

KOZLOVA, O.G. 1961. Quantitative content of diatoms in the Indian Ocean sector of the Antarctic. *Akademiya Nauk SSSR*, *Doklady*, **38**, 207-10.

KOZLOVA, O.G. 1962. Specific composition of diatoms in the waters of the Indian sector of Antarctica. *Trudy̆ Instituta Okeonologii. Akademiya Nauk SSSR*, **61**, 3-18.

KOZLOVA, O.G. 1964. *Diatoms of the Indian and Pacific sectors of the Antarctic*. Institute of Oceanology, Academy of Sciences, Moscow. Translated from Russian by the Israel Program for Science Translations (1966). 191 pp.

KOZLOVA, O.G. 1970. Diatoms in suspension and in bottom sediments in the southern Indian and Pacific Oceans. (*In* HOLDGATE, M.W. *ed. Antarctic ecology. Volume 1*. New York, Academic Press, 148-53).

KOZLOVA, O.G. 1971. The main features of diatom and silicoflagellate distribution in the Indian Ocean. (*In* FUNNEL, B.M. *and* RIEDEL, W.R. *eds The micropalaeontology of oceans*. Cambridge, Cambridge University Press, 271-5).

KOZLOVA, O.G. *and* MUCHINA V.V. 1967. Diatoms and silicoflagellates in suspension and floor sediments of the Pacific Ocean. *International Geology Review*, **9910**, 1322-42. (Translated from Geokhimiya Kremnezema, N.K. 65-12(51), 192-218, 1966).

KRANCK, K. *and* MILLIGAN, T.G. 1988. Macroflocs from diatoms: *in situ* photography of particles in Bedford Basin, Nova Scotia. *Marine Ecology – Progress Series*, **44**, 183-9.

KRAVITZ, J.H., BURCKLE, L.H. *and* BROMBLE, S.L. 1987. Distribution of diatoms in the surface sediments of the Kane Basin. *Arctic and Alpine Research*, **19**, 89-94.

KREBS, W.M. 1977. *Ecology and preservation of neritic marine diatoms, Arthur Harbor, Antarctica*. PhD thesis, University of California at Davis.

KREBS, W.M. 1983. Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. *Micropaleontology*, **29**, 267-97.

KREBS, W.M., LIPPS, J.H. *and* BURCKLE, L.H. 1987. Ice diatom floras, Arthur Harbor, Antarctica. *Polar Biology*, **7**, 163-71.

LABRACHERIE, M., ARNOLD, M., PICHON, J.-J. *and* DUPLESSY, J.-C. 1989. The last deglaciation in the Southern Ocean. *Paleoceanography*, **4**, 629-38.

LAKE, R.A. *and* LEWIS, E.L. 1970. Salt rejection by sea ice during growth. *Journal of Geophysical Research*, **75**, 583-97.

LARSEN, L. 1980. Sediment-laden sea ice: concepts, problems and approaches. *Outer Continental Shelf Environmental Assessment Program (NOAA) Arctic Project Bulletin*, **29**, 59-73.

LAWS, R.M. 1985. The ecology of the Southern Ocean. *American Scientist*, **73**, 26-40.

LEBLOND, P.H. 1980. On the surface circulation in some channels of the Canadian Arctic Archipelago. *Arctic*, **30**, 189-98.

LEDBETTER, M.T. 1983. Magnetostratigraphy of middle-upper Miocene and upper middle Eocene sections in Hole 512. (*In* LUDWIG, W.J., KRASHENINNIKOV, V.A. *and others. eds Initial Reports of the Deep Sea Drilling Project. Volume 71*. Washington, United States Government Printing Office, 1093-6).

LEDBETTER, M.T. *and* CIESIELSKI, P.F. 1986. Post-Miocene disconformities and paleoceanography in the Atlantic sector of the Southern Ocean. *Palaeogeography, Palaeclimatology, Palaeoecology*, **52**, 185-214.

LEGECKIS, R. 1977. Ocean polar front in the Drake Passage - satellite observations during 1976. *Deep-Sea Research*, **24**, 701-4.

LEGENDRE, L., INGRAM, R.G. *and* POULIN, M. 1981. Physical control of phytoplankton production under sea ice (Manitounuk Sound, Hudson Bay). *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1385-92.

LEGENDRE, L., INGRAM, R.G. *and* SIMARD, Y. 1982. Aperiodic changes of water column stability and phytoplankton in an arctic coastal embayment, Manitounuk Sound, Hudson Bay. *Naturaliste Canadienne*, **109**, 775-86.

LEGENDRE, L., ROCHET, M. *and* DEMERS, S. 1986. Sea-ice microalgae to test the hypothesis of photosynthetic adaptation to high frequency light fluctuations. *Journal of Experimental Marine Biology and Ecology*, **97**, 321-6.

LEMKE, P. 1987. A coupled one-dimensional sea ice-ocean model. *Journal of Geophysical Research*, **92**, 13 164-72.

LEMKE, P. *and* MANLEY, T.O. 1984. The seasonal variation of the mixed layer and pycnocline under polar ice. *Journal of Geophysical Research*, **89**, 6494-504.

LEVENTER, A. *and* DUNBAR, R.B. 1987. Diatom flux in McMurdo Sound, Antarctica. *Marine Micropaleontology*, **12**, 49-64.

LEVENTER, A. *and* DUNBAR, R.B. 1988. Recent diatom record of McMurdo Sound, Antarctica: Implications for history of sea ice extent. *Paleoceanography*, **3**, 259-74.

LEY, A.C. *and* MAUZERALL, D. 1982. Absolute absorption cross sections for photosystem II and the minimum quantum requirement for photosynthesis in *Chlorella vulgaris*. *Biochimica et Biophysica Acta*, **680**, 95-106.

LIGOWSKI, R. 1982. Phytogenic food of *Euphausia superba* Dana caught in the Southern Drake Passage and the Bransfield Strait, February-March 1981. (BIOMASS-FIBEX). *Polish Polar Research*, **3**, 281-8.

LIGOWSKI, R. 1983. Phytoplankton of the Olaf Prydz Bay (Indian Ocean, East Antarctica) in February 1969. *Polish Polar Research*, **4**, 21-32.

LIGOWSKI, R. 1986. Net phytoplankton of Admiralty Bay (King George Island, South Shetland Islands) in 1983. *Polish Polar Research*, **7**, 127-54.

LIPSKI, M. 1982. The distribution of chlorophyll *a* in relation to the water masses in the southern Drake Passage and the Bransfield Strait (BIOMASS-FIBEX, February-March 1981). *Polish Polar Research*, **3**, 143-52.

LISITZIN, A.P. 1971. Distribution of siliceous microfossils in suspension and in bottom sediments. (*In* FUNNELL, B.M. *and* RIEDEL, W.R. *eds The micropalaeontology of the oceans*. Cambridge, Cambridge University Press, 173-95).

LOENG, H. 1989. Ecological features of the Barents Sea. (*In* REY, L. *and* ALEXANDER, V. *eds Proceedings of the Sixth Conference of the Comité Arctique International 13-15 May 1985*. Leiden, The Netherlands, M.M. Brill, 327-65).

LORENZEN, C.J. *and* WELSCHMEYER, N.A. 1983. The *in situ* sinking rates of herbivore faecal pellets. *Journal of Plankton Research*, **5**, 929-933.

McCOLLUM, D.W. 1975. Diatom stratigraphy of the Southern Ocean. (*In* HAYES, D.E., FRAKES, L.A. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 28*. Washington, United States Government Printing Office, 515-71).

McCONVILLE, M.J. *and* WETHERBEE, R. 1983. The bottom-ice microalgal community from annual ice in the inshore waters of East Antarctica. *Journal of Phycology*, **19**, 431-9.

McCONVILLE, M.J., MITCHELL, C. *and* WETHERBEE, R. 1985. Patterns of carbon assimilation in a microalgal community from annual sea ice, East Antarctica. *Polar Biology*, **4**, 135-41.

McCOY, F.W. *and* SANCETTA, C. 1985. North Pacific sediments. (*In* NAIRN, A.E.M., STEHLI, F.G. *and* UYEDA, S. *eds The ocean basins and margins. Volume 7a: The Pacific Ocean*. New York, Plenum, 1-64).

McROY, C.P *and* GOERING, J.T. 1974. The influence of ice on the productivity of the Bering Sea. (*In* HOOD, D. *and* KELLEY, E. *eds. The oceanography of the Bering Sea*. Fairbanks, University of Alaska, 403-21).

MACAULAY, M.C., ENGLISH, T.S. *and* MATHISEN, O.A. 1984. Acoustic characterization of swarms of Antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait. *Journal of Crustacean Biology*, **4**, (Spec. no.1) 16-44.

MACDONALD, R.W., CARMACK, E.C., McLAUGHLIN, F.A., BRIAN, M.O., *and* PAPADAKIS, J.E. 1987. Modification of Arctic water properties in the Mackenzie Shelf/Estuary II. Water mass composition. *Journal of Geophysical Research*, **92**, 2934-52.

MAESTRINI, S.Y, ROCHET, M., LEGENDRE, L. *and* DEMERS, S. 1986. Nutrient limitation of the bottom-ice microalgal biomass (Southeastern Hudson Bay, Canadian Arctic). *Limnology and Oceanography*, **31**, 969-82.

MAMAEVA, N.V. 1986. Composition and distribution of planktonic infusorians in the Pacific sector of the Antarctic. *Soviet Journal of Marine Biology*, **12**, 17-20.

MANDELLI, E.F. *and* BURKHOLDER, P.R. 1966. Primary productivity in the Gerlache and Bransfield Straits of Antarctic. *Journal of Marine Research*, **24**, 15-27.

MANGIN, L. 1914. Sur le polymorphisme de certaines diatomées de l'Antarctique. *Compte rendu hebdomadaire des Séances de l'Académie des Sciences*, **159**, 476-84.

MANGIN, L. 1915. Phytoplancton de l'Antarctique. *Deuxième Expédition Antarctique Française (1908-1910) commandée par le Dr. Jean Charcot. Sciences naturelles: documents scientifiques*, **18**, 1-95.

MANGIN, L. 1917. Sur le *Chaetoceros criophilus* Castr., espèce charactéristique des mers antarctiques. *Compte rendu hebdomadaire des Séances de l'Académie des Sciences*, **164**, 704-9.

MANGIN, L. 1922. Phytoplancton antarctique. Expédition antarctique de la "Scotia" 1902-1904 dirigée par Sir William S. Bruce LLD. *Mémoires de l'Académie des Sciences (de l'Institut de France)*, **57**, 134.

MANGUIN, É. 1954. Diatomées marines provenant de l'Ile Heard (Australian National Antarctic Research Expedition). *Revue Algologique, n.s.*, **1**, 14-24.

MANGUIN, É. 1957. Premier inventaire des Diatomées de la Terre Adélie Antarctique. Espècies nouvelles. *Revue Algologique, n.s.*, **3**, 111-34.

MANGUIN, É. 1960. Les diatomées de la Terre Adélie Campagne du "Commandant Charcot" 1949-1950. *Annales des Sciences Naturelles, Botanique, Series 12*, **1**, 223-363.

MANN, A. 1937. Diatoms. *Australasian Antarctic Expedition 1911-14, Scientific Reports Series C*, **1**(10), 1-82.

MANN, D.G. 1978. *Studies in the Family Nitzschiaceae (Bacillariophyceae)*. PhD thesis. University of Bristol.

MARCHANT, H.J. 1985. Choanoflagellates in the Antarctic marine food chain. (*In* SIEGFRIED, W.R., CONDY, P.R. *and* LAWS, R.M. *eds Antarctic nutrient cycles and food webs*. Berlin, Springer, 277-283).

MARCHANT, H.J., DAVIDSON, A.T. *and* WRIGHT, S.W. 1987. The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. *Proceedings of the NIPR Symposium on Polar Biology*, **1**, 1-9.

MARIN, V. 1988. Qualitative models of the life-cycles of *Calanoides acutus, Calanus propinquus* and *Rhincalanus gigas*. *Polar Biology*, **8**, 439-46.

MARRA, J. 1978. Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Marine Biology*, **46**, 203-8.

MARRA, J., BURCKLE, L.H. *and* DUCKLOW, H.W. 1982. Sea ice and water column plankton distributions in the Weddell Sea in late winter. *Antarctic Journal of the United States*, **17**, 111-2.

MARSCHALL, H.-P. 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. *Polar Biology*, **9**, 129-35.

MARTIN, J.H. *and* FITZWATER, S.E. 1988. Iron deficiency limits phytoplankton growth in the northeast Pacific Subarctic. *Nature*, **331**, 341-3.

MARTIN, J.H. *and* GORDON, R.M. 1988. Northeast Pacific iron distribution in relation to phytoplankton productivity. *Deep-Sea Research*, **35**, 177-96.

MARTIN, J.H. *and* KNAUER, G.A. 1963. The elemental composition of plankton. *Geochimica et Cosmochimica Acta*, **37**, 1639-53.

MARTIN, J.H., GORDON, R.M. *and* FITZWATER, S.E. 1990. Iron in Antarctic waters. *Nature*, **345**, 156-8.

MARTINEZ MACCHIAVELLO, J.C. 1973. Caracteristicas teratologicas en *Coscinodiscus bouvet* en Puerto Paraiso y Estrecho de Bismark, Antartida. *Contribuciónes del Instituto Antárctico Argentino*, **169**, 9 pp.

MARUMO, R. 1953. On the plankton diatoms of the Antarctic Ocean in summers from 1946 to 1952. *Records of Oceanographic Works, Japan*, **1**(2), 55-9.

MARUMO, R. 1957. The surface distribution of plankton diatoms in the western part of the Pacific Ocean and in the Antarctic Ocean in 1954-1955. *Oceanographical Magazine (Tokyo)*, **9**, 143-7.

MATHEKE, G.E.M. *and* HORNER, R. 1974. Primary productivity of the benthic microalgae in the Chukchi Sea near Barrow, Alaska. *Journal of the Fisheries Research Board of Canada*, **31**, 1779-86.

MATSUDA, O., ISHIKAWA, S. *and* KAWAGUCHI, K. 1987. Seasonal variation of downward flux of particulate organic matter under the Antarctic fast ice. *Proceedings of the NIPR Symposium on Polar Biology*, **1**, 23-34.

MAY, R.M., BEDDINGTON, J.R., CLARK, C.W., HOLT, S.J. *and* LAWS, R.M. 1979. Management of multispecies fisheries. *Science*, **205**, 267-77.

MAYKUT, G.A. 1985. *An introduction to ice in the polar oceans. Report APL-UW 8510*. Department of Atmospheric Sciences/Geophysics Program, University of Washington, Seattle, U.S.A.

MEDLIN, L.K. *and* HASLE, G.R. 1990. Some *Nitzschia* and related diatom species from fast ice samples in the Arctic and Antarctic. *Polar Biology*, **10**, 451-79.

MEDLIN, L.K. *and* ROUND, F.E. 1986. Taxonomic studies of marine gomphonemoid diatoms. *Diatom Research*, **1**, 205-25.

MEGURO, H. 1962. Plankton ice in the Antarctic Ocean. *Antarctic Record*, **14**, 72-9.

MEGURO, H., ITO, K. *and* FUKUSHIMA, H. 1966. Diatoms and the ecological conditions of their growth in sea ice in the Arctic Ocean. *Science*, **152**, 1089-90.

MEGURO, H., ITO, K. *and* FUKUSHIMA, H. 1967a. Ice flora (bottom type): a mechanism of primary production in polar seas and the growth of diatoms in sea ice. *Arctic*, **20**, 114-33.

MEGURO, H., ITO, K. *and* FUKUSHIMA, H. 1967b. Bottom type "plankton ice" in the Arctic ocean. *Antarctic Record*, **28**, 33-47.

MELLING, H. *and* LEWIS, E.L. 1982. Shelf drainage flows in the Beaufort Sea and their effect on the Arctic Ocean pycnocline. *Deep-Sea Research*, **29**, 967-85.

MELLING, H., LAKE, R.A., TOPHAM, D.R. *and* FISSEL, D.B. 1984. Oceanic thermal structure in the western Canadian Arctic. *Continental Shelf Research*, **3**, 233-58.

MEL'NIKOV, I.A. *and* BONDARCHUK, L.L. 1987. Ecology of mass accumulations of diatom algae under drifting Arctic ice. *Oceanology*, **27**, 233-36.

MEYER, M.A. *and* EL-SAYED, S.Z. 1983. Grazing of *Euphausia superba* Dana on natural phytoplankton populations. *Polar Biology*, **1**, 193-7.

MILLER, D.G.M., HAMPTON, I., HENRY, J., ABRAMS, R.W. *and* COOPER, J. 1985. The relationship between krill food requirements and phytoplankton production in a sector of the southern Indian Ocean. (*In* SIEGFRIED, W.R., CONDY, P.R. *and* LAWS, R.M. *eds Antarctic nutrient cycles and food webs*, Berlin, Springer, 362-371).

MILLER, K.G., FAIRBANKS, R.G. *and* MOUNTAIN, G.S. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. *Paleoceanography*, **2**(2), 1-19.

MIZROCH, S.A., RICE, D.W., BENGTSON, J.L. *and* LARSON, S.W. 1985. Preliminary atlas of balaenopterid whale distribution in the Southern Ocean based on pelagic catch data. *CCAMLR Scientific Committee*, Report SC-CAMLR-IV/BG/21, 9 pp.

MOORE, R.M. *and* WALLACE, D.W.R. 1988. A relationship between heat transfer to sea ice and temperature-salinity properties of Arctic Ocean waters. *Journal of Geophysical Research*, **93**, 565-71.

MORECKI, V.N. 1965. Underwater sea ice. *Problems in the Arctic and Antarctic*, **19**, 32-8. (In Russian. Translation T497 R, 1968, Defence Research Board of Canada).

MORISON, J.H. *and* SMITH, J.D. 1981. Seasonal variations in the upper Arctic Ocean as observed at T-3. *Geophysics Research Letters*, **8**, 753-6.

MORK, M. 1981. Experiments with theoretical models of the Norwegian Coastal Current. (*In* SAETRE, R. *and* MORK, M. *eds The Norwegian coastal current*. Norway, University of Bergen, 518-30).

MORRIS, D.J. 1984. Filtration rates of *Euphausia superba* Dana: under- or over-estimates? *Journal of Crustacean Biology*, **4** (special issue number 1), 185-197.

MORRIS, D.J. *and* PRIDDLE, J. 1984. Observations on the feeding and moulting of the Antarctic Krill, *Euphausia superba* Dana, in winter. *British Antarctic Survey Bulletin* , **65**, 57-63.

MORTAN-BERTRAND, A. 1988. Photosynthetic metabolism of an Antarctic diatom and its physiological responses to fluctuations in light. *Polar Biology*, **9**, 53-60.

MORTAN-BERTRAND, A. 1989. Effects of light fluctuations on the growth and productivity of Antarctic diatoms in culture. *Polar Biology*, **9**, 245-52.

MOTODA, S. *and* MINODA, T. 1974. Plankton of the Bering Sea. (*In* HOOD, D.W. *and* KELLEY, E.J. *eds Oceanography of the Bering Sea*, **8**, 207-41).

MOUNTAIN, D.G. 1974. *Bering Sea Water on the North Alaskan Shelf*. Ph.D. thesis. University of Washington, Seattle.

MULLINS, B.W. *and* PRIDDLE, J. 1987. Relationships between bacteria and phytoplankton in the Bransfield Strait and Southern Drake Passage. *British Antarctic Survey Bulletin*, **76**, 51-64.

MURPHY, E.J., MORRIS, D.J., WATKINS, J.L. *and* PRIDDLE, J. 1988. Scales of interaction between Antarctic Krill and the environment. (*In* SAHRHAGE, D. *ed. Antarctic ocean and resources variability*, Berlin, Springer, 120-130).

NANSEN, F. 1906a. Northern waters: Captain Roald Amundsen's oceanographic observations in the Arctic seas in 1901. *Videnskabs-Selskabets Skrifter*. I. Mathematisk-Naturvitenskapelig Klasse, 1906, Dybwad, Christiania, **1**(3), 145 pp.

NANSEN, F. 1906b. Protozoa on the ice-floes of the North Polar Sea. *Scientific Results of the Norwegian North Polar Expedition*, **5**(16), 1-22.

NEORI, A. *and* HOLM-HANSEN, O. 1982. Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. *Polar Biology*, **1**, 33-8.

NEUMANN, G. *and* PIERSON, W.J. 1966. *Principles of Physical Oceanography*. Englewood Cliffs, NJ, USA, Prentice-Hall Inc.

NEWBURY, T. 1986. Sea ice and oceanographic conditions. *Oceanus*, **29**, 24-30.

NEWTON, J.L. 1973. *The Canada Basin: mean circulation and intermediate scale flow features*. Ph.D. Thesis. University of Washington, Seattle, 158 pp.

NIEBAUER, H.J *and* ALEXANDER, V. 1989. Current perspectives on the role of ice margins and polynyas in high latitude ecosystems.

(*In* REY, L. *and* ALEXANDER, V. *eds Proceedings of the Sixth Conference of the Comité Arctique International 13-15 May 1985.* Leiden, The Netherlands, M.M. Brill, 121-44).

NIEBAUER, H.J., ALEXANDER, V. *and* COONEY, R.T. 1981. Primary production in the eastern Bering Sea ice edge: the physical and biological regimes. (*In* HOOD, D.W. *and* CALDER, J.A. *eds The eastern Bering Sea shelf: oceanography and resources*, Seattle, University of Washington Press, 763-72).

NÖTHIG, E.-M. 1988. Untersuchungen zur Ökologie des Phytoplanktons im südöstlichen Weddellmeer (Antarktis) im Januar/Februar 1985. *Berichte zur Polarforschung*, **53**, 118 pp.

NOWLIN, W.D. *and* KLINCK, J.M. 1986. The physics of the Antarctic Circumpolar Current. *Reviews of Geophysics*, **24**, 469-91.

OKUNO, H. 1951. Electron-microscopical study on Antarctic diatoms I. *Journal of Japanese Botany*, **26**, 305-10.

OKUNO, H. 1952a. Electron-microscopical study on Antarctic diatoms II. *Journal of Japanese Botany*, **27**, 46-52.

OKUNO, H. 1952b. Electron-microscopical study on Antarctic diatoms III. *Journal of Japanese Botany*, **27**, 347-56.

OKUNO, H. 1952c. Electron-microscopical study on Antarctic diatoms IV. *Journal of Japanese Botany*, **28**, 171-8.

OKUNO, H. 1952d. Electron-microscopical study on Antarctic diatoms V. *Journal of Japanese Botany*, **29**, 18-32.

OKUNO, H. 1952e. Electron-microscopical study on Antarctic diatoms VI. *Journal of Japanese Botany*, **29**, 271-7.

O'MEARA, E. 1874. On diatomaceae from Spitzbergen. *Quarterly Journal of Microscopical Sciences*, **14**, 254-61.

ONO, N. 1967. Specific heat and heat of fusion of sea ice. (*In* OURA, H. *ed. Physics of snow and ice, Volume 1.* International Conference on Low Temperature Science, 14-19 August 1966, Sapporo, Japan, 599-610).

OSBORNE, N.I., CIESIELSKI, P.F. *and* LEDBETTER, M.T. 1983. Disconformities and paleoceanography in the southeast Indian Ocean during the past 5.4 million years. *Bulletin of the Geological Society of America*, **94**, 1345-58.

OSTLAND, H.G. 1982. The residence time of the fresh water component in the Arctic Ocean. *Journal of Geophysical Research*, **87**, 2035-43.

ØSTRUP, E. 1895. Marine Diatoméer fra Østgrønland. *Meddelelser om Grønland*, **18**, 397-476.

OVERLAND, F.E. *and* ROACH, A.T. 1987. Northward flow in the Bering and Chukchi Sea. *Journal of Geophysical Research*, **92**, 7097-105.

PAASCHE, E. 1980. Silicon (*In* MORRIS, I. *ed. Physiological ecology of phytoplankton*. Oxford, Blackwell, 259-84).

PADDOCK T.B.B. 1988. *Plagiotropis* Pfitzer and *Tropidoneis* Cleve, a summary account. *Bibliotheca Diatomologica*, **16**, 1-152.

PADDOCK T.B.B. *and* SIMS, P.A. 1977. A preliminary survey of the raphe structure of some advanced groups of diatoms (Epithemiaceae – Surirellaceae). *Beihefte zur Nova Hedwigia*, **54**, 291-322.

PADDOCK T.B.B. *and* SIMS, P.A. 1981. A morphological study of keels of various raphe-bearing diatoms. *Bacillaria*, **4**, 177-222.

PADDOCK T.B.B. *and* SIMS, P.A. 1990. Micromorphology and evolution of the keels of raphe-bearing diatoms (*In* CLAUGHER, D. *ed. Scanning electron microscopy in taxonomy and functional morphology*, Systematics Association special volume **41**, Oxford, Clarendon Press, in press).

PAINTING, S.J., LUCAS, M.I. *and* STENTON-DOZEY, J.M.E. 1985. The South African SIBEX I cruise to the Prydz Bay region, 1984. X, Biomass and production of bacterioplankton in Prydz Bay, Antarctica, and phytoplankton, detritus and bacterial relationships. *South African Journal of Antarctic Research*, **15**, 42-52.

PALMISANO, A.C. *and* SULLIVAN, C.W. 1982. Physiology of sea ice diatoms. I. Response of three polar diatoms to a simulated summer-winter transition. *Journal of Phycology*, **18**, 489-98.

PALMISANO, A.C. *and* SULLIVAN, C.W. 1983. Sea ice microbial communities (SIMCO) I. Distribution, abundance, and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. *Polar Biology*, **2**, 171-7.

PALMISANO, A.C. *and* SULLIVAN, C.W. 1985a. Pathways of photosynthetic carbon assimilation in sea-ice microalgae from McMurdo Sound, Antarctica. *Limnology and Oceanography*, **30**, 674-8.

PALMISANO, A.C. *and* SULLIVAN, C.W. 1985b. Physiological response of micro-algae in the ice-platelet layer to low-light conditions. (*In* SIEGFRIED, W.R., CONDY, P.R. and LAWS, R.M. *eds Antarctic nutrient cycles and food webs*, Berlin, Springer-Verlag, 84-8).

PALMISANO, A. C., KOTTMEIER, S.T., MOE, R.L. *and* SULLIVAN, C.W. 1985. Sea ice microbial communities. IV. The effect of light perturbation on microalgae at the ice-seawater interface in McMurdo Sound, Antarctica. *Marine Biology-Progress Series*, **21**, 37-45.

PALMISANO, A.C., SOOHOO, J.B., MOE, R.L. *and* SULLIVAN, C.W. 1987a. Sea ice microbial communities. VII. Changes in under-ice spectral irradiance during the development of Antarctic sea ice microalgal communities. *Marine Ecology – Progress Series*, **35**, 165-73.

PALMISANO, A.C., SOOHOO, J.B., MOE, R.L. *and* SULLIVAN, C.W. 1987b. Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae. *Marine Biology*, **94**, 299-306.

PALMISANO, A.C., SOOHOO, J.B., SOOHOO, S.L., KOTTMEIER, S.T., CRAFT, L.L. *and* SULLIVAN, C.W. 1986. Photoadaptation in *Phaeocystis pouchetii* advected beneath annual sea ice in McMurdo Sound, Antarctica. *Journal of Plankton Research*, **8**, 891-906.

PAQUETTE, R.G. *and* BOURKE, R.H. 1974. Observations on the coastal current of Arctic Alaska. *Journal of Marine Research*, **32**, 195-207.

PAQUETTE, R.G., BOURKE, R.H., NEWTON, J.F. *and* PERDUE, W.F. 1985. The east Greenland Polar front in autumn. *Journal of Geophysical Research*, **90**, 4866-82.

PARKINSON, C.L., COMISO, J.C., ZWALLY, H.J., CAVALIERI, D.J., GLOERSON, P. *and* CAMPBELL, W.J. 1987. *Arctic sea ice, 1973-1976. NASA SP-489.* Washington, DC, National Aeronautics and Space Administration Scientific and Technical Information Branch.

PATRICK, R. *and* REIMER, C.W. 1966, 1975. The diatoms of the United States exclusive of Alaska and Hawaii. *Monographs of the Academy of Natural Sciences of Philadelphia*, **13**, Parts 1 and 2(1).

PAYNE, M.R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London*, **B 279**, 67-79.

PERAGALLO, M. 1921. Diatomées d'eau douce et diatomées d'eau salée. (*In Deuxième Expedition Antarctique Française (1908-1910) commandée par le Dr. Jean Charcot. Sciences naturelles: documents scientifiques.* Paris, Masson 103 pp.).

PERAGALLO, J. 1924. Diatomées. (*In Expedition Antarctique Française (1903-1905). Sciences naturelles, documents scientifiques.* Paris, Masson 5-27).

PERKIN, R.G. *and* LEWIS, E.L. 1984. Mixing in the West Spitzbergen Current. *Journal of Physical Oceanography*, **14**, 1315-25.

PEROVICH, D.K., MAYKUT, G.A. *and* GRENFELL, T.C. 1986. Optical properties of ice and snow in the polar oceans 1: observations. *Proceedings of SPIE -the International Society for Optical Engineering*, **637** (Ocean Optics VII), 232-41.

PERRIN, R.A., LU, P. *and* MARCHANT, H.J. 1987. Seasonal variation in marine phytoplankton and ice algae at a shallow Antarctic coastal site. *Hydrobiologia*, **146**, 33-46.

PETIT, M. 1908. Diatomacées. (*In Expedition Antarctique Française (1903-1905). Sciences naturelles, documents scientifiques.* Paris, Masson, 1-3).

PETT, R.J., VICKERS, G.P., ACREMAN, J.C. *and* ETHIER, A.G. 1983. *A seasonal study of the epontic and planktonic communities near the Issungnak Artificial Island and McKinley Bay in the Canadian Beaufort Sea.* Report for Department of Supply and Services Canada, Sydney, Arctic Laboratories Ltd., xi + 89 pp.

PFIRMAN, S.L. 1985. *Modern sedimentation in the Northern Barents Sea: Input dispersal and deposition of suspended sediments from glacial meltwater.* PhD. thesis, Woods Hole Oceanographic Institution, Woods Hole, Mass.

PICHON, J.J., LABRACHERIE, M., LABEYRIE, L.D. *and* DUPRAT, J. 1987. Transfer functions between diatom assemblages and surface hydrology in the Southern Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 79-95.

PICKARD, G.L. *and* EMERY, W.J. 1982. *Descriptive physical oceanography: an introduction.* 4th edition. Oxford, Pergamon.

PLATT T., HARRISON, W.G., IRWIN, B., HORNE, E.P. *and* GALLEGOS, C.L. 1982. Photosynthesis and photoadaptation of marine phytoplankton in the Arctic. *Deep-Sea Research*, **29**, 1159-70.

POST, E.F., DUBINSKY, Z., WYMAN, K. *and* FALKOWSKI, P.G. 1984. Kinetics of light-intensity adaptation in a marine plankton diatom. *Marine Biology*, **83**, 231-8.

POULIN, M. 1990a. Sea ice diatoms (Bacillariophyceae) of the Canadian Arctic. I. The genus *Stenoneis*. *Journal of Phycology*, **26**, 156-67.

POULIN, M. 1990b. Sea ice diatoms (Bacillariophyceae) of the Canadian Arctic. 2. A taxonomic, morphological and geographical study of *Gyrosigma concilians* (Cleve) Okolodkov. *Nordic Journal of Botany*, **18**, in press.

POULIN, M. *and* CARDINAL, A. 1982a. Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebec, Canada). I. Family Naviculaceae. *Canadian Journal of Botany*, **60**, 1263-78.

POULIN, M. *and* CARDINAL, A. 1982b. Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebec, Canada). II. Naviculaceae, genus *Navicula*. *Canadian Journal of Botany*, **60**, 2825-45.

POULIN, M. *and* CARDINAL, A. 1983. Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebec, Canada). III. Cymbellaceae, Entomoneidaceae, Gomphonemataceae, and Nitzschiaceae. *Canadian Journal of Botany*, **61**, 107-18.

POULIN, M., CARDINAL, A. *and* LEGENDRE, L. 1983. Réponse d'une communauté de diatomées de glace à un gradient de salinité (Baie d'Hudson). *Marine Biology*, **76**, 191-202.

PRIDDLE, J. 1985. Species composition of net phytoplankton from Drake Passage, Bransfield Strait and Scotia Sea during summer, 1982. *Meeresforschung*, **30**, 240-50.

PRIDDLE, J. *and* FRYXELL, G. 1985. *Handbook of the Common Plankton Diatoms of the Southern Ocean: Centrales except the Genus* Thalassiosira. Cambridge, British Antarctic Survey.

PRIDDLE, J. *and* THOMAS, D.P. 1989. *Coscinodiscus bouvet* Karsten – a distinctive diatom which may be an indicator of changes in the Southern Ocean. *Polar Biology*, **9**, 161-7.

PRIDDLE, J., CROXALL, J.P., EVERSON, I., HEYWOOD, R.B., MURPHY, E.J., PRINCE, P.A. *and* SEAR, C.B. 1988. Large-scale fluctuations in distribution and abundance of krill – a discussion of possible causes. (*In* SAHRHAGE, D. *ed. Antarctic ocean and resources variability*, Berlin, Springer, 169-182).

PRIDDLE, J., HAWES, I., ELLIS-EVANS, J.C. *and* SMITH, T.J. 1986. Antarctic aquatic ecosystems as habitats for phytoplankton. *Biological Reviews*, **61**, 199-238.

PRIDDLE, J., HEYWOOD, R.B. *and* THERIOT, E. 1986. Some environmental factors influencing phytoplankton in the Southern Ocean around South Georgia. *Polar Biology*, **5**, 65-79.

PRIDDLE, J., WATKINS, J.L., MORRIS, D.J., RICKETTS, C. *and* BUCHHOLZ, F. 1990. Variation of feeding by krill in swarms. *Journal of Plankton Research*, **12**, 1189-205.

PRINSENBERG, S.J. *and* BENNETT, E.B. 1987. Mixing and transports in Barrow Strait, the central part of the Northwest Passage. *Continental Shelf Research*, **7**, 913-35.

PROBYN, T.A. *and* PAINTING, S.J. 1985. Nitrogen uptake by size – fractionated phytoplankton populations in Antarctic surface waters. *Limnology and Oceanography*, **30**, 1327-32.

QUADFASEL, D., GASCARD, J.C., *and* KOLTERMANN, K.P. 1987. Large scale oceanography in Fram Strait during the 1984 Marginal Ice Zone Experiment. *Journal of Geophysical Research*, **92**, 6719-28.

QUADFASEL, D., RUDELS, B. *and* KURZ, K. 1988. Outflow of dense water from a Svalbard fjord into Fram Strait. *Deep-Sea Research*, **35**, 1143-50.

RAMSFJELL, E. 1960. Phytoplankton distribution in the Norwegian Sea in June, 1952 and 1953. *Report on Norwegian Fishery and Marine Investigation*, **12**(10), 1-112.

REID, F.M.H. *and* ROUND, F.E. 1987. The Antarctic diatom *Synedra reinboldii*: taxonomy, ecology and transference to a new genus *Trichotoxon*. *Diatom Research*, **2**, 219-27.

REIMNITZ, E. *and* KEMPEMA, E.W. 1987. Field observations of slush ice generated during freeze-up in Arctic coastal waters. *Marine Geology*, **77**, 219-31.

REIMNITZ, E., KEMPEMA, E.W. *and* BARNES, P.W. 1987. Anchor ice, seabed freezing and sediment dynamics in shallow Arctic seas. *Journal of Geophysical Research*, **92**, 14671-8.

REINKE, M. 1987. Zur Nahrungs- und Bewegungsphysiologie von *Salpa thompsoni* und *Salpa fusiformis*. *Berichte zur Polarforschung*, **36**, 89 pp.

REY, F. *and* LOENG, H. 1985. The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. (*In* GRAY, J.S. *and* CHRISTIANSEN, M.E. *eds Marine biology of polar regions and effects of stress on marine organisms.* New York, John Wiley and Sons, 49-63).

RILEY, G.A. 1963. Theory of food chain relations in the ocean. (*In* HILL, M.N. *ed. The sea, volume 2.* New York, John Wiley and Sons, 438-63).

RIVERA RAMIREZ, P. 1981. Beiträge zur Taxonomie und Verbreitung der Gattung *Thalassiosira* Cleve (Bacillariophyceae) in den Küstengewässern Chiles. *Bibliotheca Phycologica*, **56**, 1-225.

RIVERA, P. 1983. A guide for references and distribution for the class Bacillariophyceae in Chile between 18°25'S and 58°S. *Bibliotheca Diatomologica*, **3**, 386 pp.

ROCHET, M., LEGENDRE, L. *and* DEMERS, S. 1985. Acclimation of sea-ice microalgae to freezing temperature. *Marine Ecology – Progress Series*, **24**, 187-91.

RÖNNER, U., SORENSSON, F. *and* HOLM-HANSEN, O. 1983. Nitrogen assimilation by phytoplankton in the Scotia Sea. *Polar Biology*, **2**, 137-47.

ROSENBERG, A.A., BEDDINGTON, J.R. *and* BASSON, M. 1986. Growth and longevity of krill during the first decade of pelagic whaling. *Nature*, **324**, 152-154.

ROSS, R.M. *and* QUETIN, L.B. 1986. How productive are Antarctic krill? *BioScience*, **36**, 264-9.

ROUND, F.E., CRAWFORD, R.M. *and* MANN, D.G. 1990. *The diatoms. Biology and morphology of the genera.* Cambridge, Cambridge University Press.

RUDELS, B. 1987a. *On the exchange of water masses between the Polar Ocean and the North Atlantic.* Ph.D. thesis, University of Gothenburg.

RUDELS, B. 1987b. On the mass balance of the Polar Ocean, with special emphasis on the Fram Strait. *Norsk Polarinstitutt Skrifter*, **188**, 53 pp.

RUNGE, J.A. and INGRAM, R.G. 1988. Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. *Limnology and Oceanography*, **33**, 280-6.

SAAR, A. DU *and* WOLF, H. DE 1973. Marine diatoms of sediment core from Breid Bay and Brekilen, Antarctica. *Netherlands Journal of Sea Research*, **6**, 339-54.

SAITO, K. *and* TANIGUCHI, A. 1978. Phytoplankton communities in the Bering Sea and adjacent seas. II. Spring and summer communities in seasonally ice-covered areas. *Astarte*, **11**, 27-35.

SAKSHAUG, E. 1989. The physiological ecology of polar phytoplankton. (*In* REY, L. *and* ALEXANDER, V. *eds Proceedings of the 6th conference of the Comité Artique International.* Leiden, The Netherlands, E.J. Brill, 61-89).

SAKSHAUG, E. *and* ANDRESEN, K. 1986. Effect of the light regime upon growth rate and chemical composition of a clone of *Skeletonema costatum* from the Trondheimsfjord, Norway. *Journal of Plankton Research*, **8**, 619-37.

SAKSHAUG, E. *and* HOLM-HANSEN, O. 1984. Factors governing pelagic production in polar oceans. (*In* HOLM-HANSEN, O., BOLIS, L. *and* GILLES, R. *eds Marine phytoplankton and productivity. Lecture notes on coastal and estuarine studies, volume 8.* Berlin, Springer Verlag, 1-18).

SAKSHAUG, E. *and* HOLM-HANSEN, O. 1986. Photoadaption in Antarctic phytoplankton: variations in growth rate, chemical composition, and P vs I curves. *Journal of Plankton Research*, **8**, 459-73.

SAKSHAUG, E., DEMERS, S. *and* YENTSCH, C.M. 1987. *Thalassiosira oceanica* and *T. pseudonana*: two different photoadaptational responses. *Marine Ecology – Progress Series*, **41**, 275-82.

SAKSHAUG, E., ANDRESEN, K. *and* KIEFER, D.A. 1989. A steady-state description of growth and light absorption in the marine plankton diatom *Skeletonema costatum*. *Limnology and Oceanography*, **34**, 198-205.

SALLOWAY, J.C. 1983. Paleomagnetism of sediments from Deep Sea Drilling project Leg 71. (*In* LUDWIG, W.J., KRASHENINNIKOV, V.A. *and others. Intitial Reports of the Deep Sea Drilling Project. Volume 71.* Washington, United States Government Printing Office, 1073-92).

SANCETTA, C. 1979. Oceanography of the North Pacific during the last 18,000 years: evidence from fossil diatoms. *Marine Micropaleontology*, **4**, 103-23.

SANCETTA, C. 1981. Oceanography and ecologic significance of diatoms in surface sediments of the Bering and Okhotsk Seas. *Deep-Sea Research*, **28**, 789-817.

SANCETTA, C. 1983a. Effect of Pleistocene glaciation upon oceanographic characteristics of the North Pacific Ocean and Bering Sea. *Deep-Sea Research*, **30**, 232-45.

SANCETTA, C. 1983b. Diatoms in sediments as indicators of the shelf-slope break. (*In* STANLEY, D.J. *and* MOORE, G.T. *eds The shelfbreak: critical interface on continental margins.* Society of Economic Paleontologists and Mineralogists Special Publication No.33, Oklahoma, U.S.A. 373-80).

SANCETTA, C. *and* ROBINSON, S.W. 1983. Diatom evidence on Wisconsin and Holocene events in the Bering Sea. *Quaternary Research*, **20**, 232-45.

SANCETTA, C. *and* SILVESTRI, S. 1984. Diatom stratigraphy of the late Pleistocene (Brunhes) Subarctic Pacific. *Marine Micropaleontology*, **9**, 263-74.

SANINA, L.V. 1973. Qualitative composition and quantitative distribution of phytoplankton in the Scotia Sea and adjacent areas. *Trudy Vniro* **84**, 41-54. (In Russian).

SASAKI, H. and HOSHIAI, T. 1986. Sedimentation of microalgae under the Antarctic fast ice in summer. *Memoirs of National Institute of Polar Research*, Special Issue No. **40**, 45-55.

SASAKI, H. *and* WATANABE, K. 1984. Underwater observations of ice algae in Lützow-Holm Bay, Antarctica. *Antarctic Record*, **81**, 1-8.

SAVILLE, A. 1987. Comparisons between cephalopods and fish of those aspects of the biology related to stock management. (*In* BOYLE, P.R. *ed. Cephalopod life cycles, volume 2*, London, Academic Press, 277-290).

SCHNEIDER, A. 1983. *Verbreitung und Ökologie des Phytoplanktons in atlantischen Sektor der Antarktis*. Doctoral thesis, Christian-Albrechts-Universität zu Kiel.

SCHRADER, G.C., HORNER, R. *and* SMITH, G.F. 1982. An improved chamber for *in situ* measurement of primary productivity by sea ice algae. *Canadian Journal of Fisheries and Aquatic Science*, **39**, 522-4.

SCHRADER, H.J. 1976. Cenozoic planktonic diatom biostratigraphy of the Southern Pacific Ocean. (*In* HOLLISTER, C.D., CRADDOCK, C. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 35*. Washington, United States Government Printing Office, 605-71).

SCHRADER, H.J. *and* FENNER, J. 1976. Norwegian Sea Cenozoic diatom biostratigraphy and taxonomy. (*In* TALWANI, M., UDINTSEV, G. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 38*. Washington, United States Government Printing Office, 921-1099).

SCHRADER, H.J. *and* KARPUZ, N. 1990. Recent sediment distribution of marine diatoms in two Norwegian-Iceland Seas transects: Paleoceanographic implications. (*In* BLEIL, U. *and* THIEDE, J. *eds Geological history of the polar oceans: Arctic versus Antarctic*. Kluwer, 337-62).

SCHRADER, H.J., BJOERKLUND, K., MANUM, S., MARTINI, E. *and* HINTE, J. VAN 1976. Cenozoic biostratigraphy, physical stratigraphy and paleoenography in the Norwegian-Greenland Sea, DSDP Leg 38 Paleontological Synthesis. (*In* TALWANI, M., UDINTSEV, G., *and others. Initial Reports of the Deep Sea Drilling Project. Volume 38*. Washington, United States Government Printing Office, 1197-211).

SEMINA, H.J. 1981. A morphological examination of the diatom *Thalassiothrix longissima* Cleve et Grunow. *Bacillaria*, **4**, 147-60.

SEMTNER, A.J. 1987. A numerical study of sea ice and ocean circulation in the Arctic. *Journal of Physical Oceanography*, **17**, 1077-99.

SHEMESH, A., BURCKLE, L.H. *and* FROELICH, P.N. 1989. Dissolution and preservation of Antarctic diatoms and the effect on sediment thanatocoenoses. *Quaternary Research*, **31**, 288-308.

SIEBURTH, J. McN. 1979. *Sea microbes*. New York, Oxford University Press.

SIMONSEN, R. 1975. On the pseudonodulus of the centric diatoms, or Hemidiscaceae reconsidered. *Beihefte zur Nova Hedwigia*, **53**, 83-97.

SIMONSEN, R. 1982. Note on the diatom genus *Charcotia* M. Peragallo. *Bacillaria*, **5**, 101-16.

SKJOLDAL, H.R., HASSEL, A., REY, F. *and* LOENG, H. 1987. Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979 – 1984. (*In* LOENG, H. *ed. The effect of oceanographic conditions on distribution and population dynamics of commerical fish stocks in the Barents Sea, Proceedings of the 3rd Soviet-Norwegian Symposium, Murmansk, May 1987*. Bergen, Institute of Marine Research, 59-60).

SLAGSTAD, D. 1982. A model of phytoplankton growth – effects of vertical mixing and adaptation to light. *Modeling, Identification and Control*, **3**, 111-30.

SMAYDA, T.J. 1958. Phytoplankton studies around Jan Mayen Island March-April, 1955. *Nytt Magasin for Botanikk*, **6**, 75-96.

SMAYDA, T.J. 1969. Experimental observations on the influence of temperature, light, and salinity on cell division of the marine diatom, *Detonula confervacea* (Cleve) Gran. *Journal of Phycology*, **5**, 150-7.

SMAYDA, T. 1970. The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology Annual Review*, **8**, 353-414.

SMETACEK, V. *and* POLLEHNE, F. 1986. Nutrient cycling in pelagic ecosystems: a reappraisal of the conceptual framework. *Ophelia*, **26**, 401-28.

SMETHIE, W.M. Jr., CHIPMAN, D.W., SWIFT, J.H. *and* KOLTERMANN, K.P. 1988. Chlorofluoromethanes in the Arctic Mediterranean Seas: evidence for formation of bottom water in the Eurasian Basin and deep-water exchange through Fram Strait. *Deep-Sea Research*, **35**, 347-69.

SMITH, W.O. *and* NELSON, D.M. 1985a. Phytoplankton bloom production by a receding ice edge in the Ross Sea: spatial coherence with density field. *Science*, **227**, 163-6.

SMITH, W.O. *and* NELSON, D.M. 1985b. Phytoplankton biomass near a receding ice-edge in the Ross Sea. (*In* SIEGFRIED, W.R, CONDY, P.R. *and* LAWS, R.M. *eds Antarctic nutrient cycles and food webs*, Berlin, Springer-Verlag, 70-7).

SMITH, W.O., KEENE, W.K. *and* COMISO, J.C., 1988. Interannual variability in estimated primary productivity of the Antarctic Marginal Ice Zone. (*In* SAHRHAGE, D. *ed. Antarctic ocean and resources variability*, Berlin, Springer-Verlag, 131-139).

SOURNIA, A., GRALL, J.R. *and* JACQUES, G. 1979. Diatomées et dinoflagellés planctoniques d'une coupe meridienne dans le sud de l'Ocean Indien (Campagne "Antiprod I" du *Marion-Dufresne*, mars 1977). *Botanica Marina*, **22**, 183-98.

SPAULDING, M., ISAJI, T., MENDELSOHN, D., *and* TURNER, A.C. 1987. The numerical simulation of wind-driven flow through the Bering Strait. *Journal of Physical Oceanography*, **17**, 1799-816.

SPINNANGER, G. 1968. Global radiation and duration of sunshine in Northern Norway and Spitsbergen. *Meteorological Annals, Oslo*, **5**, 65-137.

SPINDLER, M. 1988. Seasonal and geographic variations in sea ice community structure. *Fifth SCAR Symposium on Antarctic Biology*, Hobart, Australia, 29 August-3 September 1988. Abstracts, 82.

SPINDLER, M. and DIECKMANN, G. 1986. Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica). *Polar Biology*, **5**, 185-91.

SPOEL, S. VAN DER, HALLEGRAEFF, G.M. *and* SOEST, R.W.M. VAN 1973. Notes on variation of diatoms and silicoflagellates in the South Atlantic Ocean. *Netherlands Journal of Sea Research*, **6**, 518-41.

SRIVASTAVA, S.P., ARTHUR, M., CLEMENT, B *and* SHIPBOARD SCIENTIFIC PARTY 1987. Site 645 (*In* SRIVASTAVA, S.P., ARTHUR, M., CLEMENT, B. *and others eds Proceedings, Initial Reports (Part A), Ocean Drilling Program*, **105**, 61-418).

STABEL, B. 1986. A diatom maximum horizon in upper Quaternary deposits. *Geologische Ruindschau*, **75**(1), 175-84.

STALEY, J.T., IRGENS, R.L. and HERWIG, R.P. 1989. Gas vacuolate bacteria found in Antarctic sea ice with ice algae. *Applied and Environmental Microbiology*, **55**, 1033-6.

STEYAERT, J. 1973a. Distribution of plankton diatoms along an African-Antarctic transect. *Investigacion Pesquera*, **37**. 295-328.

STEYAERT, J. 1973b. Difference in diatom abundance between the two summer periods of 1965 and 1967 in Antarctic inshore waters (Breid Bay). *Investigacion Pesquera*, **37**, 517-32.

STEYAERT, J. 1974. Distribution of some selected diatom species during the Belgo-Dutch Antarctic Expedition of 1964-65 and 1966-67. *Investigacion Pesquera*, **38**, 259-87.

STEYAERT, J. *and* BAILLEUX, E.M. 1975a. The structure of *Eucampia balaustium* Castr. as revealed by the stereo scanning electron microscope. *Nova Hedwigia*, **26**, 195-204.

STEYAERT, J. *and* BAILLEUX, E.M. 1975b. *Eucampia balaustium* n. sp. Castr. and *Mölleria antarctica* n. sp. Castr. Taxonomy and nomenclature. *Microscopy Journal of the Quekett Microscopical Club*, **32**, 461-70.

STRETCH, J.J., HAMNER, P.P., HAMNER, W.M., MICHEL, W.C., COOK, J., and SULLIVAN, C.W. 1988. Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. *Marine Ecology – Progress Series*, **44**, 131-9.

SUBBA RAO, D.V. *and* PLATT, T. 1984. Primary production of Arctic waters. *Polar Biology*, **3**, 191-201.

SULLIVAN, C.W. 1985. Sea ice bacteria: reciprocal interactions of the organisms and their environment. (*In* HORNER, R. *ed. Sea ice biota,* Boca Raton, CRC Press, 150-71).

SULLIVAN, C.W. *and* PALMISANO, A.C. 1981. Sea ice microbial communities in McMurdo Sound, Antarctica. *Antarctic Journal of the United States*, **16**, 126-7.

SULLIVAN, C.W. *and* PALMISANO, A.C. 1984. Sea ice microbial communities: distribution, abundance, and diversity of ice bacteria in McMurdo Sound, Antarctica, in 1980. *Applied and Environmental Microbiology*, **47**, 788-95.

SULLIVAN, C.W., McCLAIN, C.R., COMISO, J.C. *and* SMITH, W.O. 1988. Phytoplankton standing crops within an Antarctic ice-edge assessed by satellite remote sensing. *Journal of Geophysical Research*, **93**, 12487-98.

SULLIVAN, C.W., PALMISANO, A., KOTTMEIER, S., McGRATH GROSSI, S. *and* MOE, R. 1985. The influence of light on growth and development of the sea-ice microbial community of McMurdo Sound. (*In* SIEGFRIED, W.R., CONDY, P.R. *and* LAWS, R.M. *eds Antarctic nutrient cycles and food webs*, Berlin, Springer-Verlag 78-83).

SULLIVAN, C.W., PALMISANO, A., KOTTMEIER, S., McGRATH GROSSI, S., MOE, R. *and* TAYLOR, G.T. 1983. The influence of light on development and growth of sea-ice microbial communities in McMurdo Sound. *Antarctic Journal of the United States*, **18**, 177-9.

SUNDSTRÖM, B.G. 1980. *Rhizosolenia phuketensis* sp. nov. and *Rhizosolenia stolterfothii* H. Peragallo (Bacillariophyceae). *Botaniska Notiser*, **133**, 579-83.

SUNDSTRÖM, B.G. 1986. *The marine diatom genus* Rhizosolenia. *A new approach to taxonomy*. Ph.D. dissertation. Lund University.

SUSHIN, V.A., SAMYSHEV, E.Z., *and* GAYDAMAK, A.I. 1986. The significance of infusoria in Antarctic plankton communities. *Oceanology*, **26**, 740-744.

SUTHERLAND, P.C. 1852. *Journal of a voyage in Baffin's Bay and Barrow Straits, in the years 1850-1851, performed by H.M. Ships "Lady Franklin" and "Sophia", under the command of Mr. William Penny in search of the missing crews of H.M. Ships "Erebus" and "Terror"*. Volumes 1 and 2. London, Longman, Brown, Green and Longman.

SUTTLE, C.A., CHAN, A.M., TAYLOR, W.D. *and* HARRISON, P.J. 1986. Grazing of planktonic diatoms by microflagellates. *Journal of Plankton Research*, **8**, 393-8.

SVERDRUP, H.U. 1953. On conditions for the vernal blooming of phytoplankton. *Journal de Conseil Permanent International d'Exploration de Mer*, **18**, 287-95.

SWIFT, J.H. *and* AAGAARD, K. 1981. Seasonal transitions and water mass formation in the Iceland and Greenland Seas. *Deep-Sea Research*, **28**, 1107-29.

SWIFT, J.H. *and* KOLTERMANN, K.P. 1988. The origin of Norwegian Sea deep water. *Journal of Geophysical Research*, **93**, 3563-9.

SWIFT, J.H., TAKAHASHI, T. *and* LIVINGSTON, H.D. 1983. The contribution of the Greenland and Barents Seas to the deep water of the Arctic Ocean. *Journal of Geophysical Research*, **88**, 5981-6.

SYVERTSEN, E.E. 1984. Morphology of the Arctic, planktonic *Navicula pelagica* (Bacillariophyceae), with special reference to the "setae". *Nordic Journal of Botany*, **4**, 725-8.

SYVERTSEN, E.E. 1985. Resting spore formation in the Antarctic diatom *Coscinodiscus furcatus* Karsten and *Thalassiosira australis* Peragallo. *Polar Biology*, **4**, 113-9.

SYVERTSEN, E.E. *and* HASLE, G.R. 1983. The diatom genus *Eucampia*: morphology and taxonomy. *Bacillaria*, **6**, 169-210.

TAKAHASHI, E. 1981. Floristic study of ice algae in the sea ice of a lagoon, Lake Saroma, Hokkaido, Japan. *Memoirs of the National Institute for Polar Research., Series E*, **34**, 49-56.

TAKAHASHI, E., WATANABE, K. *and* SATOH, E. 1986. Siliceous cysts from Kita-No-Seto Strait, north of Syowa Station, Antarctica. *Memoirs of the National Institute for Polar Research, Special Issue*, **40**, 84-95.

TANDE, K.S., HASSEL, A. *and* SLAGSTAD, D. 1985. Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwestern part of the Barents Sea. (*In* GRAY, J.S. *and* CHRISTIANSEN, M.E. *eds Marine biology of polar regions and effects of stress on marine organisms*. New York, John Wiley and Sons, 141-55).

THERIOT, E. *and* FRYXELL, G.A. 1985. Multivariate statistical analysis of net diatom species distributions in the south western Atlantic and Indian Ocean. *Polar Biology*, **5**, 22-30.

THEIDE, J. 1988. Scientific cruise report of Arctic Expedition ARK IV/3. *Berichte zur Polarforschung*, **43**, 237 pp.

THOMAS, D.P. *and* JIANG, J. 1986. Epiphytic diatoms of the inshore marine area near Davis Station. *Hydrobiologia*, **140**, 193-8.

TIEN, G., JONES, D., BAILIFF, M.D., NAWROCKI, M., TILBROOK, B., HABERSTROH, P., TAYLOR, G.T. *and* KARL, D.M. 1987. RACER: spatial and temporal variations in microbial biomass. *Antarctic Journal of the United States*, **22**, 148-149.

TILZER, M.M. *and* DUBINSKY, Z. 1987. Effects of temperature and day length on the mass balance of Antarctic phytoplankton. *Polar Biology*, **7**, 35-42.

TILZER, M.M., ELBRÄCHTER, M., GIESKES, W.W. *and* BEESE, B. 1986. Light-temperature interactions in the control of photosynthesis in the Antarctic phytoplankton. *Polar Biology*, **5**, 105-11.

TIMOFEYEV, V.T. 1960. On the age of Atlantic waters in the Arctic basin. *Problemy Arktiki*, **5**, 27-31.

TRESHNIKOV, A.F. 1977. Water masses of the Arctic Basin. (*In* DUNBAR, M.J. *ed. Polar Oceans*, Calgary, Alberta, Arctic Institute of North America, 17-31).

TRESHNIKOV, A.F. 1985. *Atlas Arktiki Arkt. Antarkt.*. Nauchno-Issled. Inst., Moscow.

TRESHNIKOV, A.F. *and* BARANOV, G.I. 1977. The structure of the circulation and budget dynamics of the waters of the north Polar region. (*In* DUNBAR, M.J. *ed. Polar Oceans*. Calgary, Alberta, Arctic Institute of North America, 33-44).

TRUESDALE, R.S. *and* KELLOGG, T.B. 1979. Ross Sea diatoms: modern assemblage distribution and their relationship to ecological oceanographic, and sedimentary conditions. *Marine Micropaleontology*, **4**, 13-31.

TUCHOLKE, B.E, HOLLISTER, C.D., WEVER, F.M. *and* VENNUM, W.R. 1976. Continental rise and abyssal plain sedimentation in the Southeast Pacific Basin, Leg 35, Deep Sea Drilling Project. (*In* HOLLISTER, C.D., CRADDOCK, C. *and others. Initial Reports of the Deep Sea Drilling Project. Volume 35*. Washington, United States Government Printing Office, 359-400).

TUMANTSEVA, N.I. 1982. Biomass and production characteristics of protozoan plankton in Subantarctic and Antarctic waters of the southwestern Pacific. *Oceanology*, **22**, 604-608.

UJIIE, H., SAITO, T., KENT, D.V., TOMPSON, P.R. *and others* 1977. Biostratigraphy, paleomagnetism and sedimentology of late Cenozoic sediments in north-western Hokkaido. *Bulletin of the National Science Museum, Tokyo, Series C*, **3**(2), 49-102.

UNTERSTEINER, N. 1961. On the mass and heat budget of Arctic sea ice. *Archiv für Meteorologie, Geophysik und Bioklimatologie, Series A: Meteorologie und Geophysik*, **12**, 151-82.

UNTERSTEINER, N. 1988. On the ice and heat balance in Fram Strait. *Journal of Geophysical Research*, **93**, 527-31.

URIBE, E. 1982. Influence of the phytoplankton and primary production of the Antarctic waters in relationship with the distribution and behaviour of krill. *INACH Scientific Series* (English edition), **28**, 147-63.

USACHEV, P.I. 1949. The microflora of polar ice. *Trudy Instituta Okeanologii*, **3**, 216-59.

VAN BENNEKOM, A.J., BERGER, G.W., VAN DER GAAST, S.J. *and* DE VRIES, R.T.P. 1988. Primary productivity and the silica cycle in the Southern Ocean (Atlantic Sector). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **67**, 19-30.

VAN HEURCK, H. 1909. Diatomées. *Expedition Antarctique Belge. Resultats du voyage du S. Y. Belgica en 1897-1898-1899 sous le commandement de A. de Gerlache de Gomery. Rapports scientifiques Botanique*, **5**(2), 1-128.

VANLANDINGHAM, S.L. 1967-79. *Catalogue of the fossil and recent genera and species of diatoms and their synonyms*. Vaduz, Germany, J Cramer Verlag.

VARGO, G.A., FANNING, K., HEIL, C. *and* BELL, R. 1986. Growth rates and the salinity response of an Antarctic ice microflora community. *Polar Biology*, **5**, 241-7.

VILLAREAL, T.A. *and* FRYXELL, G.A. 1983. The genus *Actinocyclus* (Bacillariophyceae): Frustule morphology of *A. sagittulus* sp. nov. and two related species. *Journal of Phycology*, **19**, 452-66.

VINJE, T.K. *and* FINNEKASA, O. 1986. The ice transport through the Fram Strait. *Norsk Polarinstitutt Skrifter*, **186**, 39 pp.

VORONINA, N.M. 1966. On the distribution of zooplankton biomass in the Southern Ocean. *Okeanologia*, **6**(6), 1041-54.

WADHAMS, P. 1983. Sea ice thickness distribution in Fram Strait. *Nature*, **305**, 108-11.

WALSH, J.E. *and* JOHNSON, C.M. 1979. An analysis of Arctic Sea ice fluctuations 1953-1977. *Journal of Physical Oceanography*, **9**, 580-91.

WALSH, J.J. 1971. Relative importance of habitat variables in predicting the distribution of phytoplankton at the ecotone of the Antarctic upwelling ecosystem. *Ecological Monographs*, **41**, 291-309.

WALSH, J.J. 1983. Death in the sea: enigmatic phytoplankton losses. *Progress in Oceanography*, **12**, 1-86.

WALSH, J.J., MCROY, C.P., BLACKBURN, T.H., COACHMAN, L.K., GOERING, J.J., NIHOUL, J.J., PARKER, P.L.,

SPRINGER, A.M., TRIPP, R.B., WHITGLEDGE, T.E. *and* WIRICK, C.D. 1989. The role of Bering Strait in the carbon/nitrogen fluxes of polar marine ecosystems. (*In* REY, L. *and* ALEXANDER, V. *eds Proceedings of the Sixth Conference of the Comité Arctique International*, Leiden, The Netherlands, M.M. Brill, 90-120).

WALTON, D.W.H. *and* BONNER, W.N. 1985. History and exploration in Antarctic biology. (*In* BONNER, W.N. *and* WALTON, D.W.H. *eds Key environments – Antarctica*, Oxford, Pergamon, 1-20).

WATANABE, K. 1982. Centric diatom communities found in the Antarctic sea ice. *Antarctic Record*, **74**, 119-26.

WATANABE, K. *and* SATOH, H. 1987. Seasonal variation of ice algal standing crop near Syowa Station, East, Antarctica, in 1983/84. *Bulletin of Plankton Society of Japan*, **34**, 143-64.

WATKINS, J.L., MORRIS, D.J., RICKETTS, C. *and* PRIDDLE, J. 1986. Differences between swarms of Antarctic krill and some implications for sampling krill populations. *Marine Biology*, **93**, 137-46.

WATKINS, T.P. *and* FRYXELL, G.A. 1986. Generic characterization of *Actinocyclus* (Bacillariophyceae): consideration in light of three new species. *Diatom Research*, **2**, 291-312.

WEAVER, F.M. *and* GOMBOS, A.M. 1981. Southern high-latitude diatom biostratigraphy. (*In* WARME, J.E., DOUGLAS, R.J. *and* WINTERER, E.L. *eds The Deep Sea Drilling Project: a decade of progress*. Tulsa, Oklahoma. Society of Economic Paleontologists and Mineralogists, Special Publication **32**, 445-70).

WEBB, P.N., HARWOOD, D.M., McKELVEY, B.C., MERCER, J.H. *and* STOTT, L.D. 1984. Cenozoic marine sedimentation and ice-volume variation on the East Antarctic craton. *Geology*, **12**, 287-91.

WEBER, L.H. *and* EL-SAYED, S.Z. 1987. Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. *Journal of Plankton Research*, **9**, 973-94.

WEEKS, W.F. *and* ACKLEY, S.F. 1986. The growth, structure, and properties of sea ice. (*In* UNTERSTEINER, N. *ed. The geophysics of sea ice*, New York, USA, Plenum Press, 9-164).

WEFER, G., FISCHER, G., FÜTTERER, D. *and* GERSONDE, R. 1988. Seasonal particle flux in the Bransfield Strait (Antarctica). *Deep-Sea Research*, **35**, 891-8.

WEFER, G., FISCHER, G., FÜTTERER, D., GERSONDE, R., HONJO, S. *and* OSTERMANN, D. 1990. Particle sedimentation and productivity in Antarctic waters of the Atlantic sector. (*In* BLEIL, U. *and* THIEDE, J., *eds, Geological History of the polar oceans: Arctic versus Antarctic*, Kluwer, 363-80).

WELSCHMEYER, N. *and* HOEPPFNER, N. 1986. Rapid xanthophyll cycling: an *in situ* tracer for mixing in the upper ocean. *EOS*, **67**, 972.

WERNER, D. 1978. Relations of physiological-cytological peculiarities and biogeography of marine diatoms in the southern hemisphere. *Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere*, Auckland, New Zealand, 17-20 July, 1978. New Zealand DSIR Information Series No. 137, **1**, 131-45.

WHITAKER, T.M. 1977. Sea ice habitats of Signy Island (South Orkneys) and their primary production. (*In* LLANO, G.A. *ed. Adaptations within Antarcic ecosystems*. Houston, Gulf Publishing Co., 75-82).

WHITAKER, T.M. 1982. Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. *Proceedings of the Royal Society of London*, B **214**, 169-89.

WOLFE, J.A. 1978. A paleobotanical interpretation of tertiary climates in the Northern Hemisphere. *American Scientist*, **66**, 694-703.

WOOD, E.J.F. 1959. An unusual diatom from the Antarctic. *Nature*, **184**, 1962-3.

YU, J., LI, R. *and* LU, P. 1986. List of phytoplankton in inshore water at Davis, Antarctica. (*In A collection of Antarctic scientific explorations*. National Committee for Antarctic Research, 120-9).

ZHANG, K. *and* YU, J. 1986. One dominant species of diatom communities found in the sea ice near Davis Station, Antarctica. (*In A collection of Antarctic scientific explorations*. National Committee for Antarctic Research, 72-5).

ZWALLY, H.J., COMISO, J.C., PARKINSON, C.L., CAMPBELL, W.J., CARSEY, F.D. *and* GLOERSEN, P. 1983. *Antarctic sea ice, 1973-1976: satellite passive-microwave observations. NASA SP-459*. Washington DC, USA, National Aeronautics and Space Administration Scientific and Technical Information Branch.