

The diversity, distribution and ecology of diatoms from Antarctic inland waters

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Diatoms are abundant and diverse in many Antarctic freshwaters, with a general trend of decreasing diversity moving southwards. They form an important component of many benthic algal communities in streams and standing waters but are generally less common in the phytoplankton. Diatoms are excellent ecological indicator species and, because their remains are preserved in many sedimentary environments, there appears to be a great potential for palaeoenvironmental reconstruction and the examination of past diversity. A lack of taxonomic precision and consistency, coupled with the insufficient collection from some geographical areas, makes the estimation of the number of Antarctic diatom species problematic.

Keywords: diatoms; inland waters; benthic; planktonic palaeoecology.

Introduction

Diatoms (Bacillariophyceae) are unicellular algae characterized by a silica outer shell or frustule (Round *et al.*, 1990). They comprise one of the most abundant algal groups globally and are important in benthic and planktonic algal communities in freshwater, marine and terrestrial habitats. In this paper I will consider the distribution and diversity of diatoms in inland waters from maritime and continental Antarctica. Broady (this issue) considers terrestrial habitats. Inland waters are sparsely distributed in Antarctica but there are many types which have been reviewed by Heywood (1977), Burton (1981) and Priddle (1985). These range from small melt water ponds around the edge of the continent, to oligotrophic and eutrophic lakes and streams in the maritime Antarctic. Continental inland waters can be saline, permanently ice-covered and permanently stratified.

The extent of global biodiversity in the diatoms is still being debated. Although there are something in the order of 10–12 000 described taxa (Andersen, 1992), there may be as many as 200 000 actual species (Mann and Droop, in press). This is because the current species concept is thought by many to be too broad (e.g. Theriot and Stoermer, 1984; Theriot, 1992; Mann and Droop, in press), resulting in the need to describe new species, coupled with the fact that many habitats, including Antarctic ones, have been insufficiently explored.

Diatoms have long been collected from Antarctica, partly because their silica frustules are easily preserved and thus provided good material for the collections of the early expeditions (e.g. van Heurck, 1909; West and West, 1911; Fritsch, 1912; Carlson, 1913). A detailed account of these is given in Hirano (1965). These early reports typically record low numbers of diatom species (Table 1) and almost certainly represent an underestimate

of the actual number of species found. For example, Carlson (1913) lists 13 species from the South Orkney Islands, whereas Oppenheim and Greenwood (1990) found 104 taxa in two lakes on Signy Island alone.

For some geographical areas algal and diatom floras are available (Parker *et al.*, 1972; Seaburg *et al.*, 1979; Pankow *et al.*, 1987; Pankow *et al.*, 1991). In a comprehensive review of freshwater algae in the Antarctic and Subantarctic regions, Hirano (1965) lists a total of 63 Antarctic diatom species, but notes that this may be a serious underestimation. A much more extensive species list is presented by Prescott (1979) who included a bibliography of Antarctic and Subantarctic algae, together with a checklist of freshwater taxa. He estimated that there are ca 750 diatom taxa, but if Subantarctic locations are discounted a more realistic estimate for the Antarctic is ca 280 freshwater taxa plus a further 56 marine taxa (Table 1). However, this is probably still an underestimate since long species lists have been obtained for Signy Island alone (Oppenheim, 1990; Oppenheim and Greenwood, 1990) and for the maritime Antarctic in general (Håkansson and Jones, 1994) (see Table 1). When diatoms preserved in sediment core material are included in species lists, the number of recorded species is often increased as more habitats are effectively sampled. The differences are often greatest when there has been substantial environmental change. For example Spaulding *et al.* (1994) found five taxa in the plankton from Lake Fryxell (Victoria Land) while 26 taxa are found in core material from this area (Spaulding, pers. comm.). In many Antarctic situations there is opportunity for more detailed work, which will almost certainly result in longer species lists.

As well as insufficient exploration of some areas, there are a number of other factors which account for the underestimation of numbers of diatom species in the Antarctic. There is no single Antarctic diatom flora, and workers have based their identifications on floras produced from elsewhere, and therefore may be failing to recognize new species. There has also been a lack of systematic investigation and the critical appraisal of species from preserved specimens. In addition, the use of incorrect or obsolete nomenclature has created a lack of consistency. Although there have been recent advances in molecular genetic studies which reinforce a refined taxonomy (Mann and Droop, in press), the dominance of the morphological species concept, based on the frustule, remains, and is likely to remain for many more decades. There is therefore a need for the excellent documentation and the critical appraisal of these morphotypes.

Not all the methods used to identify and enumerate diatoms are comparable. In order to assess whether a species is actually living in a particular habitat, live cell counts and examination of the chloroplast is essential; however, few workers have done this routinely, exceptions being Baker (1967) and Oppenheim and Ellis-Evans (1989).

Diatom habitats in Antarctic lakes, ponds and streams

According to Priddle (1985) two major factors affect diatom abundance and habitat availability in the Antarctic – first, the lakes are frozen for most or all of the year, and second, the catchments are barren. Although eutrophic lakes occur in the maritime Antarctic where seals and birds supply nutrients, most of the lakes are generally very nutrient poor. This results in extremely low water column productivity, and lakes in the Antarctic are probably some of the least productive and oligotrophic in the world (Grobbehaar, 1975; Laybourn-Parry and Marchant, 1992). However, production and biomass may be greater in the benthos (Opalinski, 1972a) where efficient regeneration of

Table 1. Number of diatom species found in fossil and modern Antarctic material
a. Modern samples

Author	Geographical area	Number of taxa found	Type of water body	Comments
West and West (1911)	Cape Royds	4	Freshwater and saline lakes	
Fritsch (1912)	South Orkney	5	Snow	
	Cape Adare	4	Ice	
	Bay of McMurdo	7	Ice	
Carlson (1913)	South Orkney	13	Freshwater lakes	
	Graham Land	32	Freshwater lakes	
	Victoria Land	43	Freshwater lakes	
	Cape Adare	8	Freshwater lakes	
Fukushima (1961)	Prince Olav Coast	34	Freshwater and brackish ponds	4 taxa considered endemic
Fukushima (1964)	Cape Royds, Ross Island	19		
Hirano (1965)	Antarctica	68	Freshwaters	Lists based on literature sources
	South Shetlands	11	Freshwaters	
	South Orkneys	15	Freshwaters	
	Antarctic plus Subantarctic (inc. Falklands)	203	Freshwaters	
Baker (1967)	Lake Miers, southern Victoria Land	22	Freshwater	6 taxa considered endemic
Opalinski (1972a)	Thala Hills, Enderby Land, E. Antarctic	15	Freshwater	all cosmopolitan forms
Opalinski (1972b)	Haswell Island, Queen Mary Land, E. Antarctic	9	Freshwater lake	includes some marine species, brought by birds
Parker <i>et al.</i> (1972)	Anvers Island, Antarctic Peninsula	10	Freshwater melt ponds	some marine influence
Parker and Samsel (1977)	Lake Bonney		Meromictic fresh/saline	
Priddle and Dartnall (1978)	Moss Lake, Signy Island, S. Orkney Is.	17	Freshwater lake	as epiphytes on aquatic moss
Prescott (1979)	Antarctic and Subantarctic	c. 750	Freshwater	some marine influence
	Antarctic	289	Freshwater	my estimate
Seaburg <i>et al.</i> (1979)	southern Victoria Land	32	Freshwater lakes and streams	
			Meromictic fresh/saline	
Watanuki (1979)	Langhovde and Skarvsnes, E. Antarctica	81	Saline lakes	freshwater and marine taxa
Priddle and Belcher (1981)	Adelaide Island	17	Freshwater	
Pankow <i>et al.</i> (1987)	Untersee & Schirmacher Oases, Queen Maud Land	22	Freshwater lakes and terrestrial habitats	
Oppenheim (1990)	Signy Island	89	Freshwater lakes	10 taxa noted as marine contaminants
Oppenheim and Greenwood (1990)	Sombre and Light lakes, Signy Island	104	Freshwater lakes	as epiphytes on algal mats
Pankow <i>et al.</i> (1991)	Schirmacher Oases	56	Freshwater and terrestrial habitats	

Table 1. Continued

Author	Geographical area	Number of taxa found	Type of water body	Comments
Hansson and Håkansson (1992)	Antarctic Peninsula (King George Is., Livingston Is., James Ross Is. and Horseshoe Is.	66	21 Freshwater lakes	Surface sediment samples
Kowecka and Olech (1993)	King George Island	74	Freshwater streams	
Cragg (1993)	Vestfold Hills	56	Freshwater and Saline lakes	Surface sediment samples
Izaguirre <i>et al.</i> (1993)	Hope Bay, Antarctic Peninsula	6	Lake Boeckella (freshwater)	Phytoplankton sample
Håkansson and Jones (1994)	South Orkney and South Shetland Islands	234	Freshwater lakes	Surface sediment samples Some marine influence
Spaulding <i>et al.</i> (1994)	Lake Fryxell	5	saline, meromictic lake	Plankton sample
Vinocur and Izaguirre (1994)	Hope Bay, Antarctic Peninsula	23	9 Freshwater lakes	Phytoplankton samples 60% of forms noted as cosmopolitan
Vinocur and Pizarro (1995)	Prasiola Stream, Hope Bay	18	Freshwater stream	
Spaulding (pers. comm.)	Taylor Valley	26	Freshwater to saline. Lakes (fryxell & Hoare) and streams.	3 taxa considered endemic. Includes taxa found in cores.
b. core material				
Author	Geographical area	Number of taxa found	lake type	Comments
Kellogg <i>et al.</i> (1980)	Taylor Valley, Victoria Land	27 non marine species 10 marine species	Non marine saline	9 taxa considered endemic
Schmidt <i>et al.</i> (1990)	Mondsee & Tiefersee King George Island	104	freshwater	79 (63%) considered cosmopolitan
Gillieson (1991)	Kirisjes Pond & Pup Lagoon, Larsemann Hills	36	Marine-brackish-freshwater sediment sequence	
Wasell and Håkansson (1992)	'Skua Lake', Horeshoe Island	134	Marine-brackish-freshwater sediment sequence	
Wasell (1993)	Nicholson Lake, Vestfold Hills	62	Marine-brackish-freshwater sediment sequence	
Björck <i>et al.</i> (1993)	Lake Åsa, Livingston Island	92	Freshwater	49 taxa considered to be 'aerophilic, euterestic or bryophytic'

nutrients can occur, (Kerry *et al.*, 1977; Parker *et al.*, 1977; Hawes *et al.*, 1993) and diatoms are much more common in benthic habitats than in planktonic ones.

Both the Antarctic phytobenthos and phytoplankton are well adapted for photosynthesis at extremely low light conditions (Priddle *et al.*, 1986), and benthic diatoms appear to be shade adapted. Oppenheim and Ellis-Evans (1989) found that the highest autofluorescence counts at Sombre Lake (Signy Island) were observed where only 20% of the surface radiation was available.

Benthic habitats

Probably the most important habitats for benthic diatoms throughout the Antarctic are those associated with microbial mats, which are composed primarily of cyanobacteria, heterotrophic bacteria and algae (see Ellis-Evans, this issue). Diatoms are common in mats from streams (Davey, 1993), saline and freshwater lakes (Parker *et al.*, 1977; Wharton *et al.*, 1983; Oppenheim and Patterson, 1990; Hawes *et al.*, 1993) and from terrestrial environments (Smith, 1972; Broady, 1979, 1989; Davey and Clarke, 1992). They can grow either as attached or as motile forms in the mats (Wharton *et al.*, 1983; Oppenheim and Patterson, 1990), occurring at considerable depths in some lakes, for example below 18 m in Lake Bonney (Wharton *et al.*, 1983). In some areas they contribute the largest number of algal species in the mats, for example, Wharton *et al.* (1983) found 17 diatom taxa associated with mats from southern Victoria Land. Although some species are associated with a particular mat type in a single lake, other species do not show the same faithfulness and are common in more than one mat type at one lake, and/or occur in different mat types at different lakes (Wharton *et al.*, 1983).

Low-temperature scanning electron microscope (SEM) investigation of mats frozen *in situ* allows the fine structure and three dimensional nature of the mats to be investigated. Using these techniques on mats collected by divers, Oppenheim and Patterson (1990) were able to show the attachment mechanisms of diatom species. *Achnanthes minutissima* was attached so extensively that the host filament was not visible, whereas species such as *Navicula dicephala* were found to be motile within the mats. Davey and Clarke (1992) also used SEM and light microscope (LM) techniques to investigate the fine structure of a terrestrial cyanobacterial mat from Signy Island. They observed a distinct layered structure with diatom species such as *Pinnularia* and *Achnanthes* species associated with the lower layers. The application of such techniques on different mat types from elsewhere in the Antarctic would be of great interest, especially in some of the continental systems where very thick and complex mats develop. Although Wharton *et al.* (1983) described the different types of mats from southern Victoria Land, and show that below pinnacle mats there are alternating bands of organic (containing empty diatom frustule) and inorganic material, there appears to be plenty of scope for more detailed analysis of these mats and their fine structure.

Diatoms also grow epiphytically on aquatic mosses, which can provide a diverse habitat with a variety of niches. Priddle and Dartnall (1978) found six species of diatoms as habitual epiphytes, and 11 species as casual epiphytes at Moss Lake (Signy Island). Other benthic habitats such as epipsammon (sand), epilithon (stones) and epipelon (fine mud) may also be important at some sites, and a flaky algal mat is sometimes found associated with these.

Planktonic habitats

Diatoms are generally considered rare in phytoplankton communities throughout the Antarctic (Priddle *et al.*, 1986), although in some areas they may form the most important components of the phytoplankton (Opalinski, 1972a). Where nutrient enrichment occurs the phytoplankton may show enhanced growth at the expense of the phytobenthos through the effects of self shading or winter deoxygenation (Priddle, 1985; Hawes, 1990), but even in such situations, where in more temperate regions a diatom phytoplankton commonly becomes important, there is little development of this community in the Antarctic.

However, planktonic forms do occur in the Antarctic. Spaulding *et al.* (1994) collected a *Cyclotella* species in Lake Fryxell and Kellogg *et al.* (1980) reported *Cyclotella compta*, *C. glomerata* and *C. stelligera* and a *Melosira* species in sediments from lakes in the Taylor Valley.

Pankow *et al.* (1987) found *M. granulata* var. *angustissima* and *Asterionella formosa* from Schirmacher and Untersee Oases, and at Lake Miers Baker (1967) reported *C. stelligera* which is a cosmopolitan species also found in Arctic regions. Fukushima (1961) reported *Cyclotella compta* from Prince Olav coast. It is interesting that these reports of centric taxa, such as *Cyclotella*, and species such as *Asterionella formosa*, which are often regarded as being truly planktonic, appear to be restricted to more continental locations in Antarctica. In maritime locations, such as Signy Island, these species appear to be absent, although at Livingston Island, Björck *et al.* (1993) found *Fragilaria crotonensis* in the sediments from Lake Åsa, which is often considered to be a planktonic species. They did not, however, collect live material from this site.

The reason why *Cyclotella* and other true planktonic species are absent from the maritime Antarctic is intriguing since the lakes are deep enough to support a diatom phytoplankton and there is little obvious difference in water quality between maritime and continental situations.

Marine diatom phytoplankton can also occur in inland freshwaters. For example, Kerry *et al.* (1977) reported *Coscinodiscus* species, and Cragg (1993) found *Thalassiosira antarctica* in hypersaline lakes in the Vestfold Hills.

Some species found in plankton samples may not actually be truly planktonic. Spaulding *et al.* (1994) found three *Navicula* and *Nitzschia* species in the plankton of Lake Fryxell which probably represent dislodged benthic species. Vinocur and Izaguirre (1994) found 23 species of diatom in phytoplankton samples from Hope Bay but note that many of these are typically epilithic or associated with terrestrial habitats. Similarly, Light *et al.* (1981) reported *Stauroneis anceps* and *Pinnularia microstauron*, which are common terrestrial/benthic diatoms, in plankton samples from Heywood Lake (Signy Island), and Laybourn-Parry and Marchant (1992) found *Navicula* species in Lake Braunsteffer in the Vestfold Hills. The movement of live and dead diatoms into the plankton, therefore, seems to be a common phenomenon, and at Lake Bonney Parker *et al.* (1977) noted that the plankton contains nearly all the algae found in the mat community at some time during the Austral summer. Diatoms can also be dislodged from terrestrial environments into lakes; Björck *et al.* (1993) consider that an important factor in the composition of sedimentary diatom assemblages is the erosion and transport of minerogenic soils containing terrestrial forms into the lake resulting in a mixture of autochthonous and allochthonous taxa.

As well as dislodged forms, diatoms tend to occur in more than one habitat, and the association of a species with a particular habitat needs to be confirmed by live cell counts.

For example, in the Arctic, Douglas and Smol (1995) found that many taxa were common to rock and moss substrates. Of 66 taxa only three were found exclusively on moss and 14 exclusively on mud. In the Antarctic, Kawecka and Olech (1993) found terrestrial and aerial forms in stream habitats, including species often described as soil algae, and Kellogg *et al.* (1980) reported 'soil' forms in lakes. Seaburg *et al.* (1979) sampled littoral benthic mat and planktonic communities from lakes in southern Victoria Land as well as habitats in soils and glacial melt water streams. They found that some species (e.g. *Navicula muticopsis* and *Hantzschia amphioxys*) were present in all four habitats, while several other species were common in two of the four habitats. It is apparent that a great number of common freshwater species are able to live in terrestrial or semi-terrestrial habitats. There is a need to sample live diatoms from habitats around lakes in Antarctica and not just rely on reports of habitat preference from the literature. Habitats tend to overlap and this may be especially important in the Antarctic where many habitats are ephemeral.

Stream communities

In contrast to work conducted in standing water bodies, there is very little information available on the diatom communities in running waters, although it is likely that diatoms are found in melt streams throughout the Antarctic. Diatoms are present in streams from the Vestfold Hills (Kerry *et al.*, 1977). In glacial streams from southern Victoria Land, Seaburg *et al.* (1979) found 11 species of diatom, and diatoms were found to be more abundant in these habitats than elsewhere in the Dry Valleys. Diatoms are often the most predominant organisms on the alluvial sands and gravels of streams with a low slope angle (e.g. those in the McMurdo Sound area (Vincent *et al.*, 1993)). Kawecka and Olech (1993) investigated stream diatom communities on King George Island (South Shetland Islands) and found that these were characterized by cosmopolitan species plus those which grow in aquatic habitats subject to desiccation, together with those which grow in wet terrestrial habitats (e.g. *Navicula atomus*, *N. mutica* and *Hantzschia amphioxys*). Vinocur and Pizarro (1995) identified 18 species of diatom from Prasiola Stream in the Hope Bay area, which included many of the taxa that Håkansson and Jones (1994) found to be common in lakes in the maritime Antarctic (e.g. *Achnanthes subatomoides* and *Nitzschia hamburgensis*) as well as species more commonly, although not exclusively, associated with aerophilic habitats (e.g. *Hantzschia amphioxys*). In some locations, though, diatoms do appear to be absent, for example Hirano (1979) records no diatom species in the Yukidori stream, East Antarctica, despite 57 species of algae being found.

Diatom diversity and richness

Hirano (1965) suggested that there is a decrease in the number of diatom species as one moves southwards, and it is apparent from Table 1 that continental regions appear to be less diverse than the maritime Antarctic. Often continental systems are dominated by a single species or a few species which are best adapted to the extreme fluctuations in the environment (Vincent, this issue), but other factors, such as the degree of geographical isolation, the length of time since ice retreat and fewer available habitats are also important.

Hansson and Håkansson (1992) felt that factors related to latitude (e.g. length of the growing season) were most important in determining species richness along a productivity

gradient in the Antarctic. Species richness and diversity can also be influenced by water quality. Cragg (1993) found that species diversity fell as salinity increased at sites in the Vestfold Hills, with only a few species being abundant in hypersaline lakes. Historical changes in species diversity have been investigated using diatom remains in sediment cores; for example, Gillieson (1991) found increasing species diversity in cores following marine incursion, and also noted that early proglacial diatom floras were low in species diversity (although high in numbers). Bronge (1992) investigated the number of diatom taxa through time from Nicholson Lake in the Vestfold Hills and found 37 taxa at 6250 BP which declined to eight taxa at 4250 BP, after which it remained virtually constant to the present day. This change corresponded to a change from a marine phase before 4250 BP to a freshwater phase thereafter.

Diatom ecology and palaeoecology

Diatom responses to water quality

The most important variables affecting diatom species abundance in lakes from more temperate areas are usually those related to water chemistry, in particular nutrient (Nygaard, 1949; Stockner 1971, 1972), salinity (Kolbe, 1927; Hustedt, 1957) and pH (Hustedt, 1937–9; Nygaard, 1956) gradients. As elsewhere, these factors are increasingly seen as being important in determining species distribution in the Antarctic. Hansson and Hakansson (1992) investigated diatom community response along a productivity gradient and found that some species (e.g. *Caloneis* cf. *bacillum* and *Navicula* cf. *seminulum*) showed an increase in abundance with increasing nutrients, while others (e.g. *Achnanthes* cf. *mollis*) showed a decrease. Oppenheim and Greenwood (1992) used redundancy analysis to demonstrate that diatom species composition was correlated to the concentration of nitrogen and phosphorus. Similar relationships have also been found by Jones *et al.* (1993) who, in a study of 59 maritime Antarctic lakes (Signy Island and Livingston Island), showed that the variance in diatom community composition could be statistically accounted for by conductivity, potassium, chlorophyll-*a* and ammonium concentrations in the lake water. Diatom species associated with various lake types were also identified. Oligotrophic inland Livingston Island sites were characterized by *Achnanthes lanceolata*, *Achnanthes exigua*, *Navicula seminulum*, *Navicula tantula* and *Stauroneis* species No. 1, while high-conductivity, high-nutrient Livingston Island sites were characterized by *Fragilaria construens* var. *binodis* and *Nitzschia* species No. 1. Low-conductivity, high-nutrient sites at Signy Island were characterized by *Achnanthes pinnata*, *Gomphonema angustatum* var. *productum*, *Achnanthes subatomoides* and *Fragilaria construens* var. *venter*.

A recent approach has been to quantify these relationships using multivariate statistical methods (e.g. Birks *et al.*, 1990). This involves constructing a training, or calibration set for a region, relating contemporary lake water chemistry to the surface sediment diatom assemblage which is representative of an integrated sample of the various diatom communities growing in different habitats in the lake. Such samples have a greater species diversity than single habitats, and they can also provide a means of checking whether all habitats within a lake have been sampled. Because diatoms are well preserved in the surface sediments of lakes and because they are excellent ecological indicator species (see above), modern-day species responses to, for example, nutrients and/or salinity can be

modelled using a variety of statistical approaches (e.g. weighted averaging which allows individual species' optima and tolerances to be estimated). Quantitative relationships between diatoms and environmental gradients have now been established in many parts of the world for pH (e.g. Birks *et al.*, 1990), nutrients (e.g. Hall and Smol, 1992) and for salinity (e.g. Fritz *et al.*, 1991), and such an approach is now being undertaken in the Antarctic (Jones and Juggins, 1995; Roberts and McMinn, in press). These relationships or transfer functions can be applied to fossil assemblages from sediment cores to provide environmental reconstructions (see below).

In some continental systems, where meromixis is common, it may be more difficult to relate contemporary diatom assemblages to current water-column chemistry. Sediment diatom assemblages can be derived from a mixture of diatom communities growing at different levels within the meromictic system. Careful work is needed to understand the chemical conditions which occur where diatom growth is taking place. Despite these problems there is potential for modelling the response of diatoms to water quality in these regions.

Although perhaps the easiest way to demonstrate the relationships between species abundance and environmental gradients is using the calibration and regression approach, results can be reinforced by culture work. Antarctic diatoms have been successfully cultured (Watanuki and Ohno, 1975; Watanuki and Karasawa, 1975; Watanuki, 1979). Watanuki (1979) cultured five diatom taxa and showed *Tropodoneis laevisissima* to be halophilic, *Achnanthes brevipes* var. *intermedia* to have a wide salt tolerance and *Navicula muticopsis* to have a narrow salt tolerance, which reinforces the findings of Fukushima (1961, 1967) on the present-day distribution of these taxa in nearby lakes.

Spatial variability of diatom communities

Studies from Antarctic lakes have investigated the extent of seasonal succession (e.g. Light *et al.*, 1981; Hawes, 1983; Lizotte and Priscu, 1992) and vertical stratification (Spaulding *et al.*, 1994) in the phytoplankton. However, as diatoms do not play an important role in the phytoplankton of most Antarctic lakes, these studies make little or no mention of any diatom species successions.

There is a general paucity of information on the within-lake spatial variability of benthic algae in general and diatoms in particular compared with phytoplankton studies. Oppenheim and Ellis-Evans (1989) found a very definite depth zonation of benthic diatoms at Sombre Lake, Signy Island. For example, *Achnanthes minutissima* was most abundant in shallow water, while *Stauroneis anceps* var. *hyalina* was most common in the deeper areas. A general model can be proposed for diatom zonation in maritime Antarctic lakes (Oppenheim and Ellis-Evans, 1989). The shallow, nearshore shelf is a zone of wave action, wind-induced mixing, ice scouring and grazing, which is often characterized by low numbers of viable cells. At Sombre Lake *Fragilaria* species are present, some of which are typical of frequently disturbed shallow water environments throughout the world (e.g. Denys, 1988). The deeper water has more stable environmental conditions, and diatoms grow epiphytically on microbial mats or aquatic mosses. Oppenheim and Ellis-Evans (1989) found *A. minutissima* and *Synedra rumpens* var. *familiaris* abundant as epiphytes on filamentous algae at 4–7 m depth in Sombre Lake, and, in a more detailed study, Oppenheim and Patterson (1990) found 37 species of diatom associated with a microbial mat from a single location. The deepest water is often a zone of anoxia where mats are not

able to grow, and the substrate is commonly mud. Some epipelagic diatoms are found which are either able to withstand seasonal anoxia or able to avoid anoxia by virtue of their motility. In Sombre Lake below a water depth of 9 m no mats are present due to anoxia in winter (Ellis-Evans, 1984), but *Stauroneis anceps* var. *hyalina* has been observed to be viable (Oppenheim and Ellis-Evans, 1989).

In more continental situations such detailed work on diatom community structure has yet to be completed, but like maritime Antarctic lakes there appear to be few diatoms in the littoral moat which are characterized by complete freezing in the Austral winter and it has been suggested that diatom cells may be intolerant of freeze-thaw cycles (Wharton *et al.*, 1983).

Oppenheim (1990) investigated the seasonal diatom succession at two lakes on Signy Island and found that no seasonal trends were detectable; however, as she notes, no distinction between live and dead cells was made and therefore there is potential for further work at many sites, using, for example, appropriate sampling methods and artificial substrates.

Surface sediment and fossil diatom assemblages

Due to their siliceous nature, diatoms are the best and most frequently preserved algal group and are found in many Antarctic lake sediments in high concentrations. Chrysophyte cysts are also preserved in some situations (e.g. Wharton, unpublished data in Doran *et al.*, 1994 and personal observations), and their stratigraphy may well warrant further investigation.

Diatoms preserved in lake sediments can be used to address ecological issues, such as species and assemblage succession, diversity and persistence and rates and directions of ecological change (e.g. related to changes in productivity and climate; Anderson and Battarbee, 1994). The data can also be used to examine alternative causes for environmental change and can address time-scales of varying length (from intra-annual to 1000s of years), thus extending the scope of limnologists studying contemporary systems (Anderson and Battarbee, 1994). Together with other palaeolimnological techniques, it is possible to test ideas of evolutionary sequences such as those forwarded by Priddle and Heywood (1980) and Priddle (1985). However, in Antarctic situations, diatom-based palaeolimnological reconstruction is still in its infancy and to date there has been very little quantitative work.

Due to their well documented preferences for different salinities, diatoms are ideal indicators of changing salinity which may be caused by sea level change, and sedimentary diatoms have been used to provide evidence for former sea levels in the Vestfold Hills (Gillieson, 1991; Bronge, 1992; Wasell, 1993) and at King George Island (Mäusbacher *et al.*, 1989). Wasell and Håkansson (1992) used diatom evidence to show a transition from a marine to brackish to freshwater environment as a result of isostatic uplift at 'Skua Lake', Horseshoe Island. The lower-most samples were dominated by true marine diatoms, such as *Navicula directa* and *Cocconeis costata*, there followed a phase of disturbance with a high abundance of *Fragilaria* species, then finally, at ca 1860 BP basin isolation occurred and a freshwater diatom flora with *Nitzschia* cf. *perminuta* and *Achnanthes* cf. *renei* was established.

Changes in salinity in some continental closed basins may also be related to climate change, for example through changes in evaporation. Here, quantitative salinity estimates

using calibration and regression techniques may give more quantitative information on former climates (e.g. Roberts and McMinn, in press).

Diatoms also respond to climate in maritime situations, Schmidt *et al.* (1990) used changes in sediment pattern and diatom species composition to infer climatic change, and an increase of halophilic and alkaliphilic diatoms between 4700 and 3200 BP was interpreted as being due to increased erosion and/or enhanced sea spray influence. Björck *et al.* (1991, 1993) used diatoms together with other palaeolimnological variables to reconstruct climatic conditions on Livingston Island. At Midge Lake (Björck *et al.*, 1991) significant environmental changes occurred between ca 3200 and 2700 BP, which were interpreted as reflecting a milder and more humid maritime climate. A greater proportion of alkaliphilous diatoms were found in this period, possibly indicating higher productivity as a result of increased nutrient input from the catchment and/or greater diatom production.

In the Dry Valleys of Victoria Land, fossil diatoms have been used to investigate lake level changes and to elucidate former environments (Kellogg *et al.*, 1980). Factor analysis was used to identify species assemblages associated with deltas of different ages and species indicative of non-marine saline environments at the present day were found in the perched deltas. This supported the hypothesis of a grounded ice sheet blocking the mouths of the Dry Valleys during the last glacial maximum.

Such models can also be used for predictive purposes and in palaeolimnological studies will allow changes in water chemistry to be quantified as the modelled modern response is applied to dated sediment core sequences. Jones and Juggins (1995) illustrate how sedimentary diatoms can be used to reconstruct the nutrient histories of Signy Island lakes. There appears to be great potential in this approach, and more multivariate work is needed.

As well as the importance of water quality (e.g. salinity and nutrients) affecting diatom assemblages fluctuations in diatom community structure can also be dependent on short-term ice cover fluctuations or on the patchy distribution of mosses on the sediment surface. Changes in lake level could also affect the amount of terrestrial diatoms being incorporated into the lake sediment. For reliable palaeoecological interpretation, we need more modern analogues of both lake sites and diatom samples.

Although there are potential problems with the sedimentary record, for example, due to poor preservation and breakage (e.g. Gillieson, 1990) there is great potential for using diatoms for palaeoecological reconstruction at a range of time scales from tens to thousands of years and there are long sedimentary records in non-glaciated continental areas which would merit investigation. For example, Victoria Land palaeolake sediments are estimated to be 180–130 000 years old (Doran *et al.*, 1994). Studies already completed show the potential of quantitative palaeoecological reconstruction, which could be extended to many more areas to address impacts of human pressures and to assess climate change.

Conclusions

Taxonomy

Underlying all work in diatom ecology, ecosystem function, and palaeoecological reconstruction is the need for an accurate and precise taxonomy. A consistent taxonomy is

crucial to future ecological monitoring programmes which consider environmental changes. However, the absence of an Antarctic diatom flora has undoubtedly led to different workers assigning the same morphotype to different species and much of previously published work is of little help in creating a standard taxonomy unless it is supported by good photographs or museum specimens.

With the exception of *Achnanthes* by Oppenheim (1994), there have been few comprehensive revisions of freshwater taxa. Genera such as *Nitzschia*, *Pinnularia* and *Navicula* require revision, which is not a trivial exercise. With the exception of the work of Kobayashi (1963a, 1963b, 1965), there has been very little investigation into the degree of variability within diatom species, and such research could be the basis of a finer taxonomy. There needs to be some re-evaluation of current species concepts and if a narrower species concept is adopted this will result in greater precision of ecological monitoring and palaeoecological reconstruction.

There is also a need for better documentation of the taxa found with detailed descriptions and good quality light and scanning electron micrographs (e.g. those provided by Kellogg *et al.* (1980), Schmidt *et al.* (1990) and Wasell and Håkansson (1992)). This needs to be supplemented by workshops, as it is only by the exchange of slides, photographs and illustrations that we can start to produce an Antarctic flora. Preliminary work has been started with a series of Antarctic and Arctic diatom workshops (e.g. Hamilton, 1994) which detail taxonomic discussions and attempt to address analytical quality control issues, as well as nomenclatural and taxonomic issues. Such workshops are essential if an eventual aim is to bring training sets together with the aim of modelling current environmental conditions over a wide geographical area. It may also be possible to exchange image and data resources over the INTERNET (Kociolek, 1994).

The number and diversity of Antarctic diatom species and implications for conservation

It is clear that the exact number of Antarctic diatom species is unknown at present due to a lack of taxonomic consistency and the insufficient exploration of many geographical areas. When detailed surveys are made the general conclusion is that there is a greater diversity than previously supposed (e.g. Parker *et al.*, 1972; Pankow *et al.*, 1987). Although authors (Prescott, 1979) have attempted to create a species list for Antarctica using sources from the literature, unless this can be supplemented by a well-researched flora, such lists are bound to be unreliable.

There are probably well over 300 diatom species in the Antarctic, with a trend of decreasing species number southwards into more continental locations. The maritime Antarctic flora has a high proportion of cosmopolitan species, (e.g. an estimate of 63% were by Schmidt *et al.*, 1990) with a strong influence of elements from the South American and Subantarctic flora (Krasske, 1939, 1949; Cleve-Euler, 1948; Bourelly and Manguin, 1949, 1954). Overall, there appears to be a rather low proportion of endemic taxa (Table 1); however, the adoption of a finer species concept may well reveal a greater number of endemic species, but until sufficient studies have been made using a more reliable taxonomy it will not be clear how many species are endemic and how many are truly cosmopolitan (cf. Mann and Droop, in press). This has important implications for conservation: if there are numbers of narrow endemics, and Antarctica contains unique diatom species, then species may become extinct as a result of human disturbance or climate change.

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