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Biodiversity in extreme aquatic environments: lakes, ponds and streams of the Ross Sea sector, Antarctica

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The Ross Sea Sector (RSS) of Antarctica lies between the lines of longitude 150°E and 150°W and contains diverse landscapes with a variety of lakes, ponds and streams. Neither insects nor crustacean species have been recorded in these ecosystems but most contain planktonic and/or benthic communities that are composed exclusively of microscopic organisms. Microbial biodiversity is low with a small number of species (e.g. filamentous cyanobacteria of the family Oscillatoriaceae) occurring under a broad range of environmental conditions throughout the region. There is no evidence to date of microbial endemism in the RSS; however, there is a need to apply molecular and cellular techniques to compare biodiversity and genetic characteristics with assemblages elsewhere in Antarctica and with comparable communities in the north polar zone. A series of hypotheses are advanced to help guide further work. These derive from the conclusion that environmental extremes plus biogeographical isolation control the biodiversity of RSS communities, and that biological interactions (competition, grazing, predation, parasitism) are weak and play a minor role by comparison with temperate latitude ecosystems.

Keywords: algae; Antarctica; cyanobacteria; freshwater; limnology; microbial; polar; protozoa.

Introduction

The Ross Sea Sector (RSS; Fig. 1) of Antarctica contains a remarkably diverse spectrum of aquatic and semi-aquatic environments: dilute meltwaters, hypersaline ponds, ice-shelf and glacier pools, deep mesotrophic to ultra-oligotrophic lakes, sea-spray and penguin influenced coastal waters, tidal ponds, nitrate-rich brines, many types of flowing water ecosystems, and moss or algal wetlands. In other parts of the world, including the north polar zone, such a diversity of physical and chemical conditions might be expected to support a concomitant richness of species. Contrary to this expectation, the RSS is generally thought to contain a much reduced biodiversity, even by comparison with other parts of Antarctica. Higher plants are absent from the catchments, and even moss stands are sparsely distributed, particularly in the McMurdo Sound region and further south. Unlike the situation in Arctic lakes and streams, fish and insects do not occur within the non-marine aquatic ecosystems of the RSS, and in contrast to many lakes elsewhere in

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Antarctica, even crustacean zooplankton are conspicuously absent. The result is a unique array of aquatic ecosystems that are largely, and often exclusively, inhabited by microscopic life-forms.

Although there is now a large and rapidly growing literature on the biological composition of RSS aquatic habitats, our understanding of biodiversity in this region is still in its infancy. Floristic analyses began soon after the turn of this century (Fig. 2); however, the information available to date is still restricted to a small number of taxonomic groups and is derived mostly from species collections from a few biologically-rich sites within this region. Biogeographical isolation as well as the environmental extremes that organisms must face within the RSS are both likely to have played a role in shaping community structure, but the relative importance of these factors in controlling biodiversity has been little considered. Polar communities and their environments were once considered 'simple systems' (Rigler, 1978), but many studies over the last decade have underscored the complexity of air–ice–water systems, as well as our still rudimentary understanding of microbial food webs. With the advent of new techniques for studying

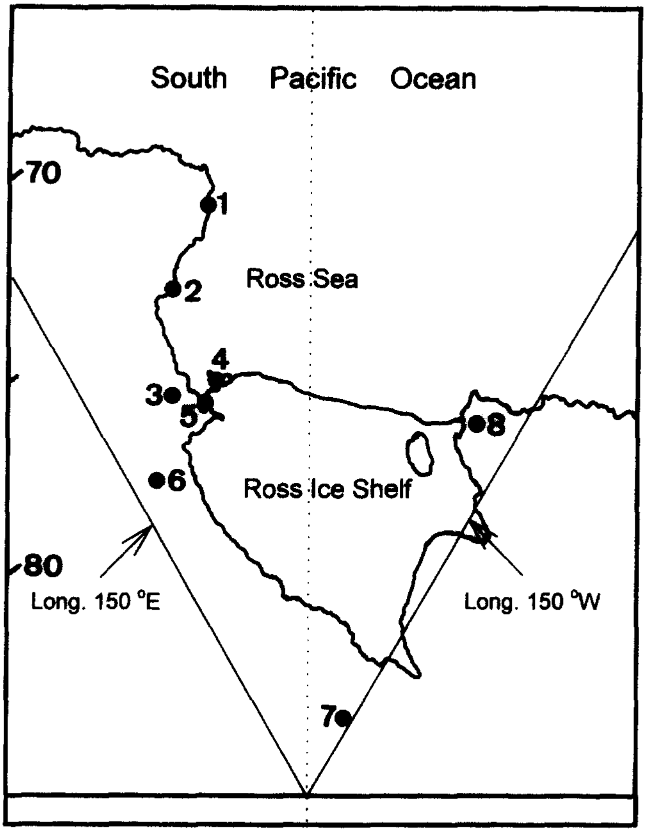
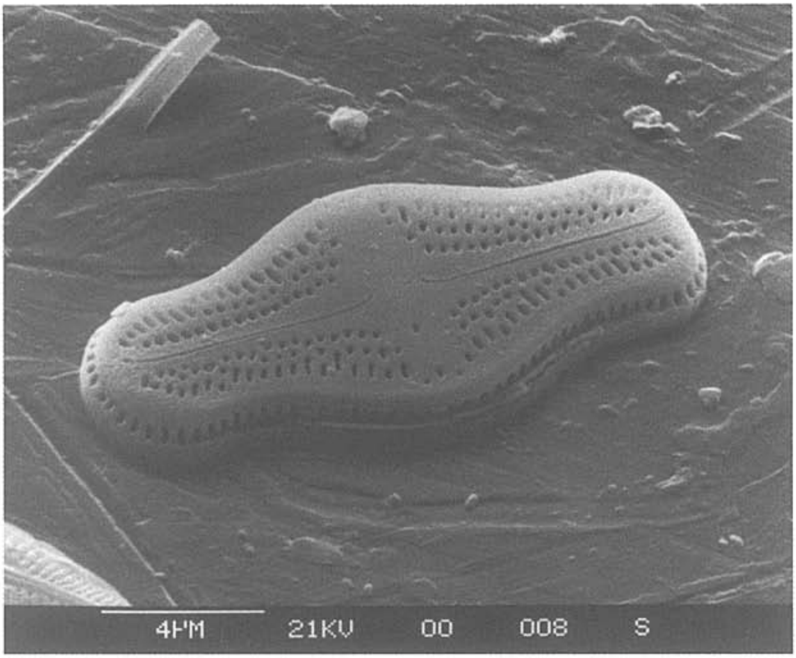


Figure 1. The Ross Sea Sector (RSS) showing the location of major sites mentioned in the text: 1 = Cape Hallett; 2 = Mt Melbourne and Terra Nova Bay; 3 = McMurdo Dry Valleys; 4 = Ross Island; 5 = McMurdo Ice Shelf; 6 = Darwin Glacier Region; 7 = Mt Howe; 8 = Rockefeller Mts.



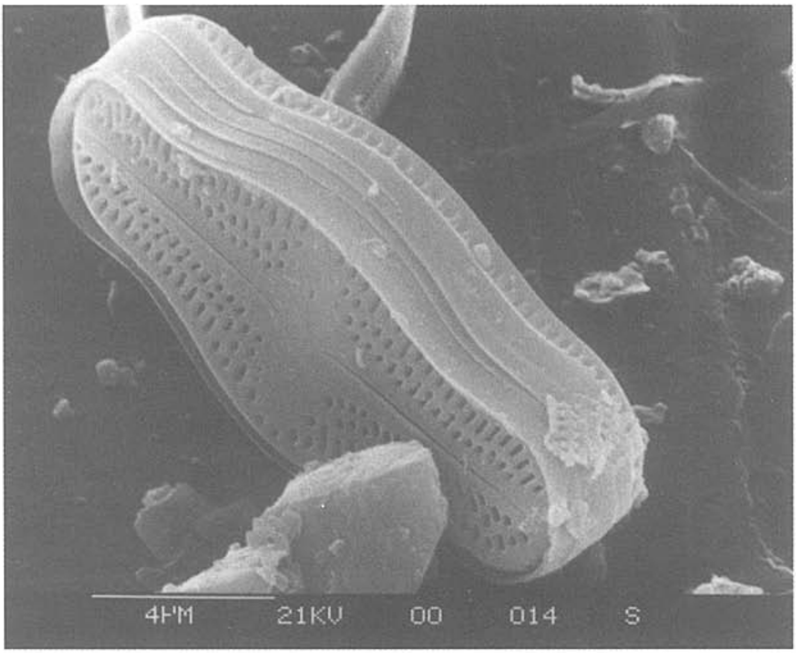


Figure 2. Scanning electron micrographs of the diatom *Luticola murrayi* from the surficial sediments of Lake Fryxell, McMurdo Dry Valleys. This genus is characteristic of brackish water, soils and aerophilic habitats. The species was first described from collections made on Shackelton's 1907–09 expedition to the Ross Sea region. The scale in µm is given at the bottom of the micrographs (upper = valve view; lower = girdle view), taken by Sarah Spaulding, United States Geological Survey.

natural microbial communities, and the long-term commitment to environmental research at several RSS sites, it is timely to identify some of these major unknowns.

The aim of the present review is to summarize our current knowledge of biodiversity in the lakes, ponds and streams of the RSS, and to raise some of the outstanding questions. We first briefly describe the geographic features of this Antarctic region, and then review the studies to date on biological communities in each of the three types of aquatic environment. These environments span a gradient of habitat stability, from permanently stratified waters in deep ice-covered lakes to the highly variable regime of ephemeral streams. We examine to what extent such differences translate into species composition and diversity. Finally, we consider overall features of RSS aquatic communities, and advance a series of hypotheses concerning the potential controls on their biodiversity.

Geographic features of the RSS

The RSS can be defined as that region extending from the South Pole to approximately 66°S in the west, the latitude of the Balleny Islands, and to 77°S in the east, the northern limit of the Saunders Coast. The sector is bound by the lines of longitude at 150°E and 150°W (Fig. 1). It includes coastal environments along the western and eastern sides of the Ross Sea, associated offshore islands and the mountains, valleys and glaciers of the Transantarctic Mountain Range. In the northernmost part of the region the Ross Sea is covered by annual sea ice through much of the year, and in the south it is covered by the permanent ice of the Ross Ice Shelf. This in combination with the influence of the ice-capped continent results in extremely low air temperatures throughout the year, even in the coastal environments.

An introduction to the climate, landscapes and geology of the RSS is given in Hatherton (1990). The largest expanses of ice-free land within Antarctica are found in the McMurdo Dry Valleys, a 15 000 km^2 area in southern Victoria Land centred at 77°S, 163°E. About 30% of this area is largely devoid of snow and ice (Vincent, 1996). Meltwater streams and seeps flow each summer within this polar desert environment, from source glaciers to downstream ponds and lakes. Meltwater is also produced within the ablation zone of ice shelves. The most extensive of these meltwater systems is the McMurdo Ice Shelf at 78°S where a 1500–2000 km^2 region of moraine-coated ice is up to 60% covered by water at the end of the summer season (Vincent, 1988). This vast flooded system is the habitat for a particularly rich and varied microbiota.

The continental climate of this region is ameliorated near the coast by the influence of the Ross Sea, resulting in large annual fluctuations, and substantial differences between sites in terms of extremes and annual range. At Cape Hallett (72.3°S, 170.3°E) in the northern part of the sector, the mean daily maximum temperature in January is +1.1°C, while the July average daily minimum is –23.9°C. Much further to the south at Lake Vanda in the McMurdo Dry Valleys (77.5°S, 161.4°E), summer conditions are similar (mean maximum of +1.2°C in January), but temperatures plunge 10°C lower to a mean July minimum of –33.4°C (details in Vincent, 1988). Even within the McMurdo Sound region there can be major differences in climate between sites in relatively close proximity, for example between valleys.

The RSS is a region that is greatly isolated from other sources of biota. The northern tip of Victoria Land lies 2700 km to the south of New Zealand, and the McMurdo Sound region is another 850 km south. This contrasts with the Antarctic Peninsula which is about

1000 km from South America. The nearest neighbours to the RSS known to contain lakes and streams are the Bunger Hills (66°S, 101°E) and Vestfold Hills. These northern coastal regions are across the other side of the polar plateau in East Antarctica, about 2400 km from McMurdo Sound, and they support aquatic species not found in the RSS, for example copepods and cladocera.

Lakes

Deep lakes containing liquid water throughout the year are to be found in several parts of the RSS, but most studies to date have focused on the lakes of southern Victoria Land: Lakes Fryxell, Hoare and Bonney in the Taylor Valley, Lakes Vanda and Brownworth in the adjacent Wright Valley, and Lake Miers further to the south. Studies have recently begun on Lake Wilson, a similar but deeper (100 m) lake 300 km to the south of the Dry Valleys in the Darwin Glacier region (Webster *et al.*, 1996). All of these systems are permanently capped by thick (3.5–5.5 m) ice, however a 1–10 moat of open water melts out for 1–2 months each year around the periphery of these lakes. This edge environment is an important exchange zone for gases, surface inflows and biota. The Dry Valley lakes range in depth up to 75 m and contain a subsurface layer of dilute meltwater overlying strata of increasing salinity. This gives rise to strong gradients in the chemical and physical properties of the water column, and thus a wide spectrum of potential niches for microbial colonization and growth. Micro-organisms have in turn had a strong reciprocal influence on the depth distribution of biologically reactive chemical species. Water temperatures in these lakes vary little throughout the year, but there are major differences between lakes. Temperatures are within the range 0 to 1°C in Lake Hoare, for example, but rise to +23°C in the solar-heated bottom waters of Lake Vanda. There are also major lake-to-lake differences in chemical properties and biological productivity that could potentially influence microbial diversity. Detailed limnological information on the Dry Valley lakes is summarized in Vincent (1987), Green and Friedmann (1993) and Simmons *et al.* (1993).

The key elements of microbial food webs in aquatic ecosystems in general are given in Fig. 3. In lakes and streams of the temperate zone this component is connected via many linkages to communities of larger organisms such as higher plants, macrozooplankton and fish. The microbial food web constitutes the entire biota of the Dry Valley lakes, with the exception of Lake Vanda where there is a report of benthic moss communities (Kaspar *et al.*, 1982). The moss resembles the terrestrial species *Bryum algens*, considered to be the most widespread bryophyte throughout Antarctica. It occurred at all depths sampled in Lake Vanda, but this community appears to be poorly developed relative to the rich, multi-species bryophyte stands found in lakes of the Antarctic maritime zone. In general the benthos of Dry Valley lakes is dominated by filamentous cyanobacteria while the plankton is dominated (in biomass terms) by flagellates and non-colonial cyanobacteria. Even the moss stands in Lake Vanda are coated in cyanobacteria.

The upper water columns of Dry Valley lakes contain low concentrations of nutrients and planktonic cells. In oligotrophic environments elsewhere the plankton is typically dominated by cells less than 2 μm, the so-called picoplankton, however little is known about the picoplankton of Dry Valley lakes. The counts of heterotrophic bacteria fall in the range 10^5–10^6 cells ml^{-1} (Vincent, 1987) which is typical of oligotrophic lakewaters at most latitudes. Larger celled bacteria have been recorded in the anoxic bottom waters, but

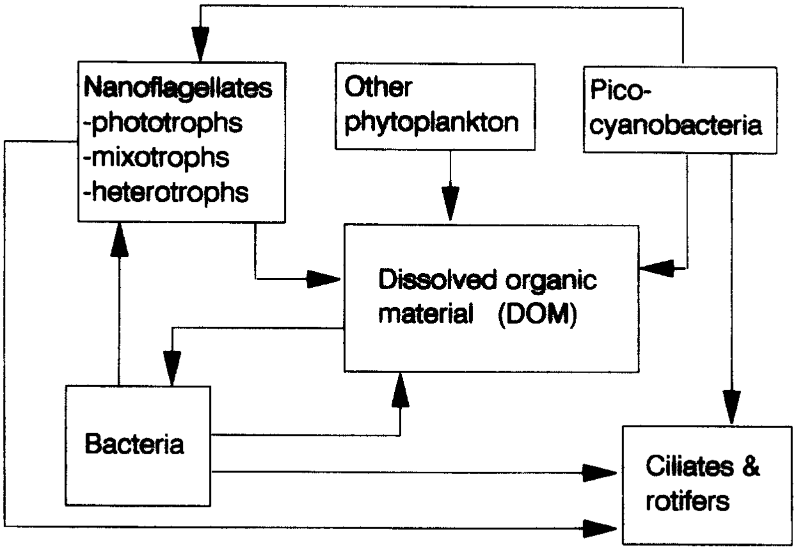


Figure 3. Microbial food web components and the main pathways of carbon flux in planktonic systems. In many RSS ecosystems these processes are most active in the benthic environment, with exchanges with the overlying water column via sedimentation of plankton and detritus, and by DOM release from the benthos.

the species composition is unknown. The presence of certain groups of bacteria in these lakewaters has been inferred indirectly by the presence of key biogeochemical intermediates, or more rarely, by specific rate determinations. For example in Lake Vanda, the nitrification intermediate nitrous oxide has accumulated to concentrations in excess of 20 000% of air equilibrium; even higher concentrations of N_2O, up to several hundred thousand percent of air equilibrium, have been recorded in Lake Bonney (Priscu, Downes and McKay, 1996). Similarly there is biogeochemical evidence of photosynthetic sulphur bacteria in Lake Fryxell, methylotrophs and methanogens in Lakes Fryxell and Vanda, and denitrifying bacteria in Lake Vanda.

For the most part the genetic diversity of these communities is not known, but molecular techniques are now being applied towards understanding the structure of these microbial ecosystems. For example, polymerase chain reaction (PCR) assays have recently been applied to Dry Valley lakes to detect ammonium oxidizing bacteria belonging to the beta and gamma subclasses of the Protobacteria (Voytek *et al.*, 1995), and immunofluorescence techniques have been used to determine the depth distribution of denitrifying bacteria in Lake Bonney (Ward and Priscu, 1995).

Autotrophic picoplankton assemblages in the oligotrophic environment are typically dominated by picocyanobacteria of the genus *Synechococcus*; however, there is little information from the Dry Valleys in this regard. Previous phytoplankton enumerations have identified *Synechocystis* and *Synechococcus* (e.g. Goldman *et al.*, 1967), but there do not appear to have been detailed epifluorescence or electron microscopic analyses to date. Studies further to the north in lakes of the Terra Nova Bay region have shown that up to 50% of the planktonic chlorophyll *a* is in the picoplankton fraction. Cultures of the < 2 μm fraction from these waters contained *Synechococcus*, eukaryotic species (*Chlorella* spp) and two unidentified entities that were possibly prochlorophytes (Andreoli *et al.*, 1992).

The phytoplankton of the Dry Valley lakes show a relatively low species diversity, but strong vertical differentiation in community structure (Table 1). In Lake Vanda, the upper community is dominated by phytoflagellates and small-cell chlorophytes, but the highest phytoplankton concentrations occur much deeper in the water column (Vincent and Vincent, 1982). As in many Antarctic lakes, the algal population maximum, the so-called deep chlorophyll maximum (DCM), occurs in the region of the sharp oxygen gradient (oxycline), immediately over the region of anoxic, nutrient-rich bottom water. This deep (57 m) community in 1981 was dominated by picoplanktonic cyanobacteria ('*Synechocystis*'), thin-trichome (thus also picophytic) cyanobacteria of the genus *Phormidium* and a green phytoflagellate. This contrasted with the DCM community previously examined in Lake Fryxell (Vincent, 1981) which in 1979 was dominated by *Chroomonas lacustris* and a species of *Pyramimonas*. The latter prasinophyte resembles *P. gelidicola*, an important constituent of the DCM in Ace Lake, an ice-covered waterbody in

Table 1. Vertical niche partitioning of the algal and microzooplankton dominants in Lakes Vanda, Fryxell and Miers; from Vincent and Howard-Williams (1985), James (1995) and Laybourn-Parry *et al.* (1996)

	Lake Vanda	Lake Fryxell	Lake Miers
Upper community:			
Depth range	3.25–15 m	4.5–6.5 m	4.5–6.5 m
Phytoplankton	*Ochromonas miniscula* *Polytomella* *Chlorella*	*O. nannos* *Chlamydomonas*	*Nannochloris* *Chlorosarcina consociata* *Chroomonas lacustris* *Ochromonas*
Microzooplankton	*Askenasia* *Monodinium* *Urotricha*	*Askenasia* *Monodinium*	
Middle community:			
Depth range	15–40 m	6.5–8.5 m	6.5–12 m
Phytoplankton	*Phormidium fragile* *P. antarcticum* *Chlamydomonas globosa* *Chlorella* *O. miniscula*	*Chlamydomonas* *C. lacustris* biflagellate	*Nannochloris* *P. frigidum* *Monoraphidium* *Ochromonas* *C. lacustris*
Microzooplankton	*Askenasia* heliozoa	*Askenasia* *Monodinium* *Vorticella*	
Lower community:			
Depth range	40–60 m	8.5–9.5 m	12–18 m
Phytoplankton	*Synechocystis* *P. antarcticum* *P. frigidum* *P. fragile* *C. globosa*	*Chroomonas lacustris* *Pyramimonas cf. gelicola*	*Gloeocystis* *Arthrospira* *Chlorella antarctica* *P. frigidum* *Nannochloris*
Microzooplankton	heliozoa *Euplotes*	*Askenasia* *Monodinium* *Strombidium*	

the Vestfold Hill region of Antarctica that shares a number of other attributes with Lake Fryxell. However another algal group found commonly in similar lakes of the Vestfold Hills, dinoflagellates, are rarely observed in waterbodies of the Dry Valleys (Seaburg *et al.*, 1979).

A unique multi-year study of the phytoplankton of Lake Fryxell has revealed large interannual variations in community structure (Spaulding *et al.*, 1994) which has important implications for the assessment of biodiversity in Antarctic aquatic habitats. Over the period 1987 to 1992 a total of 56 taxa were identified in lakewater samples. This compares with typical species lists of several hundred taxa in temperate lakes, and probably reflects competitive exclusion in the stable, stratified waters beneath the ice-cap of the lake. Some of the Fryxell species were vertically stratified (*Oscillatoria limnetica*, *Phormidium angustissimum*, *Pyramimonas* sp, *Oscillatoria* sp), while others showed no characteristic depth preferences (*Chlamydomonas subcaudata*, *Cryptomonas* sp). There were major changes in species composition relative to the 1979 study. In particular, high concentrations of filamentous cyanobacteria were observed; they had been detected in Lake Vanda in the 1981 study, and Lake Miers in 1983, but were not found in the 1979 study on Lake Fryxell (Table 1). There were also large year-to-year variations in dominants: *Chroomonas lacustris* dominated the phytoplankton community in 1987–88, while *Cryptomonas* sp. was the biovolume dominant in the subsequent four years. This interannual variability is seen to be spectacular when the phytoplankton data are expressed in terms of cell counts (Fig 4); there are major changes in dominants and little correspondence between years. In this lake there appears to be slow or minimal species succession during the summer sampling period, but clearly the community structure is unstable at longer time scales.

Paleolimnological investigations of the Dry Valley lakes will provide important new insights into the long-term scales of change in biodiversity, and will provide a historical context in which to interpret the current year-to-year variability. Diatoms are a traditional group of indicator species used for paleolimnological studies at temperate latitudes

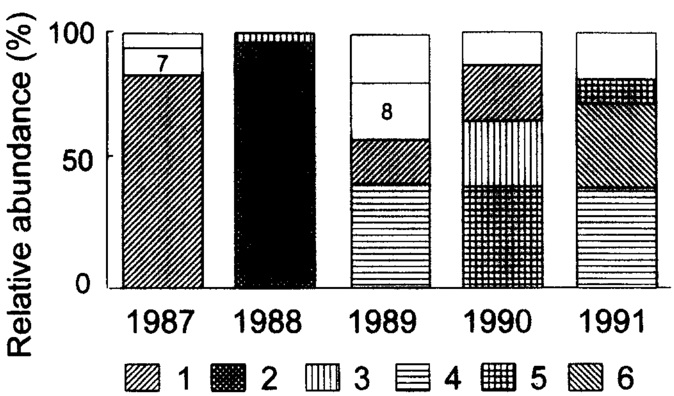


Figure 4. Inter-annual variations in phytoplankton community structure in Lake Fryxell, redrawn and reproduced by permission from Spaulding *et al.* (1994). Key: 1 = *Oscillatoria* sp; 2 = *Phormidium* sp; 3 = *Cryptomonas* sp; 4 = *Oscillatoria limnetica*; 5 = *Phormidium angustissimum*; 6 = unidentified coccoid; 7 = *Coccomyxa dispar*; 8 = *Chlorella vulgaris*.

because of their abundance within the plankton and the excellent preservation of their silicon frustules as microfossils within lake sediments. In ice-covered polar lakes the interpretation of this record may be more difficult. Diatoms are relatively rare in the plankton of Dry Valley lakes, reflecting the absence of wind-induced mixing that is required to maintain these fast-sinking organisms in suspension. A variety of diatom species have been recorded in the water column and sediments (Figs 2, 5) but many of these may be derived from algal mat communities in the lake and in the inflowing streams. Baker (1967), for example, recorded 22 species of diatom in a bottom sample of Lake Miers in the southern Dry Valleys, but most of these were as empty frustules, only five of the species were recorded in the water column, and most were benthic forms.

The lakes of southern Victoria Land are noted for their absence of crustacean zooplankton but there is increasing information about their protozoa-dominated, microzooplankton communities. The observations provide a compelling reminder that our estimates of biodiversity are very much a function of the sampling methodology adopted. Parker *et al.* (1982) only recorded two ciliate taxa in Lakes Vanda and Bonney East, three in Joyce and Hoare, four in Fryxell and no taxa in Miers. Cathey *et al.* (1981) recorded five taxa in Lake Fryxell when they sampled by net tows but found a surprisingly diverse microfauna in the water column and benthos using artificial substrates. Polyurethane foam squares incubated for up to 5 weeks in the water column of the lake collected 35 species of protozoa comprising 15 ciliate taxa, 19 flagellated phytoplankton taxa and one sarcodine. A parallel incubation on the lake floor in the littoral zone yielded 55 species. Additionally the substrates were colonized by the rotifers *Philodina gregaria* and *P. alta*, and the tardigrade *Hypsibius antarcticus*. *P. gregaria* and the tardigrade are both endemic to Antarctica. The same set of incubations in Lake Hoare recorded 20 protozoan taxa in the limnetic zone and 31 in the littoral zone. This protozoan diversity is low by comparison with lower latitudes. The same protocol but with a shorter incubation time resulted in over 150 species in temperate lakes and ponds, but comparative data are lacking for sites elsewhere in Antarctica, including the other lakes of southern Victoria Land. Based on settled water bottle samples only two ciliate taxa, a Didinidae and *Urotricha* were recorded from Lake Wilson, a large deep lake at latitude 80°S. James *et al.*, (1995) recorded 15 ciliate taxa using settled samples from the limnetic zone of Lake Fryxell in 1992. Only two of these, a small oligotrich *Halteria* and the prostome *Urotricha* had not been previously recorded from the lake. A total of 12 ciliate taxa were recorded from Lake Fryxell in 1994 (Laybourn-Parry *et al.*, 1996). One group of ciliated protozoans which are conspicuously absent from all of these collections, from Antarctic lakes in general, as well as from lakes elsewhere in the southern hemisphere, are the loricate tintinnids; this group is common in northern hemisphere lakes (James *et al.*, 1995).

It is difficult to assess year-to-year variations in protozoan community structure because of the range of sampling methods used and also taxonomic difficulties, but there is some evidence of interannual differences. *Halteria* was one of the dominant ciliates in Lake Fryxell in 1992, but was not recorded in collections from this lake in 1994; at this latter time *Askenasia* was dominant. (Laybourn-Parry *et al.*, 1996). These large differences parallel those noted above for the phytoplankton of Lake Fryxell.

Heliozoans, which are generally associated with oligotrophic lakes, have been identified as a component of the microfauna in ultra-oligotrophic Lake Vanda. Goldman *et al.* (1967) observed a species that resembled *Actinophrys* at several depths in mid to late summer 1963. Heliozoans were again recorded in this lake in 1993 and in 1994 (with zoochlorellae

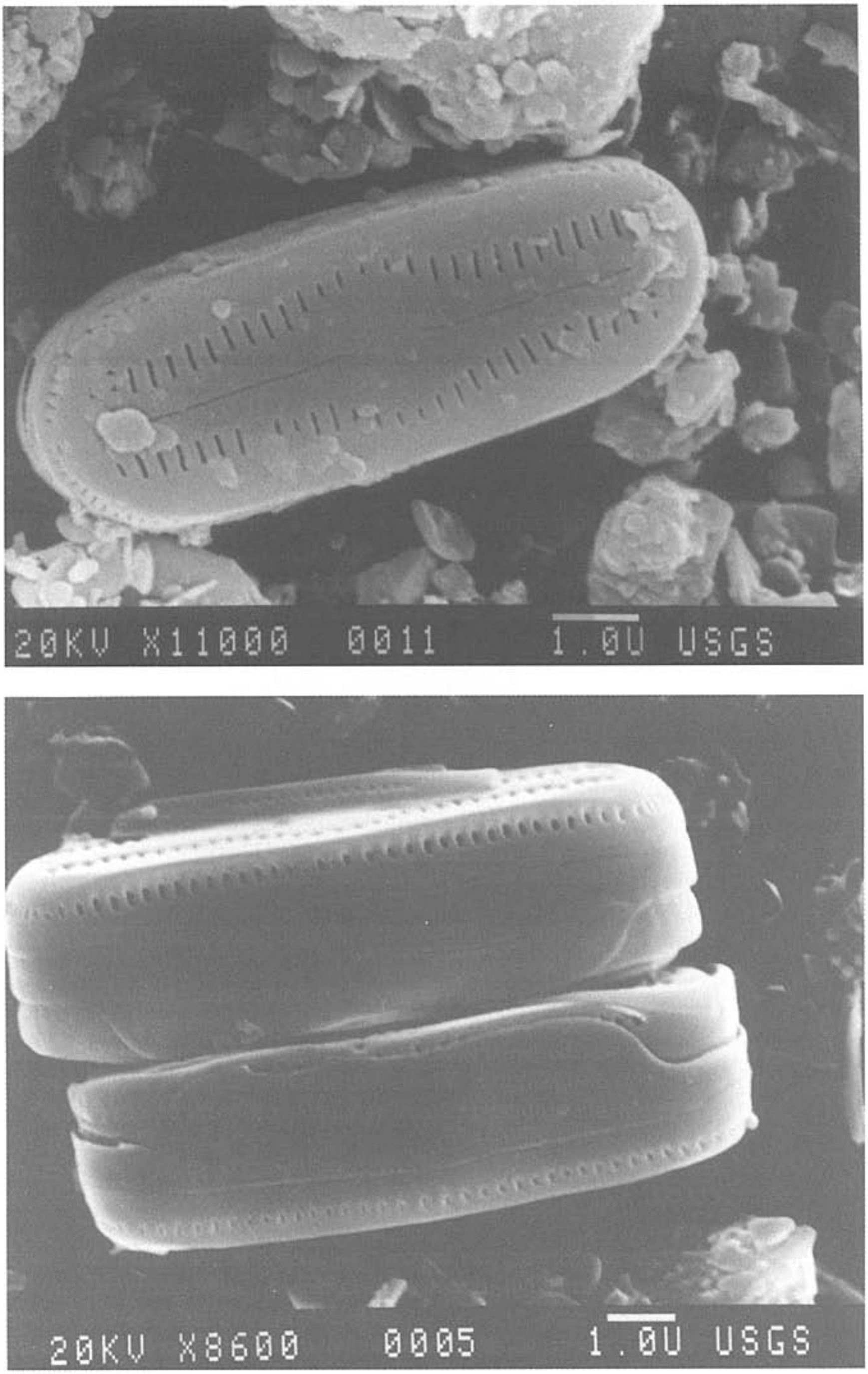


Figure 5. *Diadesmis contenta* from the surficial sediments of Lake Fryxell, McMurdo Dry Valleys. This is an attached species likely to have been brought into the lake from the catchment. The scale in µm is given at the bottom of the micrographs (upper = valve view; lower = girdle view), taken by Sarah Spaulding, United States Geological Survey.

symbionts, M. James, unpublished) but not in 1977 (Cathey *et al.*, 1981). Heliozoa have also been found in other Dry Valley lakes, specifically Lakes Miers, Brownworth, Chad and Joyce (Cathey *et al.*, 1981), but they were absent from a set of microzooplankton collections from Lake Bonney (James, unpublished) and were recorded (albeit in low concentration) in samples from Lake Fryxell in 1992 (James, 1995) but not 1994 (Laybourn-Parry *et al.*, 1996). The suctorian *Sphaerophyra* has been recorded in several of the Dry Valley lakes (Joyce, Bonney, Hoare and Fryxell), but not in Lake Vanda nor lakes elsewhere on the Antarctic continent (Laybourn-Parry *et al.*, 1996). These inconsistent records of presence and absence may reflect real differences between sites and years, an influence of trophic state on protozoan community structure (e.g. heliozoa are consistently present in Lake Vanda, the most oligotrophic of the Dry Valley lake series, but *Sphaerophyra* is an ambush predator that may not survive on the low prey densities in Vanda; Laybourn-Parry *et al.*, 1996), or simply the difficulty of reliably assessing those species which typically occur in low population densities.

The only metazoan zooplankton found in lakes in the RSS are members of the Rotifera. The endemic and ubiquitous *Philodina gregaria* is the most common and has been recorded from the limnetic zones of most RSS lakes (Cathey *et al.*, 1981). Four genera were recorded in Lake Brownworth and Lake Chad. Most taxa are bdelloids but the monogonont rotifer *Collotheca* has also been recorded from several lakes. Bdelloids are morphologically adapted to a benthic habitat, but the relative importance of benthic versus planktonic food sources for these limnetic populations in Dry Valleys lakes is at present unknown. This community is likely to be derived in part from individuals washed in from the extensive algal mats coating the streambed of inflows to the lakes, and also from the littoral sediments. The endemic tardigrade *Hypsibus antarcticus* has been recorded in several of the lakes (Bonney, Fryxell, Miers and Brownworth) and nematodes have been found in Lakes Bonney, Miers, Brownworth, Chad and Hoare (Cathey *et al.*, 1981). Generally the benthic fauna has not received the same attention as the limnetic fauna of lakes in the RSS.

Ponds

Ponds are widely distributed throughout the RSS region and range from small ephemeral pools on glaciers to larger, perennial systems in the Dry Valleys. They are chemically diverse, from dilute meltwaters to sulphate- or chloride-rich brines. Most of these waters freeze solid during winter, although the hypersaline ponds may be too concentrated to allow freeze-up. In Don Juan Pond, for example, the dissolved solids reach more than 500g l^{-1} (Vincent, 1987). The dominant salt is calcium chloride which precipitates out as antarctite ($CaCl_2.6H_2O$), a mineral found only in the Don Juan Basin. Several bacterial species and a yeast have been isolated from this habitat, but the results are controversial, and may simply reflect species washed in from the catchment (see Wright and Burton, 1981).

The coastal ponds of Ross Island have been the subject of biological study from the turn of this century onwards. Many of these are enriched by skuas and/or penguins, as well as sea spray. A study of the winter limnology of two such ponds has shown that the benthos experiences especially harsh conditions during freeze-up (Schmidt *et al.*, 1991). These ponds had conductivities of a few hundred $\mu S\ cm^{-1}$ during summer, but salts were oncentrated into the remaining water during ice formation, ultimately resulting in a chloride-rich brine with conductivities more than five times that of seawater and liquid water temperatures below −10°C. Such conditions may be a severe constraint on the range of life-forms that can survive in these environments, and may be a more important control on biodiversity than the limnological conditions measured during our usual period of field operations in summer.

When James Murray dug through the thick ice of Blue Lake at Cape Royds, Ross Island in 1908, he discovered a bottom layer of algal material which upon careful thawing revealed 'multitudes of living things for study' (Murray, 1910). Subsequent taxonomic analyses revealed that this benthic layer was composed of cyanobacteria (including a species to be named after this initial discovery, *Phormidium murrayi*) and diatoms (West and West, 1911). The ponds at Cape Royds were later visited briefly during summer by Goldman *et al.* (1972) who noted the species dominants of the brightly pigmented (red or orange) microbial mats. The most detailed taxonomic analysis of the ponds at Cape Royds as well as at other sites on Ross Island (Cape Bird, Cape Evans and Cape Crozier) is provided by Broady (1989a). He found that most of the ponds over the full range of salinities contained microbial mats or 'felts' dominated by *Phormidium, Lyngbya* and *Oscillatoria*. The saline ponds often contained a dense plankton dominated by the cryptomonad *Chroomonas lacustris*, or in the saline, nutrient-rich ponds within penguin rookeries, the chlorophyte *Chlamydomonas* cf. *snowiae*. The saline ponds also contained rich benthic growths of the filamentous chlorophyte *Ulothrix*, and abundant diatoms, notably *Navicula shackletoni, Tropidoneis laevissima* and *Melosira setosa*.

The most extensive region of ponds is on the ablation zone of the McMurdo Ice Shelf (MIS), arguably the richest site of non-marine biota in the RSS. This interconnected meltwater system contains two types of topography: undulating ice (or ice-cored moraine) which is covered by a 10–20 cm layer of moraine, with variations in surface relief of ±5–10 m; and pinnacle ice which is flatter but with ice columns up to 1–2m. Ponds ranging in size from 1 m^2 to 30 000 m^2 occur in the hollows of the undulating ice, which accounts for about 30% of the ablation zone. The pinnacle ice is a much less stable regime, with temporary pools and streams, and continuous ice erosion during the summer melt period. The ponds on the undulating ice span a particularly broad range of salinities (de Mora *et al.*, 1994), from very fresh (12 mg total dissolved solids l^{-1}) to saltier than seawater (60 400 mg l^{-1}), while those on the pinnacle ice spanned the lesser range from fresh (36mg l^{-1}) to brackish (2270 mg l^{-1}).

The biomass dominants in the MIS region are mat-forming cyanobacteria, diatoms, and planktonic flagellates. Most of the ponds are lined with cohesive mats of cyanobacteria, and planktonic chlorophyll *a* concentrations range from less than 1 μg l^{-1}, to more than 100μg l^{-1} (Howard-Williams *et al.*, 1991). A detailed survey of the algal benthos revealed 58 taxa, with 17 of these occurring in more than 25% of the samples (Howard-Williams *et al.*, 1990). There were significantly more taxa in the undulating ice ponds than in the pinnacle ice samples (Fig. 6). In part this may result from the decreased habitat stability of the latter; however, it may also reflect the greater physical and chemical diversity of potential niches on the undulating ice. There were significant differences in community structure between the two ice zones. The most common species in the undulating ice were *Phormidium autumnale, Oscillatoria deflexa* and large cell (> 10 μm) chlorophytes; in the waters of the pinnacle ice the most common species were *Phormidium laminosum* and small cell (< 10 μm) chlorophytes. One species of tardigrade, three nematodes species and

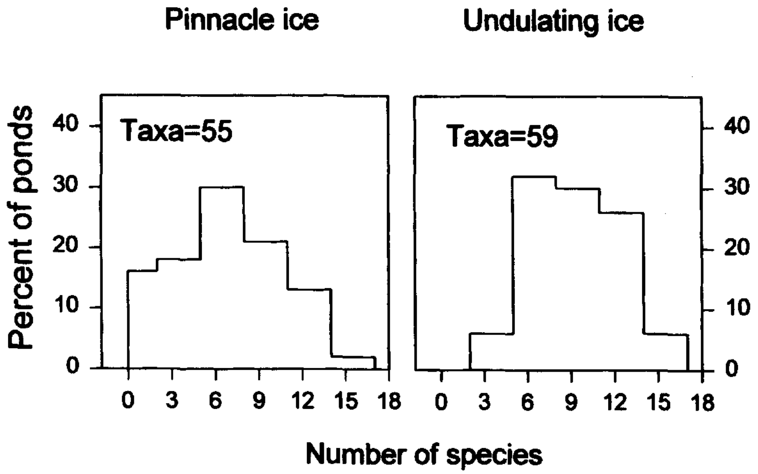


Figure 6. Biodiversity, as measured by number of taxa per sampling site, on the undulating and pinnacle ice regions of the McMurdo Ice Shelf. Redrawn from Howard-Williams *et al.* (1991).

seven rotifer taxa were found associated with the algal mats in ponds on the McMurdo Ice Shelf (Suren, 1989). Seven of the rotifer taxa were bdelloids.

Salinity appears to be an important factor controlling the distribution of algal species (Howard-Williams *et al.*, 1989). *Nostoc* and *Anabaena* were not recorded in the most saline waters. Thin trichome oscillatoriaceans dominated in the freshwater habitats, whereas thicker trichome species such as *Oscillatoria priestleyi* occurred in the saline environments. Within the diatom assemblages, the species *Pinnularia cymatopleura*, *Nitzschia antarctica* and *Navicula* sp. were characteristic of freshwater habitats, while species such as *Navicula shackeltoni* and *N. muticopsis* occurred in waters from fresh to brackish (11 mS cm^{-1}). Another species of *Navicula* as well as *Tropidoneis laevissima* were restricted to the highest salinity waters (11–60 mS cm^{-1}). The measurements of Schmidt *et al.* (1991) on Ross Island suggest that winter salinities during freeze-up may be extreme in these environments which remain saline even after melt-out, and could be a factor excluding many of the species found in the freshwater pond environments.

A survey of the plankton in the ice shelf pond waters showed that each pond contained two to nine algal taxa, with dominance usually by the phytoflagellates *Ochromonas* or *Chroomonas* (James *et al.*, 1995). *Chlamydomonas* was also found over a broad range of salinities. The highest salinity water sampled had an unusual planktonic assemblage including *Oscillatoria priestleyi* and dense populations of *Synechococcus*. This study also included a detailed inspection of the ciliate community. A total of 22 genera were recorded, with most assemblages dominated by benthic, bactivorous forms such as *Vorticella* and *Euplotes*. The number and type of genera identified in the McMurdo ponds was similar to those recorded by Armitage and House (1962) in coastal ponds on Ross Island although they missed many of the smaller nanociliates. Dillon and Bierle (1980) recorded 48 protozoan species from Coast Lake, Ross Island. There is some evidence that trophic state has an influence on protozoan's community structure in the ice shelf pond environment. While smaller, more productive ponds were dominated by small bactivorous species like *Vorticella, Euplotes* and hymenostomes, the larger, more oligotrophic ponds had lower numbers and were dominated by *Halteria* and the prostome *Bursellopsis* (James *et al.*, 1995). Benthic species such as *Nassula* and *Chilodonella* were also common in the plankton of many of the ponds. These species feed on algal filaments and were observed to have orange pigmentation derived from the benthic mats. *Euplotes* was absent from many of the larger ponds. It was also noted that the lowest number of ciliated protozoa (four taxa) was recorded in Salt Pond which had a conductivity of 54 mS cm^{-1}, suggesting an influence of the chemical environment on ciliate biodiversity.

Parts of the McMurdo Ice Shelf system experience a daily flood and ebb of freshwater caused by tidal pumping through cracks in the ice. The biota of these intertidal habitats is poorly documented but a recent study by Hawes *et al.* (1995) of a tidal lagoon at Bratina Island revealed three distinct communities. The algal community in the dry mudflat areas was dominated by motile diatoms (species of *Nitzschia* and *Navicula*). Shallow ponds contained a community similar to those in the meltponds in undulating ice (Howard-Williams *et al.*, 1990; James *et al.*, 1995). Deeper ponds were strongly stratified with a warm, saline bottom layer. These ponds contained a very different biotic community including the flagellate *Pyramimonas* which has not been recorded in other ponds of the McMurdo Ice Shelf, although it is known from Lake Fryxell (see above). This flagellate, along with a diatom *Amphiprora* which was also found in the deep water layer of tidal ponds, are commonly associated with sea-ice algae. Both habitats provide similar brine conditions. Two taxa of ciliated protozoa were also found in these ponds, a haptorid and the prostome *Urotricha*. The latter taxon was not found in any of the nearby meltponds (James *et al.*, 1995).

Ponds further northwards, in the Terra Nova Bay region, have now been studied by several research groups (Broady, 1987; Guilizzano, 1992; Fumanti *et al.*, 1995). The species assemblages appear to be quite similar to those recorded in the McMurdo Sound region, with benthic mats dominated by cyanobacteria (diatoms as subdominants), and the phytoplankton typically dominated by phytoflagellates. For example, the majority of ponds at Inexpressible Island had thick benthic felts of cyanobacteria (Broady, 1987). In the ponds outside the influence of a penguin rookery these benthic communities were dominated by oscillatoriaceans with thin (0.5–2.0 μm) trichomes; inside the penguin rookery the ponds were dominated by phytoplankton, in particular a species resembling *Chlamydomonas subcaudata*, and benthic diatoms typical of saline or nutrient-enriched waters *Tropidoneis laevissima, Melosira setosa* and *Navicula muticopsis*. At Edmonson Point spherical colonies of *Nostoc sphaericum* were often associated with the rich oscillatoriacean felts, and on the lateral moraines of the Campbell Glacier (near Gondwana Station) the felt was unusual in that it was dominated by *Microcoleus vaginatus*. Diatoms were also commonly found in the benthos of the unenriched ponds at each of these sites, and included *Pinnularia cymatopleura, Nitzschia* sp., *Navicula muticopsis* and *Stauroneis anceps*.

The southernmost aquatic systems studied to date are in the Brown Hills and Darwin Glacier region at latitude 80°S, about 300 km to the south of McMurdo Sound (Vincent and Howard-Williams, 1994). Oscillatoriacean mats occurred in many of the freshwater and saline lakes, ponds and streams of this region and contained species including *Phormidium autumnale, P. fragile* and *Schizothrix* sp. Neither *Nostoc* nor diatoms were recorded in these far south benthic communities.

Diatoms were also conspicuously absent in samples from pond environments sampled on the western side of the RSS, in Marie Byrd Land (Broady, 1989c). Oscillatoriacean felts were again common in various freshwaters sampled in this region. Many of the cryoconite ponds (meltwaters contained within ice basins) at Washington Ridge had an unusual benthic flora with the rare cyanobacterial species *Homeothrix* cf. *rivularis*, as well as the chlorophytes *Dictyochlopsis* sp. and *Stichococcus bacillaris*. Elsewhere in this region the cryoconite pools had a similar flora, but without *Homeothrix* and with the N_2-fixing cyanobacterium *Nostoc*. Although *Homeothrix* had not been previously observed in this type of habitat, *Nostoc* and oscillatoriaceae are well represented in the cryoconite ponds on glaciers in the western side of the RSS such as in the Dry Valleys (Wharton *et al.*, 1981), on Ross Island and in Northern Victoria Land. Such pools, however, typically also contain diatoms such as the widely distributed species *Pinnularia cymatopleura*, but neither this species nor other diatoms contributed to the communities sampled in the cryoconite waters of Marie Byrd Land (Broady, 1989c).

Streams

A great variety of flowing water environments occur throughout the RSS and are important foci for microbial colonization and growth. These waters are all fed by snow and glacier melt, but they encompass a broad spectrum of mean and maximum flow regimes, nutrient content and sediment loads. The streams are ephemeral, although many occupy perennial streambed channels, and flow for only a few weeks each year. In general, they are highly unstable systems that are subject to large variations in their chemical and physical properties from timescales ranging from time of day to interannual (Vincent *et al.*, 1993).

Cyanobacteria are often the species dominants in the stream microbial ecosystems of the RSS (Fig. 7), but there is considerable site-to-site variation in community structure, including downstream gradients in floristic composition. Four types of cyanobacterial community are typically found within the flowing water environments: epilithic crusts and films, cohesive mats dominated by oscillatoriaceae, black mucilaginous layers of *Nostoc commune*, and communities associated with moss banks (Howard-Williams *et al.*, 1986a; Vincent *et al.*, 1993).

The epilithic communities are typically black, red or brown in colour and are dominated by *Gloeocapsa* and *Schizothrix*. In the headwaters of the Alph River system in the southern Dry Valleys the black crusts form an almost continuous coating over the rocks and contain the heterocystous species *Calothrix* in addition to *Gloeocapsa, Schizothrix* and sometimes *Nostoc* (Howard-Williams *et al.*, 1986b). Although green algae also occur in some of the stream environments they appear to be of much lesser importance relative to the Antarctic maritime zone. Diatoms are commonly found in many of the stream environments, particularly in sandy substrata.

The macro-algal species *Prasiola* occurs in several types of stream habitat. On the coast the species *P. crispa* is especially common in streams enriched by nearby penguin colonies. In the Dry Valley streams the species *P. calophylla* is often found in shaded habitats such as within, between or on the undersurface of rocks (Broady, 1986b). This taxon resembles a species found in similar habitats in high Arctic streams (Hamilton and Edlund, 1994).

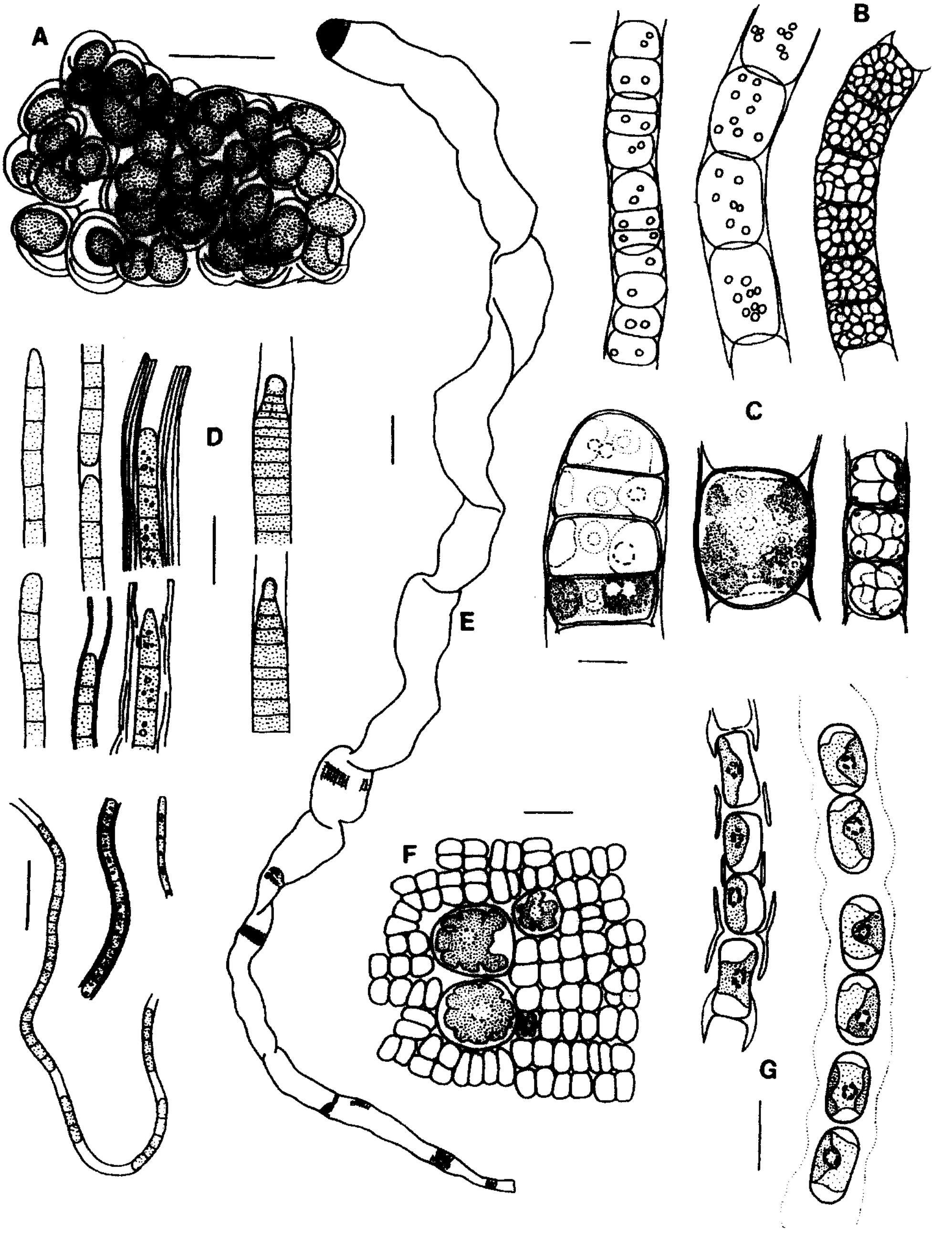


Figure 7. Dominant cyanobacteria and eukaryotic algae found in RSS streams. Drawings by P.A. Broady, and reproduced by permission from Vincent *et al.* (1993). Key: A, *Gloeocapsa kuetzingiana*; B, *Urospora* sp.; C, *Urospora* sporangia; D, various oscillatoriaceans; E, ribbon form of *Prasiola calophylla*; F, detail of E showing cell arrangement and enlarged reproductive cells; G, *Binuclearia tectorum*. All scale bars are 10 μm, except for E, which is 100 μm.

The fungal biodiversity of the RSS is poorly known in general, but preliminary data are available from a Taylor Valley stream. Three species of filamentous yeasts (*Leucosporidium antarcticum, Cryptococcus jungaricus, Vanrija foliorum*) as well as several unidentified species of *Vanrija* were identified from the sediments (Klinger, 1987).

Biodiversity in the RSS

Our ability to define and measure biodiversity in microbial ecosystems is still limited, but a number of interesting features emerge from the work conducted to date in the RSS. First, there is little evidence of endemism. Most of the microbial species found to date in this region are cosmopolitan taxa that are well known from outside the south polar region. On first inspection this is perhaps surprising given the long period of isolation (>20 million years) of Antarctica from the rest of the world. Endemism is well illustrated in the Antarctic marine flora and fauna for example (Knox, 1994), including some micro-organisms (e.g. Miceli, 1994). This suggests that, at a microbial level, there is continuous exchange with biota from other latitudes, for example by air currents or bird migration. Alternatively it may indicate that the severe and highly variable environmental conditions of Antarctica have selected for a small subset of generalist species that can do well and survive in a broad range of conditions in Antarctica as well as elsewhere in the world. A third potential explanation is that this apparently low endemism reflects the inadequacies of criteria we currently use, especially morphological criteria, to differentiate genetically distinct micro-organisms. In the future, it will be especially interesting to examine with molecular techniques species such as *Phormidium laminosum* which occur in both the North and South polar zones as well as in diverse temperate (including geothermal) and tropical latitude habitats. Molecular analyses of widely distributed protozoan species will also be highly informative in this regard.

Microbial biodiversity, as measured to date, appears to be low in the RSS, with the frequent occurrence of a small number of genotypes that occur under an extremely broad range of conditions. These include members of the Oscillatoriaceae (although the genetic variability in this important Antarctic group is poorly understood), other cyanobacteria such as *Nostoc commune* and *Gloeocapsa* spp., flagellates such as *Chroomonas lacustris* and *Chlamydomonas subcaudata*, and certain diatoms, notably *Pinnularia cymatopleura*. In the eastern and southern extremes of the RSS even *Nostoc* and diatoms appear to be rare or absent. This low diversity suggests that such ecosystems could change substantially, even rendered abiotic, by the extinction of only a few species. Perturbations such as contaminant release, continued UV increases or global warming effects may push some of these species beyond their current limits of tolerance.

The low microbial diversity of the RSS is mirrored by the small number of multicellular plants and animals in the aquatic environments of this sector. Mosses, for example are an important component of lake ecosystems in the maritime Antarctic, but are sparsely distributed in the RSS with the exception of a few specific sites (e.g. Fryxell Stream in the Dry Valleys; Schwarz *et al*., 1992). Several rotifer species are found throughout the region, to as far south as at least 85°S (Wise and Gressitt, 1965), but no crustacean zooplankton have yet been recorded in non-marine habitats of the RSS. In part this may reflect the great distance between the RSS and northern sources of biota. It has been suggested for example that *Daphniopsis studeri*, a cladoceran species found in East Antarctica but not in the RSS, colonized the Vestfold Hills lakes from the Iles Kerguelens and Marion Islands. The depauperate RSS fauna might also indicate a lack of suitable refugia during periods of cooling and glacier advance. Bayly and Burton (1993) have suggested that epishelf lakes (ice-capped freshwater floating on more saline water that is in direct connection with the sea) may be a critical habitat for refuge populations of zooplankton during such periods. There are no large systems of this type known to occur in the RSS. On the other hand, cryoconite habitats, and ice-shelf pond systems of the type now found on the McMurdo Ice Shelf, may have been suitable refugia and major sources of re-seeding populations for hardier organisms such as rotifers, nematodes, protozoa and other microbiota.

An important new development for ecological research in the RSS has been the commitment to studies beyond one year with the establishment of the NSF Long-Term Ecological Research site in the Taylor Valley, and with ongoing studies in the Italian Terra Nova Bay programme. The enormous year-to-year variations in phytoplankton structure of Lake Fryxell attest to the potentially severe interannual variability that has affected our observations to date on the aquatic communities of this region. Both of these programmes have begun to attract much-needed, additional taxonomic expertize into the region. Most of the research to date in the RSS has focused on the phototrophs, and the distribution and population structure of most of the heterotrophic communities is very poorly understood. Even the phototrophic groups, however, such as diatoms and the cyanobacteria require much further taxonomic scrutiny and community analysis using traditional approaches as well as new cellular and molecular techniques. There is considerable potential for paleolimnological studies, particularly of the Dry Valley lakes, to place the current biodiversity of these systems and their variability in a historical context.

The RSS is now a region of increasing research and tourism activity. In the 1993/94 season tourists entered the Taylor Valley (McMurdo Dry Valleys) for the first time, and up to several hundred tourists now visit this area each season. This increased human activity will require careful management to minimize disturbance and biological contamination of these unique landscapes and polar microbial ecosystems (Vincent, 1996). Although many of these systems contain high levels of microbial biomass, the communities are slow growing and depauperate in species; their rate of recovery from environmental disturbance may therefore be extremely slow.

In concluding, we propose three hypotheses to help guide future research on the microbial biodiversity of the RSS. These hypotheses rest on the central tenet developed in this review that environmental extremes plus biogeographical isolation control the biodiversity of communities in these non-marine aquatic habitats:

1. Colonization of the RSS lakes, ponds and streams has been primarily from northern, temperate latitudes rather than from elsewhere in Antarctica. *The low biodiversity of this region reflects its biogeographical isolation from northern source biota.* A prediction of this hypothesis is that there should be decreasing biodiversity from north to south over the >15 degrees span of latitude within the RSS. This effect may be compounded by the increasing severity of environmental conditions with distance southwards. A second prediction is that microbial biodiversity in the RSS should be lower than in aquatic habitats at equivalent latitudes in the north polar zone which is much less isolated from source microbiota.

2. The primary selective pressure on organisms entering the RSS is the set of physical and chemical extremes which characterize this region, particularly those associated with

freezing and thawing. *Biodiversity is therefore mostly limited to species which have broad tolerances rather than an ability to grow fast.* A prediction of this hypothesis is that apart from their resilience to certain types of environmental stress, many microbial species in the RSS have slow maximum growth rates and/or occur in habitats where maximum growth is rarely achieved.

3. Competitive interactions, grazer activities, parasitism (viruses, bacteria, fungi) and predation are all likely to occur within the microbial ecosystems of the RSS. However, the absence of 'top-down' control from invertebrate grazers such as insects and crustaceans, the small population size of micro-invertebrate grazers such as nematodes and rotifers, the small number of competing species and the inhibiting effect of low temperature on biological processes, in combination with (1) and (2), lead to the hypothesis that *the ability to compete for resources, or to resist grazing, parasitism and predation, are not major factors contributing towards the biodiversity of the RSS.* A prediction of this hypothesis is that the micro-organisms in these habitats show less niche-specialization and less biological adaptation ('goodness-of-fit') to specific conditions during growth than in planktonic or benthic communities in other regions of the world.

Evaluating these three hypotheses will require more detailed field studies of the distribution of microbiota throughout the RSS. It will also require a close reciprocal coupling between laboratory experiments and field measurements to determine the microbial responses to gradients and extremes in the south polar environment.

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