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Ciliated protozoa of two antarctic lakes: analysis by quantitative protargol staining and examination of artificial substrates

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Abstract Planktonic and artificial substrate-associated ciliates have been identified in two perennially ice-covered antarctic lakes of the McMurdo Dry Valleys. Abundances estimated by quantitative protargol staining ranged from < 5 to $31690 \text{ cells} \cdot \text{l}^{-1}$, levels that are comparable to those previously obtained using other methods. Nineteen ciliate taxa were identified from these lakes, with the most frequently encountered genera being *Plagiocampa*, *Askenasia*, *Monodinium*, *Sphaerophrya* and *Vorticella*. The taxonomic findings compare favorably with those of previous investigators; however four previously unreported genera were observed in both Lakes Fryxell and Hoare. The variability in the depth distributions of ciliates in Lake Fryxell is explained in terms of lake physicochemical properties and ciliate prey distributions, while factors related to temporal succession in the Lake Hoare assemblage remain unexplained. Local marine or temperate zone freshwater habitats are a more likely source than the surrounding dry valleys soils for present ciliate colonists in these lakes. Although the taxonomic uncertainties require further examination, our results suggest that ciliate populations in these antarctic lakes undergo significant fluctuations and are more diverse than was previously recognized.

Introduction

Perennially ice-covered antarctic lakes are examples of aquatic ecosystems existing at the extremes of conditions

found on Earth. These are habitats in which biogeochemical cycles are mediated almost entirely by microbial populations, and multicellular life is virtually absent. Continental antarctic lakes provide unique opportunities to understand the structure and function of microbially dominated ecosystems. In these extreme environments the role of protozoa as trophic links may be of great significance.

The microbial loop is recognized as a major pathway of energy and nutrient flow in aquatic systems, in which protozoa are the major grazers of bacteria and phytoplankton (Azam et al. 1983; Pomeroy and Wiebe 1988). Most investigations into the fate of aquatic microbes have focused on the following as direct regulators of bacterioplankton numbers and productivity: (1) availability of inorganic nutrients (primarily nitrogen and phosphorus); (2) dissolved organic matter availability; (3) microprotozoan grazing pressure; and (4) feeding by larger, metazoan bacterivores. In the water columns of the antarctic lakes considered here, the role of planktonic metazoan bacterivores is minimal due to their virtual absence. Low concentrations of inorganic nutrients and low solar radiation (light levels are greatly attenuated by overlying ice covers) are both known to limit primary production in these systems (e.g., Goldman 1964; Vincent 1981, Priscu et al. 1989, Priscu 1995). Although some of the physical and chemical factors that influence microbial productivity have been studied in these lakes, the distribution and role of microprotozoan grazers as regulators of bacterial and phytoplankton dynamics remains relatively unstudied.

In addition to conducting process-oriented studies of protozooplankton in antarctic lakes, it is also important to understand the basics of taxonomic diversity in these systems. In this paper, we evaluate the distribution of ciliate (Protozoa, Ciliophora) taxa with respect to depth in Lake Fryxell, and the distribution of taxa at a single depth, with respect to time in Lake Hoare, using the quantitative protargol staining (QPS) method. The QPS method is regarded in many ways as the best method

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currently available for obtaining both accurate identifications and quantitative abundance estimates of ciliates (Montagnes and Lynn 1993). We also report on ciliate identifications made by examining live material collected on colonized artificial substrates. The degree of similarity in ciliate community composition between the two lakes is discussed, and we compare our taxonomic findings with those obtained in previous studies of antarctic lakes. The data presented here provide a quantitative evaluation of ciliate community structure in these unique aquatic systems.

Study sites

The McMurdo Dry Valleys

The McMurdo Dry Valleys (77°00'S, 162°52'E) of southern Victoria Land, Antarctica, are characterized as a cold desert ecosystem. Our study lakes are within the largest ice-free area of continental Antarctica, roughly 5000 km² in size. Minimal precipitation (< 10 cm · year⁻¹) along with cold, arid winds from the polar plateau, make the region as climatically extreme as any on the planet. The fieldwork was based at the NSF-funded McMurdo Dry Valleys Long-Term Ecological Research site located in Taylor Valley. The ecosystem characteristics in the McMurdo Dry Valleys are summarized elsewhere (e.g., Vincent 1988; Green and Friedmann 1993; Priscu 1998).

Study lakes

Located at the eastern end of Taylor Valley, Lakes Hoare and Fryxell are morphologically, chemically, and biologically distinct lakes which are separated by the Canada Glacier. Neither Fryxell nor Hoare have outlet streams and there appears to be no groundwater discharge from the lakes. The vast majority of water loss occurs through direct sublimation from the surface lake ice (Henderson et al. 1965; McKay et al. 1985). Water columns are exceptionally stable from season to season and year to year with respect to physical and chemical properties (Spigel and Priscu 1998), although recent studies suggest that limited mixing may occur (Miller and Aiken 1996; Tyler et al. 1998).

Lake Hoare waters are very cold, dilute (conductivity < 700 µmhos · cm⁻¹), and change only gradually with depth. Anoxic conditions exist below 28 m in Hoare, which has a maximum depth of 34 m. Major features in Lake Hoare include: (1) a double oxycline with a slight decrease in dissolved oxygen (DO) at 11–14 m and large decrease below 25 m, (2) a minor increase in specific conductance (9–14 m) which then increases more gradually with depth, (3) a decrease from pH 9 to 7 between 9 and 14 m, and (4) a narrow range of temperatures throughout the water column (0–1.0°C). Lake Fryxell has a maximum depth of 20 m, and other characteristics

include: (1) a strong permanent oxycline (8.5–10 m), with anaerobic (DO < 1 mg · l⁻¹, high-H₂S) waters below 11 m, (2) low epilimnetic nutrient concentrations, (3) a constant increase in conductivity below 7 m, and (4) a gradual increase in temperature between 5 and 10 m (from 0 to 2.5°C). Light also attenuates more rapidly in Lake Fryxell than in Hoare, for example the net incident solar radiation at 11 m was 0.4% and 2.1% in Fryxell and Hoare, respectively (Kepner et al. 1997). Detailed descriptions of these antarctic lakes can be found elsewhere (Lawrence and Hendy 1985; Green et al. 1988, 1989; Vincent 1988; Wharton et al. 1989; Green and Friedmann 1993; Spigel and Priscu 1998).

Microbial community structure

Due to their relative biotic simplicity, ice-covered dry valley lakes act as excellent model systems for investigating trophic interactions and materials/energy flows in which protozoa may play important roles. By most criteria, Lake Fryxell would be considered to be oligotrophic, while Lake Hoare would be considered to be an ultra-oligotrophic lake. Nevertheless, the lakes have seasonally abundant phytoplankton populations, dominated by a few dozen cyanobacterial, phytoflagellate, and non-flagellated chlorophyte taxa. Given the unusually stable water columns of these lakes, microbial populations – including motile flagellates and ciliates – are typically stratified with depth (Vincent 1981; Parker et al. 1982a; Lizotte et al. 1996; Laybourn-Parry et al. 1997). Flagellate genera such as *Cryptomonas* and *Chroomonas* (Cryptomonadida), *Ochromonas* (Chrysoomonadida), *Pyramimonas* (Prasinomonadida) and *Chlamydomonas* (Volvocida) – some of which may be active mixotrophs – congregate seasonally at particular depths in both Lakes Hoare and Fryxell (Vincent 1988; Spaulding et al. 1994; Laybourn-Parry et al. 1997; James et al. 1998). Total bacterial densities in Hoare and Fryxell are not substantially different from those commonly encountered in temperate, oligotrophic lakes (Vincent 1987; Konda et al. 1994; Kepner et al. 1997; Laybourn-Parry et al. 1997; Takacs and Priscu 1998), although heterotrophic activity is relatively low (e.g., Smith and Howes 1990; Takacs and Priscu 1998).

Few prior studies have considered the protozoan assemblages of either Lakes Hoare or Fryxell (Cathey et al. 1981, 1982; Laybourn-Parry et al. 1997). In general, the pristine lakes of continental Antarctica have been considered to have low species diversity and depauperate ciliate assemblages relative to antarctic marine (Perriss and Laybourn-Parry 1997), arctic lake, temperate and tropical systems (Laybourn-Parry et al. 1991). The freshwater protozoan communities of Antarctica have been considered to be relatively species-poor and comprised almost entirely of cosmopolitan forms (e.g., Sudzuki and Shimoizumi 1967; Vincent and James 1996). The results presented in this paper examine the validity of these generalizations as they apply to these

particular dry valley lakes and add to our knowledge of ciliate diversity in these unique systems.

Materials and methods

Sample collection

Water samples were collected from ice-covered Lakes Fryxell (26 December 1996) and Hoare (3, 13, and 23 December 1996, and 12 January 1997). Water was obtained using a 2.0-l Niskin bottle following drilling with a 10-cm-diameter, motor-powered ice auger through approximately 4 m of ice at each site. Samples were collected from a single site in the deepest parts of both Lakes Fryxell (77°36'42.7"S, 163°08'49.5"E) and Hoare (77°37'40.5"S, 162°54'42.7"E).

Quantitative protargol staining

Subsamples of whole water samples were preserved in Bouin's solution (Lee et al. 1985a), poured into 500-ml graduated cylinders and allowed to settle for 5–7 days. The top 455 ml of sample was then aspirated off and the remaining 45 ml, plus 5 ml of deionized water used to rinse the cylinder was concentrated by low-speed centrifugation (approximately 2000 g) to a final volume of 2.0 ml. Following return from Antarctica, concentrates were resuspended in 50 ml of filter-sterilized (2.0 µm pore-size) 5% Bouin's solution. Aliquots (25 ml) of these Bouin's-preserved samples were then concentrated on 0.45 µm Millipore (Type HA) filters, coated with a thin layer of agar and stained by the QPS technique of Montagnes and Lynn (1993). Prepared slides were examined under brightfield illumination using Zeiss optics (Carl Zeiss, Thornwood, N.Y. USA) at a magnification of $\times 1250$. Preparations were systematically evaluated for taxonomic composition by direct microscopic observation of material prepared using the QPS method. Estimates of ciliate abundance were obtained by either counting all cells present on the filter, or by enumerating specimens in 400 randomly selected microscope fields. In the latter case, at least 100 ciliates were counted for each slide preparation. Ciliates were sorted by morphotype during counts and, with rare exception, were subsequently identified to genus using established criteria (Small and Lynn 1985; Foissner et al. 1991, 1992, 1994, 1995).

Artificial substrate samples

Live samples were also collected during the austral summer of 1995–96 using artificial substrates. Polyurethane foam units (PFUs) were deployed at several depths in Lakes Hoare and Fryxell and left *in situ* for a period of 3 weeks. Protists from substrates were identified at least to genus, and to species when possible, using a Zeiss Standard 16 microscope with phase contrast, at the Lake Hoare field camp. Standard protozoological keys were used (e.g., Kudo 1966; Lee et al. 1985b). Identified protozoa were classified according to the system of Levine et al. (1980). Quantitative data on ciliate abundances from PFU samples are not presented here. Details of the PFU technique are provided elsewhere (Pratt and Kepner 1992).

Results and discussion

QPS abundance estimates

Total QPS abundances in the whole water samples from Lake Fryxell exceeded the maximum abundance estimates obtained in the summers of 1992 and 1994

(7720 · l⁻¹, Laybourn-Parry et al. 1997). However, our QPS abundances (Table 1) did not exceed the high ciliate density estimates (as many as 22195 · l⁻¹, obtained following Sedgewick-Rafter cell counts of Lugol's-preserved Fryxell samples collected on 27 November 1996. The mean densities in the aerobic zone on this date ranged from 391 · l⁻¹ at 6 m to 18490 · l⁻¹ at 10 m (Kepner et al., to be published). One month later, total ciliate abundances in Fryxell were still greatest near the oxycline and lower in nutrient-poor upper waters. Ciliate taxa were rarely observed in samples from artificial substrates colonized in either oxic or anoxic waters, and ciliates were generally undetectable in anoxic Fryxell waters below a depth of 11 m.

A large range in ciliate abundances was observed in Lake Hoare over time (Table 2). At a depth of 12 m in Lake Hoare, several changes in the distribution of taxa occurred over the 6-week sampling period. The virtual absence of ciliates in the 13 December sample is striking. *Plagiocampa* was abundant early in December (1001 cells · l⁻¹, 74% of observed ciliates) and then disappeared completely from waters at 12 m. This does not appear to be related to food availability since bacterial abundance and production remained relatively constant at this depth during the 1996–97 austral summer (Takacs and Priscu 1998).

The depth distributions of ciliates in Lake Fryxell, on the other hand, appeared to be closely related to the distribution of bacterial cells. Peaks in bacterial production were commonly observed between 9 and 10 m in Fryxell (Takacs and Priscu 1998), and bacterial densities increased below 9 m (Smith and Howes 1990; Konda et al. 1994). Likewise, peaks in heterotrophic and phototrophic flagellate abundances have been observed at this chemocline (Kepner et al. to be published). Interestingly, the peak ciliate abundance in Lake Hoare (1353 cells · l⁻¹) corresponds to the 12-m, 3 December peak observed in extracellular, planktonic virus abundances (Kepner et al. 1998). We suggest that in addition to bacteria, perhaps ciliates in these systems ingest virus-

Table 1 Ciliate abundances from Lake Fryxell at various depths. All samples were collected on 26 December 1996

Ciliate taxa	Depth (m)				
	4.5	6	8	9	10
<i>Askenasia</i> sp. 1	7	3	3	0	2
<i>Cyclidium</i> sp. 1	0	0	0	1	0
<i>Cyclotrichium</i> sp. 1?	1	0	0	0	0
<i>Enchelydon</i> sp. 1?	5	0	0	0	0
<i>Euplotes</i> sp. 1	0	0	1	0	0
<i>Frontonia</i> sp. 1	0	0	1	1	0
<i>Monodinium</i> sp. 1	5	9	5	1	1
<i>Plagiocampa</i> sp. 1	0	0	0	265	122
<i>Vorticella</i> sp. 1	0	2	2	1	3
<i>Uronema</i> sp. 1	0	0	0	2	0
Unknown genus	1	0	0	0	0
Total no. of cells counted	19	14	12	271	128
Total cells · l ⁻¹	96	69	60	31690	14968

Table 2 Ciliate abundances from Lake Hoare on various dates. All samples were collected at a depth of 12 m

Ciliate taxa	Date			
	3 Dec. 1996	13 Dec. 1996	23 Dec. 1996	12 Jan. 1997
<i>Askenasia</i> sp. 1	58	0	9	100
<i>Blepharisma</i> sp. 1	1	0	4	0
<i>Cyclidium</i> sp. 1	0	0	0	1
<i>Euplotes</i> sp. 1	1	0	0	0
<i>Monodinium</i> sp. 1	6	0	10	12
<i>Plagiocampa</i> sp. 1	196	0	0	0
<i>Vorticella</i> sp. 1	2	0	0	0
<i>Urotricha</i> sp. 1	1	0	0	0
Total no. of cells counted	265	0	23	113
Total cells · l ⁻¹	1353	< 5	110	548

sized particles, as has been demonstrated for heterotrophic marine flagellates (Gonzalez and Suttle 1993).

Ciliate densities in these antarctic lakes are likely to be controlled by bottom-up forces. This is also the most probable scenario in oligotrophic, open ocean habitats, where ciliate densities are comparable to those in Lakes Fryxell and Hoare (e.g., Suzuki et al. 1998). The dominance of bottom-up forces in structuring ciliate assemblages is likely to be evident in other systems that are devoid of crustacean zooplankters or other consumers of protozoa, as is the case in the dry valleys lakes.

Taxonomic richness and diversity

A total of 19 ciliate taxa were observed in Lakes Hoare and Fryxell during this study. The greatest richness (14 taxa) was observed in the more productive Lake Fryxell. As is typical, data showed a skewed distribution of species abundances with number of species (i.e., there were many more infrequently occurring than frequently occurring taxa). On a sample-by-sample basis, the most frequently encountered genera in QPS-prepared samples were *Plagiocampa*, *Askenasia* and *Monodinium*. In observations of live samples collected from PFUs, the most frequently encountered ciliates were *Sphaerophrya* and *Vorticella*. This is reasonable given that stalked peritrichs such as *Vorticella* spp. will have an affinity for surfaces on which to attach. Suctorians, including stalkless forms such as *Sphaerophrya*, may also have an affinity for surfaces and benthic environments, given their lack of cilia and inability to swim in the adult trophic state.

The highest ciliate diversity was observed in the upper waters of Lake Fryxell (Table 3). Diversity was lowest where the ciliate community was dominated by *Monodinium* or, in the case of Lake Hoare, when ciliates were extremely sparse. The detection limit of the QPS method, given the sample volumes examined, is about 5 cells · l⁻¹, thus a reported total ciliate density of zero (as at Hoare on 13 December) is more accurately reported as < 5 · l⁻¹. Although not statistically significant ($r = 0.549$, $0.05 < P < 0.10$) taxonomic diversity (the average of Simpson and Shannon diversity indices) ap-

pears to be negatively correlated with total ciliate density. The degree to which we can generalize a relationship between overall antarctic lake trophic status (i.e., primary productivity) and ciliate diversity remains to be established.

In our samplings of PFUs from Lakes Hoare and Fryxell, non-ciliate taxa that were frequently encountered included *Bodo globosa*, *Ochromonas* sp. (probably *O. minuta* or *O. miniscula*), *Chlamydomonas globosa*, *Chroomonas lacustris*, and *Pyramimonas* sp.; all of which were observed in approximately half the substrates collected (Kepner and Wharton 1997). Phytoflagellate groups were often numerically dominant in our collections, and the majority of species encountered also occur in temperate lakes.

Regarding the functional diversity of planktonic protozoa in these antarctic lakes, we can only speculate. Artificial-substrate assemblages were dominated by bacterivorous taxa based on functional group classification by taxa (Pratt and Cairns 1985). This is also the case for assemblages from ponds of the McMurdo Ice Shelf, where 83% of ciliates are bacterivores (James et al. 1995). It is possible that some of these ciliate taxa are algivores or facultative mixotrophs which may sequester chloroplasts from consumed prey. The methods used here for quantifying and identifying ciliates do not yield useful information regarding the nutritional modes of these organisms.

Community similarity

Euclidean distance measures were used to evaluate community similarity between sampling holes using the QPS data (Tables 1, 2). A distance of zero would indicate that the exact same taxa were found in the exact same densities in two different samples (i.e., that communities in the two samples were identical). Distance measures indicate that, depending upon the time and depth of sampling, assemblages in Lakes Hoare and Fryxell can be quite similar (Fig. 1). Chemocline samples from Fryxell are similar to non-chemocline samples from Hoare when dominant taxa are found in each (e.g., *Plagiocampa*), and despite a greater overall abundance

Table 3 Taxonomic richness and Simpson and Shannon diversity indices computed for samples analyzed for ciliate taxonomic diversity using the quantitative protargol staining technique

	Lake								
	Fryxell					Hoare			
Depth or date	4.5 m	6 m	8 m	9 m	10 m	3 Dec.	13 Dec.	23 Dec.	12 Jan.
"Label"	F45	F6	F8	F9	F10	H123	H1213	H1223	H112
Richness	5	3	5	6	4	8	0	3	3
Simpson (H')	0.60	0.39	0.62	0.06	0.10	0.32	0.00	0.45	0.17
Shannon (D)	0.72	0.52	0.72	0.04	0.09	0.40	0.00	0.63	0.21

of ciliates in Fryxell, intra-lake spatial and temporal variability in community composition is as great as the differences between the two lakes. This is in agreement with the observation that significant intra-lake differences in protozoan community structure occur at spatial scales of as little as 3 m in the vertical, and that within-lake differences can be as great as those between these two lakes (Kepner and Wharton, 1997).

Comparisons to prior studies

The ciliate identifications made during the course of this study compare favorably with those obtained in previous studies (Table 4). Twenty-four ciliate genera have been positively identified from Lake Fryxell during prior studies and we have observed 13 of these same genera. Seventeen genera have been positively identified from Hoare during prior studies and we have observed 11 of these. We observed four previously unreported genera in Lake Fryxell (*Cyclidium*, *Cyclotrichium*, *Frontonia* and *Plagiocampa*), and four previously unreported genera in Hoare (*Chilodonella*, *Cyclidium*, *Monodinium* and *Plagiocampa*). The occurrence of these ciliates implies

that we have not yet obtained a complete picture of protozoan diversity in these lakes and that increased sampling efforts are likely to reveal an even greater diversity of ciliate taxa than is herein described. Seasonal dynamics in the protozooplankton are also not well understood. While a recent study considered phytoplankton community composition changes in Lake Fryxell over the dark antarctic winter (McKnight et al., in press), protozoan assemblages in these lakes have only been studied during austral summers (October through February). Seasonal community succession and year-to-year variability in protozoan species composition (e.g., Laybourn-Parry et al. 1997) remain unexplained.

The occurrence of *Chilodonella* and *Monodinium* in Lake Hoare is not surprising given that they have previously been reported from nearby Lake Fryxell. *Cyclidium* has not been observed before in any of the McMurdo Dry Valley lakes, even though it is one of the most commonly encountered freshwater scuticociliates. *Cyclidium* were not common in either Fryxell or Hoare samples, possibly due to their preference for more eutrophic environments (e.g., Lake Nakaru, Finlay et al. 1987). Only two individual *Frontonia* cells were identified, one each in the whole water samples from 8 and 9 m in Lake Fryxell. *Frontonia* was not collected on PFUs, nor has it been previously reported from any of the McMurdo Dry Valley lakes. Bierle (1969), however, reported the occurrence of antarctic *Frontonia* in Coast Lake, a small freshwater lake in Victoria Land.

A total of 11 ciliate taxa were found in Lake Fryxell by Laybourn-Parry et al. (1997). We have observed the majority of these same taxa (Table 4). James (1995) observed 15 ciliate taxa in Lake Fryxell during the 1992 austral summer. At that time, only two of the taxa identified by James (*Urotricha* and *Halteria*) had not been previously recorded from this lake. Comparisons can also be made with the ciliate communities observed in nearby Lakes Vanda and Bonney (James et al. 1998). Lake Vanda appears to have a seasonally fluctuating ciliate community which is low in diversity relative to Lakes Bonney, Fryxell and Hoare. The number of ciliate taxa in Vanda ranged from two to five over four samplings in 1994 and 1995, while up to nine taxa were observed in the water column of Bonney (James et al. 1998). Generalizing to the McMurdo Dry Valley region, we can say that the most commonly encountered genera appear to be *Askenasia*, *Euplotes*, *Halteria*, *Monodinium*,

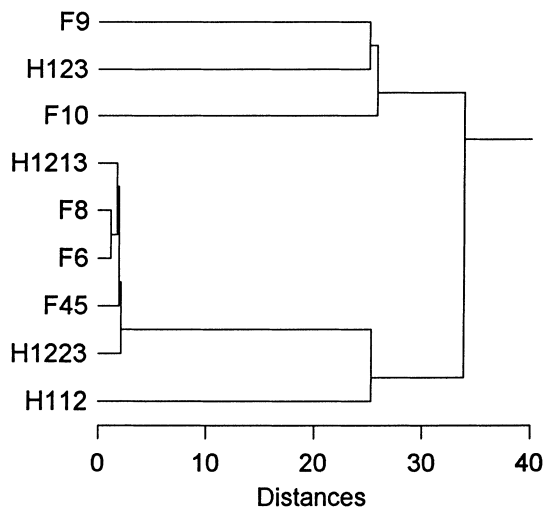


Fig. 1 Hierarchical Euclidean distance cluster tree formed from quantitative protargol staining data using the single linkage (nearest neighbor) method (Hartigan 1975). The site "labels" are as given in Table 3

Table 4 Summary of ciliate taxa identified in Lakes Fryxell and Hoare. The font in which the year observed appears indicates the type of sample in which each ciliate type was identified i.e. in the water column (normal typeface), benthic or on artificial substrates (*italic typeface*), or both of these (**bold typeface**)

Genus	Species	Lake Fryxell		Lake Hoare	
		Year(s) observed	Citation(s)	Year(s) observed	Citation(s)
<i>Askenasia</i>	sp	1978–1979, 1992, 1994, 1996	1, 3, this study	1978–1979, 1996–1997	1, this study
<i>Askenasia</i>	<i>volvox</i>	1978–1979	1		
<i>Blepharisma</i>	<i>hyalinum</i>			1978–1979	1
<i>Blepharisma</i>	sp			1978–1979, 1996	1, this study
<i>Bursaria</i> (?)	sp	1994	3		
<i>Chaenea</i>	sp	1978–1979	1		
<i>Chilodonella</i>	<i>algivora</i>			<i>1995–1996</i>	This study
<i>Chilodonella</i>	sp	<i>1978–1979, 1994</i>	1, 3		
<i>Cinetochilum</i>	<i>margaritaceum</i>	<i>1977, 1978–1979</i>	1, 2	1978–1979	1
<i>Cinetochilum</i>	sp	<i>1978–1979</i>	1	<i>1978–1979</i>	1
<i>Colpoda</i>	sp			1978–1979	1
<i>Cyclidium</i>	sp	1996	This study	1995–1996 , 1997	This study
<i>Cyclotrichium</i> (?)	sp	1996	This study		
<i>Didinium</i>	<i>balbianii</i>	<i>1977, 1978–1979</i>	1, 2	1978–1979	1
<i>Didinium</i>	sp	1978–1979, 1992	1, 3	1978–1979	1
<i>Enchelyodon</i>	sp	1978–1979, 1996	1, this study		
<i>Enchelys</i>	<i>mutans</i>			<i>1978–1979</i>	1
<i>Enchelys</i>	sp	<i>1977–1978</i>	2		
<i>Euplotes</i>	<i>c.f. aediculatus</i>	1994	3		
<i>Euplotes</i>	<i>eurystomus</i>	1978–1979	1		
<i>Euplotes</i>	sp	1978–1979, 1995–1996	1, this study	<i>1977, 1978–1979,</i> 1995–1996	1, this study
<i>Euplotes</i>	sp 1	1978–1979	1	<i>1978–1979</i>	1
<i>Frontonia</i>	sp	1996	This study	<i>1978–1979</i>	1
<i>Halteria</i>	sp	1992, 1994, <i>1995–1996</i>	3, this study	<i>1978–1979</i>	1
<i>Holophrya</i>	<i>simplex</i>			<i>1978–1979</i>	1
<i>Holophrya</i>	sp	1978–1979	1, 2	1978–1979	1
<i>Holophrya</i>	sp 1	<i>1978–1979</i>	1		
<i>Holophrya</i>	sp 2	<i>1978–1979</i>	1		
<i>Holosticha</i>	sp	<i>1978–1979</i>	1		
<i>Holosticha</i>	<i>vernalis</i>	1978–1979	1		
<i>Homalozoon</i>	sp	<i>1977</i>	1		
<i>Lacrymaria</i>	sp	1978–1979	1	<i>1978–1979</i>	1
<i>Lacrymaria</i>	sp 1	1978–1979	1	<i>1978–1979</i>	1
<i>Loxophyllum</i>	sp	<i>1978–1979</i>	1		
<i>Mesodinium</i>	sp	<i>1978–1979, 1995–1996</i>	1, 2, this study		
<i>Monodinium</i>	sp	1995–1996	This study	1996–1997	This study
<i>Monodinium</i>	sp 1 (<i>large</i>)	1994	3		
<i>Monodinium</i>	sp 2 (<i>small</i>)	1994	3		
<i>Nassula</i>	sp	<i>1977, 1977–1978, 1994</i>	1, 2, 3	<i>1978–1979</i>	1
<i>Oxytricha</i>	sp	<i>1977, 1995–1996</i>	1, this study	<i>1978–1979</i>	1
<i>Oxytricha</i>	sp 1			<i>1978–1979</i>	1
<i>Plagiocampa</i>	sp	1996	This study	1996	This study
<i>Podophrya</i>	sp	1978–1979	1		
<i>Spathidium</i>	sp	<i>1977</i>	1		
<i>Sphaerophrya</i>	<i>magna</i>			1978–1979	1
<i>Sphaerophrya</i>	sp	<i>1978–1979, 1992, 1994,</i> 1995–1996	1, 3, this study	1995–1996	This study
<i>Strombidium</i>	<i>viride</i>	1992, 1994	3	1992, 1994	3
<i>Strombidium</i>	sp	<i>1977–1978</i>	4, 5	1977–1978, 1995–1996	4, 5, this study
<i>Urotricha</i>	sp			1978–79, 1996	1, this study
<i>Vorticella</i>	<i>convallaria</i>	1978–1979	1	<i>1978–1979</i>	1
<i>Vorticella</i>	<i>mayeri</i>	1992, 1994, 1995–1996	3, this study	1995–1996	This study
<i>Vorticella</i>	<i>microstoma</i>	1978–1979	1	<i>1978–1979</i>	1
<i>Vorticella</i>	sp	1978–1979, 1996	1, this study	<i>1977, 1978–1979, 1996</i>	1, this study
<i>Vorticella</i>	sp 1	<i>1978–1979</i>	1		
Unidentified gymnostome		1978–1979	1		
Unidentified hymenostome 1		<i>1978–1979</i>	1	<i>1978–1979</i>	1
Unidentified hymenostome 2		<i>1978–1979</i>	1	<i>1978–1979</i>	1
Unidentified hypotrich				<i>1995–1996</i>	This study
Unidentified oligotrich		<i>1978–1979</i>	1		
Unidentified peritrich				1977–1978	5
Unidentified prostomatid		1992, 1994	3		
Unidentified suctorian 1		<i>1978–1979</i>	1	1978–1979	1
Unidentified suctorian 2		<i>1978–1979</i>	1		

¹ Cathey et al. 1981; ² Cathey et al. 1982; ³ Laybourn-Parry et al. 1997; ⁴ Parker et al. 1982; ⁵ Simmons et al. 1993

and *Strombidium*. Additionally, the lakes of Taylor Valley have frequently been reported to contain *Vorticella* and the suctorian, *Sphaerophrya*. Studies regarding the physiological adaptations of ciliates to the harsh conditions of antarctic lakes (e.g., low light, low temperature, low in nutrients) would best be focused on these apparently successful organisms.

Protozoan diversity in lakes Hoare and Fryxell is greater than that in the antarctic lakes of the Vestfold Hills (Laybourn-Parry et al. 1991, Laybourn-Parry et al. 1992, Perriss and Laybourn-Parry 1997). Ciliate abundances in Lakes Hoare and Fryxell are greater than those of the lakes in the Vestfold Hills. For example, the maximum density of planktonic ciliates in Lake Druzhby was $143 \text{ cells} \cdot \text{l}^{-1}$ (Laybourn-Parry and Bayliss 1996). Ciliate abundances are comparable to those of the more nutrient-rich Sombre and Heywood lakes (Signy Island, South Orkneys), sites at which changes in ciliate community composition over the austral summer have previously been observed (Laybourn-Parry et al. 1996). The benthos of pools and lakes in maritime Antarctica are also more diverse than in most continental lakes, with ciliate taxonomic richness comparable to that of the Taylor Valley lakes (Hawthorn and Ellis-Evans 1984). This is also true of various melt ponds on Ross Island (Armitage and House 1962) and the McMurdo Ice Shelf (James et al. 1995). However, we agree with James et al. (1998) who conclude that the protozooplankton of McMurdo Dry Valleys lakes is diverse relative to other continental antarctic lakes thus far studied.

Although the lakes of Taylor Valley are relatively diverse in terms of protozoa, antarctic assemblages overall are species-poor relative to those encountered in the vast majority of temperate and tropical waters. In addition, it has been suggested that the low species diversity of the antarctic lakes, relative to their arctic counterparts, results from the younger age and greater isolation of the southern systems (Heywood 1977). The low diversity of continental aquatic systems thus reflects biogeographical isolation, and the few taxa present seem to be limited to those that have broad tolerances (Vincent and James 1996).

Ciliate source pools

The aeolian transport of sediment and organic material is an important feature of antarctic dry valley ecosystems, and material as large as small pebbles may be moved throughout the windy valleys (Campbell and Claridge 1987). Pieces of benthic algal mat are also transported from lakes to soils and up onto glaciers (Parker et al. 1982b; Wharton et al. 1985). Presumably, material will also be transported from lake to lake, and therefore these are not isolated systems. Some degree of similarity in the ciliate assemblages of individual lakes of the McMurdo Dry Valleys is therefore to be expected.

One source of colonists to the upper water column and ice covers of these lakes are the microbial mat

communities of inflowing streams. These glacial melt-water streams flow for 6–10 weeks each year during the austral summer. The mat communities lyophilize in later months and may then provide an important aerial inoculum to lakes, glaciers, and surrounding soils. Although the algal communities of these streams have been characterized (e.g., Alger et al. 1996 and citations therein), to our knowledge, stream protozoa have received little or no attention.

The vast majority of genera observed in the lakes of the dry valleys have representatives that also occur in marine habitats. Based on the facts that: (1) many of the ciliate taxa found in Lakes Hoare and Fryxell are taxa that are also found in marine or brackish-water systems (e.g., *Askenasia*, *Euplotes*, *Monodinium*, *Plagiocampa*), (2) that high-salinity waters actually occur in the dry valleys lakes, and (3) that these lakes are located in proximity to McMurdo Sound (only 7 km in the case of Lake Fryxell), we speculate that wind transport of organic material from the marine environment may be a source for the protozoan colonists now present in the lakes.

An additional source of colonizing ciliates are traveling skuas, penguins and seals which are sometimes observed on the lakes. Long-distance transport by birds may also account for the presence of cosmopolitanly distributed taxa. For example, the skua (*Cataracta antarctica*) is known to range from New Zealand to this region of continental Antarctica (Stead 1932). For ponds on the McMurdo Ice Shelf, it has been concluded that long-distance colonization from northern regions (either by wind or animal transport) appears to be more likely than dispersal from other regions of Antarctica (Vincent and James 1996).

Although soils may be both a source pool and sink for lake organisms, soil ciliate communities in the dry valleys are extremely low in species richness and abundance. Limited data are available on soil ciliates in the Taylor Valley area, however there appear to be few taxa found in either Lakes Fryxell or Hoare that are recoverable from local terrestrial environments. For example, Foissner (1996) reports the occurrence of *Colpoda cucullus*, *Drepanomonas sphagni*, *Fuscheria lacustris*, *Homalogastra setosa* and *Oxytricha opisthomuscorum* from damp soil, wet moss and *Nostoc*, and dry moss along the shores of Lake Fryxell. Of these, only taxa of the genus *Oxytricha* have been reported from Lake Fryxell waters. In another study involving samples from several of the dry valleys, soil ciliates were found at only 7 of 50 sites. These ciliates were identified as *Tetrahymena rostrata*, *Cyclidium muscicola*, *Spathidium* sp., and *Holosticha* sp. Total soil protozoan densities were estimated at $150\text{--}700 \text{ cells} \cdot \text{g}^{-1}$ soil at five of these McMurdo Dry Valley sites, yet the vast majority of these organisms (>98%) were flagellates and amoebae, not ciliates (Bamforth, personal communication). Thus, relative to the lakes, harsh soil habitats are sparsely populated with ciliates.

The absence of colpodids in dry valley soils parallels their absence in the soils of the maritime Antarctic islands, as reported by Smith (1978). We did not observe

colpodids in Lakes Fryxell and Hoare, although Cathey et al. (1981) report *Colpoda* sp. from the water column of Lake Hoare during the 1978–79 season. Colpodids are nearly always found in soils, not in lakes. Laybourn-Parry et al. (1997) report *Bursaria* sp. from Fryxell in 1994, and we suspect that Cathey et al. (1981) may have identified *Bursaria* in their live samples as *Colpoda*. *Colpoda* and *Bursaria* are believed to be closely related and may be difficult to distinguish under the light microscope. Although further comparative work is necessary, it appears that soils that are not in direct contact with lake waters do not act as a significant source pool for aquatic ciliates in Taylor Valley. Comparative morphological and genetic (e.g., rRNA sequence) work on widely distributed ciliate taxa would do much to clarify the issue of sources and origins for the current lake populations.

Taxonomic uncertainties

There is always concern over potential confusion between morphologically similar taxa. One case regarding the potential confusion between the species of *Colpoda* and *Bursaria* has already been mentioned. Relevant to our current understanding of ciliate assemblages in Lakes Hoare and Fryxell, there are four primary issues of additional concern:

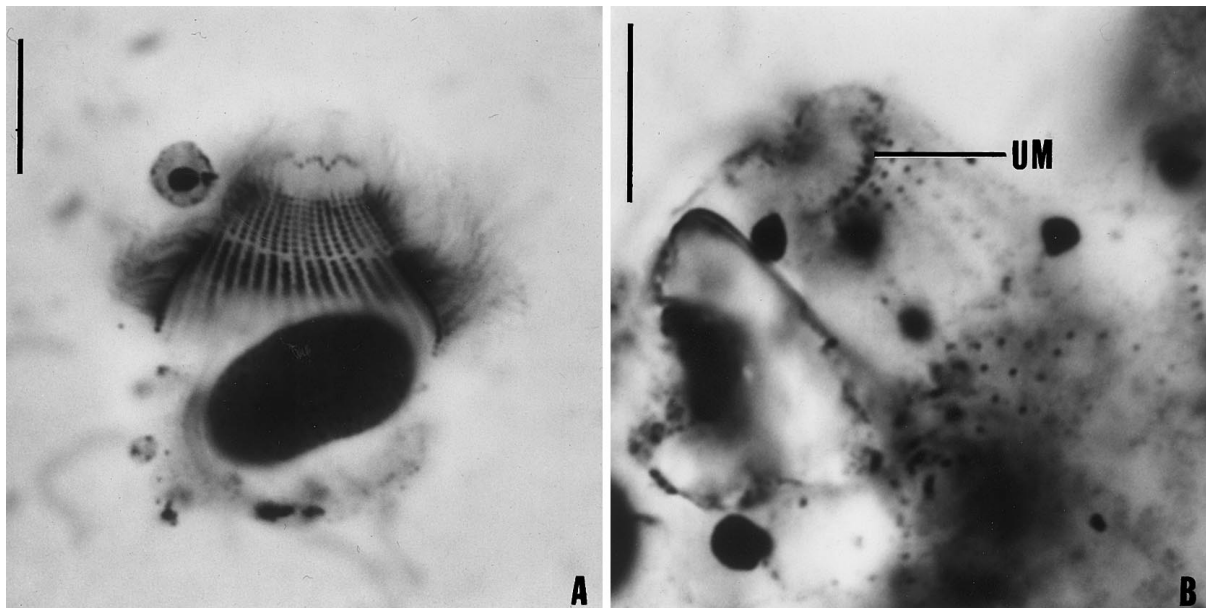
1. The possibility exists that the organisms here identified as *Cyclotrichium* have previously been confused with *Mesodinium*. This has happened in the past.

For example, Powers (1932) believed that a species of *Cyclotrichium* had earlier been misidentified as *Mesodinium rubrum* by Leegaard (1920). It would be nearly impossible to confuse our *Cyclotrichium* with chromatophore-bearing *M. rubrum* cells, however the colorless species of *Mesodinium* might be difficult to distinguish from *Cyclotrichium* without careful examination and/or silver staining. Interestingly, *M. rubrum* itself has been found to be ecologically important in other continental antarctic lakes (Perriss et al. 1995). It is also possible to confuse *Halteria* (previously reported from both Lakes Fryxell and Hoare) with *Mesodinium* if the equatorial spikes of *Halteria* are inadvertently overlooked.

2. Living *Askenasia* and *Didinium* are easily confused (Kudo 1966) and various species of these genera have been reported from the McMurdo Dry Valleys lakes (Table 4). We observed *Askenasia* (Fig. 2A) but did not find organisms identifiable as *Didinium*. *Didinium* has been reported from both water column and benthic samples in Lake Fryxell, but only from the water column of Lake Hoare (Table 4). *Askenasia* has been observed in all of the larger McMurdo Dry Valleys lakes (Fryxell, Hoare, Bonney, and Vanda). It is also possible that the organism we now know as *Monodinium* was previously referred to as *Didinium* by other investigators.

3. The gross morphology of *Plagiocampa* is very similar to that of *Holophrya*. Both belong to the class Prostomatea and have bipolar kineties and an apical cytostome. In silver stains, *Plagiocampa* is seen to possess a semicircle of oral dikinetids (the undulating membrane, UM, described by Foissner et al. 1994), which is absent in *Holophrya*. The ciliates we identify as *Plagiocampa* appear to have a semicircular UM (Fig. 2B). Thus, we believe that the organisms identified as the genus *Holophrya* in these lakes are actually *Plagiocampa*. Also, the prostomatids previously listed as unidentified may also have been *Plagiocampa*.

Fig. 2 Protargol stained *Askenasia* sp. (A) showing the close arrangement of two rings of long cilia encircling the body ($\times 1800$), and *Plagiocampa* sp. (B) showing the semicircle of oral dikinetids (UM) in one of the organisms ($\times 2300$). Scale bars = 10 μm



4. More detailed descriptions of the commonly reported, frequently abundant genera for which several unnamed species have been described is necessary. In particular, several peritrich genera have been observed, nearly all having been described as various species of *Vorticella* (Table 4). For example, Cathey et al. (1981) report the occurrence of four distinct vorticellid taxa in Lake Fryxell. Similarly, several suctorian taxa have been previously reported, including *Sphaerophrya*, *Podophrya* and two unidentified genera. Although suctorians were not identifiable using the QPS method, they were frequently observed in live samples from both study lakes. These abundant, but insufficiently known ciliate taxa require more detailed description and taxonomic placement.

Many factors control the community composition of antarctic lake ciliates. Some of these are historical in nature, for example the colonization history of the specific water body being investigated. Other factors include the availability of food resources, which are in turn regulated by frequently extreme abiotic conditions. Top-down control of ciliate populations by metazoan predators does not occur in the lakes of the McMurdo Dry Valleys. More detailed studies on both the structure and function of the protozooplankton communities in these lakes are currently being completed (Laybourn-Parry, personal communication), and efforts continue in identifying key taxa within these systems. Overall, ciliates in these lakes may play a more important role in microbial food webs relative to those in lower latitude systems due to the absence of metazoans. This makes an understanding of ciliate diversity in these antarctic lakes of particular relevance.

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