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The microbial plankton of Lake Fryxell, southern Victoria Land, Antarctica during the summers of 1992 and 1994

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Abstract Samples collected from Lake Fryxell, southern Victoria Land, Antarctica in January 1992 and 1994 were analysed for the abundance of bacterioplankton and the diversity and abundance of protistan plankton. At the times of sampling, 14 ciliate species and 10 species of autotrophic flagellate were recorded. The samples contained two species of rotifer (Philodina spp.), which formed the first record of planktonic metazoans in the Dry Valley lakes of this region of Antarctica. Bacterial concentrations ranged between 1.0 and $3.8 \times 10^8 l^{-1}$ in the upper oxic waters increasing to $20 \times 10^8 l^{-1}$ in the anoxic waters. Heterotrophic flagellates decreased in abundance down the oxygenated water column, disappearing completely at 9 m, and ranged between 0.28 and $7.39 \times 10^5 1^{-1}$ in abundance. Autotrophic flagellates were much more abundant exhibiting a number of distinct peaks down the water column $(1.89-25.3 \times 10^8 1^{-1})$. The ciliated protozoa were very abundant (up to 77201^{-1}) in relation to flagellate and bacterial numbers, typical of oligotrophic lakes world-wide. The distribution of the

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protistan plankton showed marked zonation, probably in response to the differing salinity and temperature gradients in the water column. Possible trophic interactions are discussed and comparisons with other continental Antarctic lakes made.

Introduction

The growing appreciation of the importance of microbial plankton in the nutrient regeneration and energy flow (Azam et al. 1983) has led to many investigations aimed at quantifying their biomass and role in lake systems (e.g. Weisse et al. 1990; Šimek and Straškrabová 1992; Laybourn-Parry et al. 1994). Antarctic lake systems have been less well studied from this standpoint, probably because of logistic constraints; however, the data available indicate that these lakes are dominated by microbial food webs (Laybourn-Parry et al. 1991, 1992, 1995; Laybourn-Parry and Marchant 1992a; Parker et al. 1982). Antarctic lakes are considered to have low species diversity and biomass of the microbial constituents, since almost all lakes are ultra-oligotrophic, unless they are enriched by bird and seal faeces.

Metazoan plankton are sparse or absent. The plankton of the oasis lakes of the Vestfold Hills have one sparse daphniid species (*Daphniopsis studeri*) and a few migratory benthic rotifer species (Laybourn-Parry and Marchant 1992b). The much older lakes of the Dry Valleys in Victoria Land apparently lack metazoans (Parker et al. 1982). In contrast, the maritime lakes, which have been studied in detail by the British Antarctic Survey, have a number of crustacean and rotifer components, which may become relatively abundant on occasions and impose top-down control (Heywood 1972, 1977; Laybourn-Parry et al. 1996). Continental lakes lack top-down control and are entirely driven by bottom-up forces, which in turn are related to the physical and chemical extremes of the environment.

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The low species diversity seen in continental lakes is undoubtedly related to the isolation of the continent from other land masses, and the extreme climate. While the continent has relatively few lakes, those that occur are remarkably diverse in type and age. The oasis lakes of the Vestfold and Larsemann Hills, for example, are relatively young at around 8000 years old and were formed during isostatic uplift (Adamson and Pickard, 1986), and for a few weeks each year most of the freshwater lakes become ice free. The suite of lakes in the Vestfold Hills ranges from saline relic marine systems to large freshwater lakes. In contrast, the lakes of the Dry Valleys of Victoria Land are considered to be very old, probably hundreds of thousands of years. This desert oasis has been ice-free for up to 5 million years (Armstrong et al. 1968; Hendy et al. 1977; Denton and Hughes 1981). The lakes are meromictic and permanently ice covered, though they may develop a moat in summer. Thus they have had longer for colonisation to have occurred. A study of their littoral and moat zones revealed a wide range of protozoans, six rotifer species and two tardigrades, but no crustaceans (Cathey et al. 1981). The lakes in the McMurdo Dry Valleys, although older, are not in a steady state, and the lake levels have risen steadily since they were first surveyed by the Scott expedition. This is attributed to warmer temperatures and greater meltwater inflows (Chinn 1993).

Constant ice cover means that these lakes lack windinduced mixing of the water column, which in turn has important consequences on the types of organism that can successfully colonise. Many of the dominant algal populations in Lake Fryxell occur in well-defined depth ranges within the water column (Spaulding et al. 1994), indicating that stratification of food resources as well as environmental conditions may control the position of heterotrophic plankton in the water column. Motility or some means of buoyancy is an important pre-requisite for any organism in such a stable water column, because they must be able to maintain their position at an appropriate level in the water column for their physiological functioning. This paper presents data on the protozooplankton and their food from several independent studies on Lake Fryxell, one of the most productive of the Dry Valley lakes.

Materials and methods

Sampling site

Lake Fryxell ($77^{\circ}37'$ S, $163^{\circ}07'$ E) has an area of 7 km² and a maximum depth of 19 m (Lawrence and Hendy 1985). The average depth is 9 m and therefore the lake has an extensive littoral zone (above a depth of 9 m) where microbial mats are abundant (Cathey et al. 1981). The lake is chemically stratified with an oxic zone extending down to 9.5 m (Torii et al. 1975; Lawrence and Hendy 1985). A distinct oxycline is present between 7.5 and 9.5 m below which the waters are anoxic. The lake is permanently stratified. The upper

waters are low in nutrients $(NH_4^+, NO_2^-, NO_3^- \text{ and } PO_4^-)$ but ammonium and soluble reactive phosphorus increase below the oxycline (Vincent 1981; Spaulding et al. 1994). Thus the upper waters experience a combination of low temperatures, nutrient limitation and highly attenuated light because of ice cover.

Sampling and analyses

Water was collected using either a Kemmerer bottle or a Van Dorn sampler lowered through a hole drilled in the 4-m-thick ice with a Jiffy-drill in January 1992 (by James) and in January 1994 (by McKnight and others) at a centre station (depth 18.5 m). Samples were taken at 1-m intervals down to 12 m into the anoxic zone. In 1992, 250-ml subsamples were fixed in Lugol's iodine for the analysis of ciliates, and other aliquots fixed in glutaraldehyde for bacterial counts. In 1994, 1.1-l samples were fixed in buffered glutaraldehyde for protozoological and bacterial analysis. These were kept refrigerated in the dark and flown to Australia or New Zealand for immediate analysis. Both fixatives are regarded as reliable for protistan analysis provided samples are analysed within a few months of collection (Ngando and Groliere 1991; Leakey et al. 1994). However, in our experience while Lugol's iodine is considered best for preserving abundance, it does cause more cell distortion of some species than glutaraldehyde, which may hamper identification. Moreover, we used buffered glutaraldehyde, which gives better preservation of ciliates in freshwater samples. One litre of water from each depth was preserved in Lugol's iodine for phytoplankton counts. Temperature was measured with a (YSI) Yellow Springs Instruments 54 meter and probe, and conductivity with a Radiometer Conductivity meter.

Ten milliliters of the buffered glutaraldehyde-fixed material was stained with DAPI, and filtered onto a 0.2- μ m black polycarbonate filter, and bacterial numbers were counted under epifluorescence microscopy using UV excitation. Fifty milliliters was stained with DAPI, filtered onto 1.0- μ m polycarbonate filters and viewed under epifluorescence microscopy using both blue and UV filters to determine heterotrophic and autotrophic flagellate abundances. The larger protozooplankton in each 1-1 sample of glutaraldehyde-fixed water were concentrated by settling, stained with bromophenol blue and counted in Sedgewick-Rafter counting chambers under higher magnification using both DIC and phase microscopy. For phytoplankton analysis between 5 and 50 ml was subsampled. These phytoplankton were settled and enumerated using the inverted microscope method of Utermöhl (1958).

Results

Lake Fryxell has permanent ice cover to a thickness of 4.0 m. Typically the water temperature rises from close to zero immediately under the ice to around 3.5°C at 12 m (Fig. 1). Conductivity also increases with depth so that the water environment moves from freshwater to brackish in the water column (Fig. 1). Twelve species of ciliated protozoan were identified in January 1992 and 1994 (Table 1) plus several unidentified species of heterotrich and a prostomatid. The total numbers of ciliates varied between the 2 years, but the distribution patterns were very similar (Fig. 2a). A clear distribution pattern for species emerged, with virtually no ciliates below 10 m. A large peak of ciliates occurred at 10 m on each occasion; this was largely due to an unidentified prostomatid that occurred in high numbers between 8 and 12 m. Askenasia was also common

throughout the upper 10 m in 1994 but in 1992 it was sparse; instead *Halteria* was one of the most common ciliates in the upper 10 m (Fig. 2b). A small species of *Monodinium* was particularly common immediately



Fig. 1 Typical temperature and depth profiles for Lake Fryxell in January (\bigcirc) temperature; (\bullet) conductivity. Data collected 1992

under the ice in 1994, and then decreased down the column, but was joined at 7 m by another, larger, species of Monodinium. (Fig. 3a). A plastidic species of Strombidium (probably S. viride) occurred down the water column to 10 m (Fig. 3b). Other relatively common species were Vorticella mayeri, a large ciliate $(85-120 \,\mu\text{m long})$ that showed strong autofluorescence suggesting endosymbiotic algae, was tentatively identified as Bursaria, in the upper 7 m and a suctorian Sphaerophrya (Fig. 3b). In 1992 fairly large numbers of an unidentified scuticociliate occurred throughout the upper 12 m (up to 5001^{-1}) and *Vorticella* sp. extended down to 12 m. While the abundances shown in the profiles from each year are derived from single samples taken at each depth, there is remarkable similarity in the pattern of total ciliate abundance at each depth (Fig. 2a).

Heterotrophic bacterial numbers in 1994 ranged between 1.0 and $3.8 \times 10^8 1^{-1}$ in the upper waters and then increased markedly at the oxycline to reach concentrations of up to $20 \times 10^8 1^{-1}$ (Fig. 4). In 1992 bacterial concentrations in the 6- to 12-m portion of the water column ranged between 0.9 and $15 \times 10^8 1^{-1}$ with a less well-defined peak below 9 m. The nature of the community also changed at this point from strongly DAPI-stained rods around 0.6–0.9 µm in length (typical of lake plankton), to larger yellow fluorescing populations. Heterotrophic nanoflagellates (HNAN) showed a progressive decline down the water column to zero at 9 m (Fig. 4).

Table 1 Species list and occurrence in Lake Fryxell in January 1992 and 1994 (Asterisks indicate presence of species in years of study)

Species	Occurrence		Species	Occurence	
Heterotrophic Protozoa			Autotrophic Protozoa		
Ciliophora	1992	1994	Phytomastigophora	1992	1994
Askenasia	*	*	Brachiomonas submarina		*
Bursaria?		*	Chlamydomonas spp.	*	*
Chilodonella		*	C. subcaudata	*	*
Didinium	*		Chromulina sp.		*
Euplotes c.f. aediculatus		*	Chroomonas lacustris	*	*
Halteria	*	*	Cryptomonas sp.	*	
Monodinium large sp.		*	Dinobryon sp.	*	
Monodinium small sp.		*	Ochromonas sp.	*	
Nassula		*	O. miniscula		*
Sphaerophyra		*	Pseudokephrion schilleri		*
Strombidium viride	*	*	Pyramimonas sp.	*	*
Vorticella mayeri	*	*	Algae		
Unidentifed prostomatid	*	*	Chlorophyta		
Zoomastigophora			Coccomyxa sp.		*
Choanoflagellates	*	*	Chlorella sp.		*
Sarcodina			C. vulgaris	*	
Unidentified heliozoan	*		Stichococcus bacillaris		*
			Cyanophyta		
			Chroococcus sp.	*	
			Phormidium frigidum		*
			P. angustissimum	*	*
			Oscillatoria sp.	*	
			Oscillatoria limnetica	*	
			Synechococcus sp.	*	*



Fig. 2 a Total numbers of cilated protozoans in 1992 and 1994 in the water column of Lake Fryxell. b The distribution of *Askenasia* and *Halteria* in the water column 1992 and 1994

Phytoplankton cells, which include the larger phototrophic flagellates (>10 μ m), as well as algae and cyanobacteria (see Table 1 for species), showed a distinct peak around 6 m in 1994, but not in 1992 (Fig. 5). In 1992 large numbers of cells appeared at 10 m. This peak was mostly composed of the cyanobacteria *Synechococcus* sp. and *Phormidium angustissimum*. The



Fig. 3 a The distribution of *Monodinium* spp. in the water column: large species, *hatched columns*; small species, *solid columns*. b The distribution of other common ciliate species in the water column: Strombidium viride, solid columns; Vorticella mayeri, dark-hatched columns; Bursaria, checked columns; Sphaerophyra, light hatched columns

latter looked somewhat degraded in appearance and may have been dying and accumulating at denser strata near the oxycline. The phytoplankton peak at 6 m was largely due to Phormidium angustissimum and P. frigidum together with Chlorella sp. and Chroomonas lacustris. Filamentous cyanobacteria (Phormidium sp.) were very common down the water column, peaking at 6 m, and their abundance dropping off rapidly at the oxycline (Fig. 6). Chlorella was the third most common phytoplankter (Fig. 6) in the upper waters. Where conductivity increased to around $1500 \,\mu\text{S}\,\text{cm}^{-1}$ (between 7 and 9 m), Chroomonas lacustris appeared in large numbers (Fig. 6). Phototrophic flagellates (PNAN), which like the HNAN ranged in size between 4 and 6 µm in length, varied considerably down the profile with three distinct peaks discernible, at 5 m, 7 m and 10 m below the oxycline (Fig. 4). Cell volumes of the commoner species Chlorella and Synechococcus were



Fig. 4 Bacteria (\bullet), heterotrophic flagellates HNAN (\blacksquare) and phototrophic flagellates PNAN (\bigcirc) in Lake Fryxell



Fig. 5 Phytoplankton cells in the water column of Lake Fryxell in 1992 (\bigcirc) and 1994 (\bigcirc)

 $8.0 \,\mu\text{m}^3$ and $2.0 \,\mu\text{m}^3$, respectively. These cells were smaller than their lower latitude counterparts.

In both 1992 and 1994 rotifers were recorded in low numbers. In 1992, numbers ranged from $8 \, l^{-1}$ at 6 m to



Fig. 6 Distribution of the dominant phototrophic components in the water column of Lake Fryxell in 1994. Dark columns, Chlorella sp.; dark-hatched columns, Chroomonas lacustris; checked columns, cynaobacterial species

 201^{-1} at 10 m. In 1994 they occurred throughout the top 6 m of the water column, decreasing progressively from 341^{-1} under the ice to 41^{-1} at 6 m. The 1994 samples were examined in detail. Two species were apparent, both members of the Bdelloidea. The smaller of the two species was identified as *Philodina alata* and the other larger species was also a *Philodina*. Their morphology suggests that these are benthic species that may be derived from the algal mats around the edges of the lake.

Discussion

To our knowledge metazoans have never been recorded in the plankton of the Dry Valley lakes. The lack of metazoans in samples has been noted by Parker et al. (1982) and by Spaulding et al. (1994). In this analysis we have established that rotifers are a part of the plankton, as they are in the oasis lakes of the Vestfold and Larsemann Hills (Laybourn-Parry and Marchant 1992a; Laybourn-Parry et al. 1992; Ellis-Evans et al. 1995). They are around 3 times more abundant in Lake Fryxell than in the Vestfold Hills lakes. Bdelloid rotifers are the representatives of the phylum in the Vestfold Hills as in Lake Frxyell, and in both cases the species are morphologically adapted to the benthic habit. They have migrated into the plankton from the littoral region, presumably to exploit the food resources there. Two species of Philodina, including Philodina alata, have been recorded from the littoral zone of Lake Fryxell (Cathey et al. 1981). The planktonic population has clearly come from the littoral regions of the lake, but its distribution in the water column suggests a well-established planktonic community that is undoubtedly exploiting the relatively abundant algae and protozoan communities as food.

Their arrival in the plankton may be relatively new, since they were less common in 1992. Filamentous cyanobacteria have also only recently become established in the plankton, as they were not recorded in studies undertaken before 1980 (Spaulding et al. 1994). These changes in the plankton over the past 15 years are possibly caused by greater inflow of meltwaterflushing species from the littoral zone into the main body of the lake, thereby facilitating the establishment of "new" planktonic species.

By Antarctic standards Lake Fryxell has a very great diversity of planktonic protozoans, which probably reflects the age of the systems and changes in temperature and salinity (between 1-7%) within the upper water column, which offer a range of physiochemical conditions at different strata. In a previous study covering 5 austral summers, 56 species of phototrophs (algae, phototrophic protozoans and cyanobacteria) were recorded (Spaulding et al. 1994). Some species occurred every year, while others were recorded in 1 year only. In contrast, detailed studies on the lakes in the Vestfold Hills and Larsemann Hills have revealed low species diversity (Laybourn-Parry and Marchant 1992a; Ellis-Evans et al. 1995). Only one lake, No Worries Lake adjacent to the Chinese Station of Zong Shan (Larsemann Hills), had a similar high species diversity. This lake has suffered human impact effects in the form of elevated temperatures and eutrophication (Ellis-Evans et al. 1995).

Some species of protozooplankton are confined to particular strata in Lake Fryxell: for example, the unidentified prostomatid and the phototroph Chroomonas lacustris in the deeper more saline layers, and high numbers of *Monodinium* immediately below the ice. It is likely that the prostomatid is feeding on the large bacteria and abundant filamentous cyanobacteria. Others obviously have a relatively good tolerance to changing salinity and temperature. Some of the species recorded are regular constituents of the plankton in freshwater lakes of all latitudes and the Antarctic, for example Askenasia sp., Halteria sp. and Strombidium viride (Laybourn-Parry and Marchant 1992a; Laybourn-Parry 1994). Stratification of the phototrophic protistan community has been noted previously, with the primary production of species like *Ochromonas* and Chlamydomonas in the upper euphotic zone being limited by nitrogen availability, while lower down in the water column Chroomonas and Pyramimonas were not nutrient limited and were able to undertake photosynthesis at an irradiance of $< 5 \,\mu E \,m^{-2} \,s^{-1}$ (Vincent 1981). In contrast, the brackish and saline meromictic lakes of the Vestfold Hills contain typical marine ciliates like Mesodinium rubrum and oligotrichs, including a species of Strombidium (Perriss et al. 1995; Laybourn-Parry and Perriss 1995). Thus the brackish waters of the Dry Valley lakes contain a totally different ciliate community to the meromictic, much younger, saline systems of the Vestfold Hills. They do share *Pyramimonas* as a common autotrophic component, but whereas dinoflagellates are very common in the Vestfold Hills saline lakes, they have only been recorded in the plankton of one of the Dry Valleys lakes (Lake Bonney-East) (Parker et al. 1982). However, they have been recorded from colonised polyurethane foam substrates suspended in the water column of Lake Fryxell (Cathey et al. 1981).

Interestingly, peritrichs (e.g. *Vorticella*) and the suctorian *Sphaerophyra* have also been recorded in Lakes Joyce, Bonney-East and Hoare (Parker et al. 1982; Cathey et al. 1981), but in no other continental systems so far studied. Suctorians are ambush predators of other ciliates, and would probably not be able to survive and grow in the sparse prey conditions found in most continental lakes elsewhere. They occur quite commonly in lake plankton at lower latitudes, e.g. Windermere (Laybourn-Parry and Rogerson 1993). In the Vestfold Hills lakes ciliate numbers are low in the summer $(0-2801^{-1})$ when one would expect the community to reach its maximum abundance (Laybourn-Parry and Marchant 1992) so that a ciliate dependent on chance encounters with its prey would not survive.

Heliozoans, which are regular members of the protozooplankton in the Antarctic and at lower latitudes (Laybourn-Parry 1992, 1994), were not recorded in the plankton of Lake Fryxell or any other Dry Valley lake by Parker et al. (1982). They were recorded in Lake Vanda (Goldman et al. 1967) and in several other Dry Valley lakes by Cathey et al. (1981). Recently, one of the authors (M.J.) has recorded them as abundant in Lake Vanda. At lower latitudes they tend to be sporadic in occurrence in mesotrophic and eutrophic lakes, but regular constituents of oligotrophic waters (Laybourn-Parry et al. 1994).

Bacterial abundances in Lake Fryxell were measured in the early 1980s by Vincent and Howard-Williams (1985). They recorded much higher concentrations than we found in the present study (up to $90 \times 10^8 1^{-1}$). As in our study, they also found a marked peak in numbers around 10 m. Since a similar technique was applied one must assume that bacterial numbers have declined in the last decade. The bacterial concentrations found in Lake Fryxell during the current study are comparable to densities reported from ten freshwater lakes in the Vestfold Hills $(1.3-5.1 \times 10^8 1^{-1})$ and three saline lakes in the same oasis $(0.54-1.20 \times 10^8 1^{-1})$. In the case of two of these lakes, a comparable increase in bacterial numbers occurred at the chemocline to concentrations around $30 \times 10^8 l^{-1}$ (Laybourn-Parry and Perriss 1995). Concentrations in a deeper, more oligotrophic, Dry Valleys lake (Lake Vanda) ranged from $10^7 1^{-1}$ in the upper waters to around $5.0 \times 10^9 \, l^{-1}$ below the oxycline, with the largest cells occurring just below the oxycline (Konda et al. 1987; Vincent and Howard-Williams 1985). The upper water concentrations were somewhat lower than those seen in Lake Frxvell, but the same increase in cell size in the anoxic water occurred.

On a global basis, reported values for bacterioplankton range between 0.1 and $11.8 \times 10^9 1^{-1}$ (Stockner and Porter 1988; Bloem and Bar-Gilissen 1989; Weisse et al. 1990; Vaqué and Pace 1992; Laybourn-Parry et al. 1994) depending on the trophic status of the lake. Lake Fryxell lies at the oligotrophic end of the trophic spectrum.

The HNAN that graze on bacteria typically range in abundance from 0.1 to $90 \times 10^6 1^{-1}$ (Pick and Caron 1987; Nagata 1988; Bloem and Bar-Gilissen 1989; Bennett et al. 1990; Laybourn-Parry et al. 1994) across the trophic continuum. The HNAN abundances in Lake Fryxell are typical of an ultra-oligotrophic lake. In contrast, PNAN abundances are higher than those found in other Antarctic lakes and in oligotrophic lakes at lower latitudes. In the Vestfold Hills abundances range between 0.8 and $13.3 \times 10^3 1^{-1}$ (Laybourn-Parry and Marchant 1992), and in a temperate oligotrophic system between 0.3 and $120 \times 10^3 1^{-1}$ (Laybourn-Parry et al. 1994) compared with $190-2531 \times 10^{3} l^{-1}$ in Lake Fryxell. The high numbers of ciliates (up to $7720 \, l^{-1}$ in 1992 and 46351^{-1} in 1994) are comparable to the abundances found in mesotrophic temperate lakes (Laybourn-Parry 1992).

The relative abundances of the different microbial groups allow some speculation as to the trophic interactions. Relative to the other heterotrophic protists and bacterioplankton, ciliate numbers are unusually high. The HNAN are probably exploiting the smaller bacteria in the waters above 8 m and may also be using dissolved organic carbon, as some marine flagellates have been shown to do (Marchant and Scott 1993). While some of the ciliates are also exploiting bacteria, for example Vorticella and scuticociliates, the majority are probably dependent on various specific fractions and/or combinations of the PNAN, HNAN and phytoplankton. The large population of ciliates at 8-10 m is probably using both the cyanobacteria and other abundant larger-sized bacteria at these depths. Two of the ciliate species are mixotrophic, combining heterotrophy with some donation of translocated photosynthate from sequestered plastids (Strombidium viride) and zoochlorellae (Bursaria). Among the autotrophic flagellates, at least two species (Ochromonas and *Dinobryon*) have been shown to also take up bacteria (Sanders and Porter 1988). The phenomenon of mixotrophy among phytoflagellates is believed to increase their access to nutrients and vitamins for photosynthesis, and to supplement their carbon budget. It has been suggested as a possible survival strategy for phytoflagellates in Antarctic lakes during the prolonged period of winter darkness (Vincent 1988).

The microbial plankton of Lake Fryxell are markedly different to those from the other continental Antarctic lakes that have been investigated. The biomass is higher and the community much more diverse than in other systems, both freshwater monomictic and saline meromictic, elsewhere in Antarctica. The large ciliate community in the lake indicates that, either (1) ciliates are growing very slowly, or (2) their food sources have relatively high productivity and are being heavily grazed: moreover, they are not subject to predation pressure. The data presented here suggest some interesting trophic interactions and physiological ecology that need to be addressed empirically.

One feature that is of particular note is the variability in the species composition in different years. In 1992, for example, *Halteria* was one of the dominant ciliates, whereas in 1994 *Askensia* was dominant. Other species appear to be fairly constant. Similar changes have been noted in the phytoplankton species composition (Spaulding et al. 1994). However, with data for only a few months in the summer it is difficult to draw firm conclusions. Long-term studies that span most, or all, of a year reveal much more about the successions in lake plankton. Such data for Antarctic lakes are few because of logistic constraints.

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