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Planktonic communities of melt ponds on the McMurdo Ice Shelf, Antarctica

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Abstract The planktonic community of 20 melt ponds on the McMurdo Ice Shelf was investigated to determine taxa abundance and diversity and the controlling environmental variables. Grazing rates were measured using fluorescent beads to examine trophic interactions between ciliates, bacteria and phytoplankton. The melt ponds contained a surprisingly varied planktonic community with relatively high abundance compared with Antarctic continental lakes. There was a clear distinction between small, productive ponds dominated by bactivorous small ciliates, hymenostomes and heterotrophic cryptophytes and the larger, less productive ponds where these taxa were less abundant. The benthic mats of cyanobacteria and diatoms were potentially a source of food for some ciliate species but the majority were bacterivores. The lack of large herbivorous ciliates, the heterotrophic capabilities of cryptophytes and the broad ecological tolerances contributed to a planktonic community dominated by cryptophytes.

Introduction

Protozoan ciliates and flagellates are ubiquitous elements of freshwater planktonic communities. In many regions of Antarctica, e.g., the Vestfold Hills region (Burch 1988; Laybourn-Parry et al. 1991; Laybourn-Parry and Marchant 1992), southern Victoria Land (Cathey et al. 1981; Parker et al. 1982) and coastal ponds and lakes on Ross Island (Spurr 1975; Goldman et al. 1972; Vincent and Vincent 1982; Broady 1989), these groups have been found to dominate the communities in ponds and lakes. Large herbivorous and predatory metazoan zooplankton are generally absent in Antarctic waters, although a few species of copepods and cladocerans, which dominate the zooplankton in temperate and tropical freshwaters, have been recorded in coastal lakes of the Vestfold Hills region of eastern Antarctica and the Antarctic Peninsula. On the Ross Ice Shelf protozoan ciliates and flagellates (mostly cryptophytes) are thought to be the top predators of the food chain. Very high numbers of protozoan ciliates have been found in ponds and small lakes on nearby Ross Island, particularly in the benthic mats (Armitage and House 1962; Dillon and Bierle 1980). Ciliates contributed up to 86.8% of the total fauna (Dillon and Bierle 1980), so it is likely that ciliates may play an equally important role in pond ecosystems on the McMurdo Ice Shelf.

Evidence that competition for food resources and predation, are important factors in the structuring of protozoan communities has been largely circumstantial (Laybourn-Parry 1992). Antarctic ponds offer a rare opportunity to investigate potential physical and chemical controls on planktonic community structure in the absence of predatory and competing metazoans.

In this paper we investigate the variability in the planktonic community structure of melt ponds on the McMurdo Ice Shelf to determine the controlling abiotic variables. We also examine trophic interactions to determine the importance of grazing by microherbivores, and whether this may contribute to the relatively low phytoplankton biomass recorded in these ponds.

Materials and methods

Study sites

The McMurdo Ice Shelf is an ablation region of approximately 1500–2000 km^2 in the northwest of the Ross Ice Shelf, and the melt

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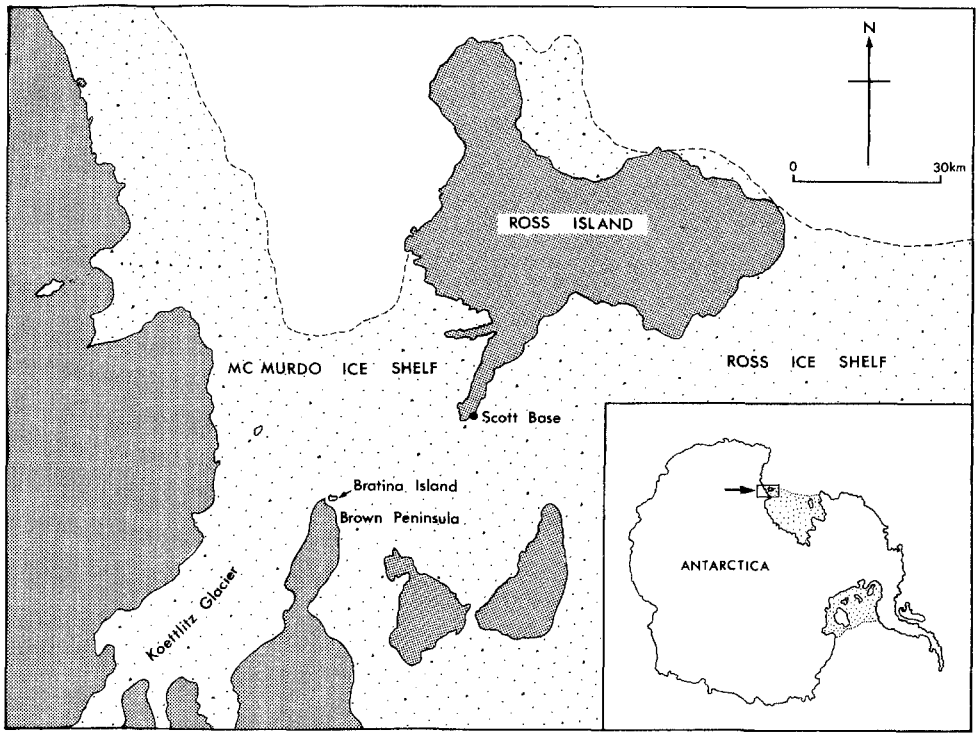

Fig. 1 Location map for Bratina Island on the McMurdo Ice Shelf, Antarctica

ponds and small lakes form one of the major freshwater ecosystems. The ponds investigated in this study were in undulating ice (cf. Howard-Williams et al. 1990), close to Bratina Island (165°30′ W, 78°00′ S) off the northern tip of the Brown Peninsula. Extensive moraine deposits, 10–30 cm thick, cover the ice with numerous melt ponds and small lakes up to 30,000 m^2 occurring in troughs. The ponds and lakes are ice covered for much of the year but melt out to varying degrees each year depending on age, salinity and depth. Most are ice free from December to February. The chemistry of the ponds is affected by lenses of mirabilite, seawater intrusion and age. Early studies of ponds on the ice shelf (Kellogg and Kellogg 1987; Howard-Williams et al. 1990) focused on the benthic diatom flora. Recent studies have examined the influence of abiotic factors on biomass and production of the benthic cyanobacteria that form mats on the bottom of many of these ponds and are the dominant autotrophic component (Howard-Williams et al. 1990; Hawes et al. 1993). The base of the ponds is often coated by dense mats of the cyanobacteria *Phormidium autumnale*, *P. laminosum*, *Oscillatoria deflexa*, *O. limosa* and *Nodularia* sp., and the diatoms *Navicula muticopsis* and *Pinnularia cymatopleura* (Howard-Williams et al. 1990). To date, little work has been conducted on the planktonic communities, which in comparison to the benthic ones, are thought to be sparse in ponds on the McMurdo Ice Shelf (Howard-Williams et al. 1990). Hawes et al. (1993) suggested that low temperatures and low concentrations of inorganic nitrogen control phytoplankton biomass but did not attempt to characterise the planktonic community. Faunal studies have focused on the rotifers and tardigrades associated with the benthic mats (Suren 1990).

Pond dimensions, mat and ice cover for each pond were noted and are given in Table 1. Pond names are unofficial. The ponds sampled varied in size from those in small hollows ($< 10\ m^2$ e.g. Hayden Pond) to large, tidally influenced Ice Ridge Pond (8000 m^2). By the end of December the ice had completely melted in most of the ponds except Bay, Ribbon, Legin, Bambi and Galore Ponds, which still retained up to 25% ice floor in the base of the ponds. Maximum water depth varied from 0.25 m (Hayden Pond, Salt Pond) to 1.5 m in VXE6 and Nicholas Ponds. The base of most ponds sampled was > 80% covered by a mat of cyanobacteria. Extra, Upper, Salt, P70E, VXE6 and Nicholas Ponds had a basal mat of orange-pigmented cyanobacteria and the base of Foghorne Pond contained predominantly *Nostoc*.

Methods

General

Twenty ponds of varying sizes were surveyed in late December 1991/early January 1992 and seven were resurveyed in late January. Replicate, depth-integrated water samples were collected from the water column by three methods, depending on the size of the pond or lake. Small ponds (< 5 m diameter) were sampled from the middle with a perspex tube (1 m long, 5 cm diameter). Medium size ponds were sampled by pumping water through a plastic tube suspended over the middle of the pond and running back to a collection bottle and hand-operated vacuum pump. Samples were collected every 10 cm and pooled to obtain a depth-integrated sample. On large ponds, integrated water samples were collected with a perspex tube from an inflatable boat. Conductivity of the ponds was measured using a Radiometer model Com 2E meter and pH was determined with a Yokogawa portable meter.

Nutrients

A water sample for nutrient analysis was collected in acid-washed polythene bottles from each pond, and filtered within a few hours of collection through Whatman GF/F filters. Samples were packed in ice until they could be frozen for transport to New Zealand. Ammonia-nitrogen (NH_4-N), nitrate-nitrogen (NO_3-N) and dissolved reactive phosphorus (DRP) concentrations were determined with a Technicon II auto analyser system. Analytical methods are given in Downes (1988). A modification of Solorzano's (1969) ammonia method was used for water from ponds with high conductivity and nitrate was reduced to nitrite by cadmium reduction followed by diazotisation.

Table 1 Physical, chemical and biological characteristics for the 20 ponds sampled on Bratina Island, Antarctica. Pond numbers refer to first (late December) and second (late January) surveys (*Chl* chlorophyll *a*; *Cond* conductivity; *Bact* bacteria; *Ice* and *mat* are the percentage of pond covered by surface ice and cyanobacterial mats)

Pond/lake	Chl mg m^{-3}	Cond $\mu S\ cm^{-1}$	pH	Bact nos $ml^{-1} \times 10^6$	NO_3 mmol m^{-3}	NH_4 mmol m^{-3}	DRP mmol m^{-3}	Length m	Width m	Depth m	Ice %	Mat %
Hayden1	78.2	7950	9.6	3.176	1.64	0	5.83	4	2	0.25	0	5
Hayden2	25.8	10790	9.7	2.147	0.08	0.11	14.48	4	2	0.25	0	5
Salt	53.2	54200	9	3.444	0.16	0.06	12.16	24	12	0.25	0	95
Skua	13.1	940	8.4	0.918	0	0	1.18	30	10	0.68	0	95
AX	12.9	1853	9.4	0.741	0	0.11	2.9	15	12	0.88	0	85
Casten1	9.2	933	9.8	1.233	0.02	0	7.36	90	30	0.9	0	90
Casten2	8.4	925	9.8	1.742	0	0.03	7.81	90	30	0.9	0	90
Upper1	8.6	9650	9.9	2.13	0.05	0.13	9.35	14	4	0.77	0	40
Upper2	6.1	7350	10.2	1.792	0.04	0.08	16.7	14	4	0.77	0	40
Nicholas	8.6	2090	9.4	1.088	0	0.49	7.2	10	6	1.5	0	100
Lunch	8.0	453	9.4	0.49	0	0	1.26	30	30	1.2	0	20
KO81	6.9	1112	9.4	0.96	0.04	0	2.84	80	50	1.2	0	100
KO82	4.6	1069	9.5	0.806	0	0.14	2.56	80	50	1.2	0	100
P70E1	5.8	5620	8.4	1.685	0	0	0.04	6	4	0.85	0	90
P70E2	1.1	6420	8.6	2.06	0	0.43	0	6	4	0.85	0	90
Galore	5.7	637	9.5	0.468	0.04	0	0.08	43	36	1.28	15	80
Bay	5.7	1309	9.6	1.005	0.02	0	1.78	40	10	0.7	25	90
ICR	4.6	3970	8.5	0.402	1.45	0	1.19	200	40	0.83	0	15
P701	4.3	3390	9.5	1.611	0.02	0	0.05	15	15	0.82	0	100
P702	1.7	3170	9.7	1.112	0	0.15	0.08	15	15	0.82	0	100
Ribbon	4.3	552	8.8	0.416	0.04	0	0.6	35	12	0.82	20	80
Foghorne1	4.3	725	9.4	0.348	0	0	0.76	20	6	0.32	0	15
Foghorne2	1.1	719	10	1.01	0	0.08	0.17	20	6	0.32	0	15
Extra	4.3	4240	8.9	1.333	0	0.71	0.09	20	6	0.26	0	100
Bambi	3.4	1510	9.9	1.615	0.02	0	1.71	18	18	0.97	15	90
VXE6	2.9	5720	8.8	1.387	0.28	0.08	0.12	7	6	1.5	15	60
Legin	2.3	1275	9.2	0.727	0	0	0.11	14	6	0.82	10	90

Phytoplankton biomass and bacteria concentrations

Chlorophyll *a* was measured on subsamples filtered onto GF/F filters, following extraction in boiling 90% ethanol for 10 min. Absorbance of GF/F-filtered pigment extract was read at 750 and 665 nm using a Shimadzu UV/120/02 spectrophotometer. Corrections for phaeophytin were made following acidification of the sample to 7.5 mmol HCI.

For bacterioplankton enumeration, 20-ml subsamples were fixed with 1% glutaraldehyde for 1 h, stained with acridine orange and filtered onto black 0.2-μm Millipore (cellulose acetate and nitrate) membrane filters (Jones and Simon 1975). Filters were placed on glass slides, sealed and packed with ice until they could be frozen for transport to New Zealand. Bacteria were enumerated on slides using a Leitz epifluorescence microscope and UV excitation.

Plankton composition

Samples for phytoplankton and microzooplankton identification and enumeration were preserved and fixed with 1% Lugol's iodine. Replicate subsamples of 5–20 ml were left for 24 h in Utermöhl settling chambers prior to enumeration. Phytoplankton were counted in 20 fields and microzooplankton were counted by scanning entire chambers with an inverted light microscope at $\times 400$, $\times 100$ and $\times 200$ respectively. To aid in identification of ciliates, live samples were observed immediately after collection and after culturing with rice grains for 2 weeks.

Potential correlations between major planktonic taxa and pond morphometry, ice and mat cover and environmental variables were determined by non-parametric Spearman rank correlations because data sets were generally not normally distributed. The degree of similarity between plankton communities in the 20 ponds was assessed by hierarchical clustering with Pearson correlations after log $(n + 1)$ transformation using SYSTAT 5.0 (Wilkinson 1988) and DECORANA (detrended correspondence analysis, Hill 1979). DECORANA ordinates pond samples in species space with minimum overlap in common causality between the two ordinates.

Grazing experiments

The grazing impact of protozoans was assessed by incubating water in 4-l polyethylene cubitainers in Nicholas Pond. Duplicate containers with the natural assemblage, < 10-μm filtrates and < 2-μm filtrate were subsampled daily for 5 days for chlorophyll *a* concentrations, bacterioplankton and flagellate counts. Chlorophyll *a* and bacteria were analysed as described above. For flagellate counts, two 50-ml samples of 20-μm size-fractionated filtrate were fixed 1 : 1 with 4% ice-cold glutaraldehyde for 1 h. The samples were filtered onto 1-μm Nuclepore filters, stained with 2 ml primulin for 5 min, mounted and the slides were packed with ice until they could be frozen and returned to New Zealand. Flagellates were counted using epifluorescence microscopy under UV excitation (Zeiss filter set 48 77 02).

Species-specific grazing rates were measured for major ciliate taxa in Upper and Skua Ponds by uptake of fluorescent beads (Polysciences), used to simulate bacteria and small phytoplankton. Bead solutions were prepared by diluting stock solutions with filtered lake water conditioned with 0.5 mg ml^{-1} bovine serum albumin. Beads were added to give final concentrations of $< 10\%$ of natural particle concentrations. Subsamples were taken after 0, 10, 20, 30, 40 and 60 mins and fixed 1:1 with ice-cold 4% glutaraldehyde. Ingested beads were counted under blue light excitation with a fluorescence microscope. Up to 50 individuals of the major taxa were examined for ingested beads.

Results

Physical and chemical variables

Conductivity of the ponds varied from 453 μS cm^{-1} in Lunch Pond to 54,200 μS cm^{-1} in Salt Pond, which was at least 5 times higher than the other ponds (Table 1). The edge of Salt Pond had deposits of mirabilite ($Na_2SO_410H_2O$). In Hayden Pond, a small pond that was slowly evaporating, the conductivity had increased from 7950 to 10,790 μS cm^{-1} by the second sampling at the end of January. Conductivity did not change over the 4 weeks in the other ponds resurveyed. Nitrate and ammonia-nitrogen concentrations were often below detection level, with an average of 0.14 and 0.10 μmol m^{-3} respectively. The nitrate-nitrogen concentration was highest at 1.64 μmol m^{-3} in Hayden Pond but declined significantly to < 0.1 μmol m^{-3} over 4 weeks. Dissolved reactive phosphorus (DRP) concentrations were relatively high (mean 3.65 μmol m^{-3}) particularly in Salt, Casten and Hayden Ponds (> 5 μmol m^{-3}). DRP concentrations more than doubled over the 4 weeks in Hayden Pond although conductivity increased by 50%. Generally, chlorophyll *a* concentrations reflected the higher nutrient concentrations in these ponds and the decline in chlorophyll *a* in Hayden Pond from 78.2 to 25.8 μg l^{-1} over the 4 weeks was associated with a decrease in nitrogen, but a doubling of DRP.

Planktonic community structure

The number of phytoplankton taxa identified in the 20 ponds ranged from 2 species of normally benthic cyanobacteria in Bambi Pond to a more diverse fauna of 9 species, including benthic cyanobacteria and diatoms, cryptophytes and chlorophytes, in Galore and VXE-6 Ponds (Table 2). Phytoplankton in the ponds was generally dominated by the cryptophytes, *Ochromonas* and *Chroomonas*. Abundance was highest in Salt (43,702 ml^{-1}) and Hayden (28,630 ml^{-1}) Ponds. 'Benthic' diatoms were found in low numbers in the plankton of several ponds. The chlorophyte, *Chlamydomonas* was found in ponds with a range of conductivity from 453 μS cm^{-1} in Lunch Pond to the highly saline Salt Pond. *Oscillatoria priestleyi*, which is only found in very saline waters, was also found in Salt Pond along with a dense population of the small cyanobacterium *Synechococcus*. The results of hierarchical cluster analysis and the ordination of ponds by DECORANA clearly identified three groups of ponds based on species presence and abundance (Figs. 2, 3), while Salt pond separated readily from all of the others with hierarchical clustering probably because of the *Synechococcus* population (Fig. 2). The three clusters separated ponds into:

1. Medium-sized moderately saline ponds dominated by *Ochromonas* and with some *Oscillatoria*.

2. Small ponds with relatively high conductivity, chlorophyll *a* concentrations and bacterial numbers. The phytoplankton community in the cluster 2 ponds was characterised by high abundance of *Chroomonas* and the presence of *Oscillatoria*.
3. Larger, lower salinity ponds with relatively low chlorophyll *a* concentrations and bacterial populations. These ponds contained very few cryptophytes and were generally dominated by the 'benthic' cyanobacteria *Phormidium* and *Oscillatoria* with diatoms sometimes co-dominant.

Similar relationships between taxa and environmental variables were also evident in Spearman Rank correlation matrices (Table 3). Significant positive relationships were found between conductivity and *Ochromonas*, and negative relationships for cryptophytes with size of ponds and *Ochromonas* with depth of ponds.

Twenty-two genera of protozoan ciliates were identified in the plankton. There was no consistent pattern between number of taxa and pond, morphometry or environmental variables; however the highest number of taxa (13) was recorded in 2 small ponds, VXE-6 and Foghorne. Only four taxa were identified from Salt Pond. Genera not included in the quantitative data (Table 2), but observed in live material or in cultures, were *Prorodon*, *Epistylis*, *Aspidisca*, *Colpoda*, *Tetrahymaena* and *Enchelys*.

The ubiquitous *Vorticella* was found in all ponds, except Salt Pond, and *Euplotes* was found in 15 ponds. Together these two genera accounted for 18% of total ciliate abundance recorded in the ponds. Ciliates < 20 µm, which accounted for 50% of total abundance were not identified to genera, but included small scuticociliates, *Cinetochilum* and *Urotricha*. High densities of small ciliates in P70E, P70 and Casten Ponds contributed to the high ciliate abundances of up to $10^5\ l^{-1}$ recorded in these ponds. The truly planktonic ciliates, the choreotrichs, contributed 8% on average and were generally found in the more 'oligotrophic' ponds with low chlorophyll *a*, while stichotrichs, *Euplotes* and Hymenostomina were more characteristic of the smaller, more productive ponds.

The benthic Nassophoria *Chilodonella* and *Nassula*, occurred in all ponds except Salt and Bay Ponds. Hymenostomes and stichotrichs were the dominant taxa in Salt Pond and were also important in the smaller, more saline ponds like Upper and Hayden. These taxa were significantly negatively correlated with size of pond (Table 3, $P < 0.01$) and positively correlated with conductivity ($P < 0.01$). There was a positive correlation between abundance of hymenostome ciliates and bacteria.

Multivariate analysis, using clustering, identified three similar groupings of ponds based on ciliates (Fig. 4), as in the phytoplankton taxa. Cluster 1 ponds in DECORANA analysis were typically small highly productive saline ponds like Hayden and Upper with high numbers of hymenostomes and stichotrichs. Cluster 2 identified medium-sized ponds with moderate salinity and microbial biomass and high ciliate species diversity. Cluster 3 contained large ponds generally with low conductivity and microbial biomass, and low numbers of stichotrichs, hymenostomes and *Euplotes*. The choreotrich, *Halteria*, and the prostome, *Bursellopsis* were important taxa in these large ponds. Salt Pond was clearly different because of the high abundance of hypotrichs and hymenostomes. Rotifers were found only in very low numbers, and were generally the benthic *Philodina gregaria* that had migrated out of the benthic mats.

There was generally a high degree of similarity for specific ponds between the first and second surveys based on phytoplankton taxa (Figs. 2, 3; Table 2). Clustering of ponds according to ciliate taxa, however, identified major changes in the ciliate community between samplings for Foghorne, Hayden and P70 Ponds according to coordinate A2 and minor changes for Upper Pond based on coordinate A1 (Fig. 4). The communities in the larger ponds, Casten and KO8, remained relatively unchanged. Foghorne, P70 and Hayden Ponds all had significantly reduced chlorophyll *a* when resurveyed (Table 1). The abundance of *Chilodonella* doubled over the 4 weeks in P70 Pond while small ciliates (< 20 µm) disappeared. Over the same period there was a 20-fold increase in choreotrichs and a five fold increase in *Vorticella* in Foghorne Pond. The major changes in Hayden Pond were an increase in *Vorticella* but a decline in small ciliates, scuticociliates and stichotrichs.

Samples were taken at four depths in Lunch Pond to determine whether there was vertical stratification. Most of the major taxa in Lunch Pond were distributed throughout the water column. *Didinium* and Didinidae (predominantly *Askenasia*) however, were more abundant at 1.0 and 1.5 m than in surface waters.

Trophic interactions

Correlations, positive or negative, between planktonic grazers and their food may suggest potential trophic interactions or controlling mechanisms but measurements of these interactions are required to eliminate partial correlations with other environmental variables.

Grazing rates were measured for major ciliate taxa feeding on fluorescent beads used to simulate bacteria and small phytoplankton-sized particles. It is now recognised that some ciliate groups exhibit higher feeding rates on natural particles (Sherr et al. 1987), but because of logistics and import restrictions in the Antarctic environment, we were limited to using artificial particles. The only taxa that were in sufficient quantities to measure grazing rates in Upper and Skua Ponds were *Euplotes*, *Vorticella*, scuticociliates and oligotrichs.

Table 2 Abundance of phytoplankton ($\times 10^3$) and major microzooplankton taxa in Antarctic ponds [numbers refer to first (1) and second (2) surveys (numbers per litre)]

Pond/lake	Upper1	Upper2	VXE6	Extra	Salt	Fogh1	Fogh2	P70E1	P70E2	Nicholas	Hayden1
Phytoplankton											
Cyanophyta											
Anabaena	523.5	18.4	73.5	0	0	174.5	45.9	0	0	18.4	9.2
Chroococcus	0	0	0	293.9	0	0	0	0	0	0	0
Merismopedia	0	0	0	0	0	0	0	0	0	0	0
Oscillatoria deflexa West and West	725.6	339.8	0	110.2	202.1	0	128.6	0	9.2	661.3	257.2
O. priestleyi West & West	0	0	0	0	73.5	0	0	0	0	0	0
O. limosa Agardh	0	0	0	0	0	0	0	0	0	0	0
O. retzii (Agardh) Gomont	0	0	0	0	0	0	0	0	0	0	0
Phormidium autumnale (Agardh) Gomont	18.4	0	27.6	0	119.4	0	0	0	0	27.5	64.3
P. augustissimum West & West	0	0	0	0	0	82.7	0	587.8	0	0	0
P. animale Agardh	0	0	0	0	0	0	0	0	0	0	27.6
Synechococcus	0	0	0	0	55082.4	0	0	0	0	0	0
Chlorophyta											
Brachiomonas submarina Boh.	64.3	0	165.3	0	0	0	0	0	0	0	0
Chlamydomonas	698.1	0	156.1	0	1487.7	27.6	0	27.6	0	0	0
Euglena/Phacus	0	0	0	0	0	0	0	0	0	0	0
Mallamonas	0	0	0	0	0	0	0	0	0	0	0
Cryptophyta											
Chroomonas sp.	0	0	4959.9	0	0	0	0	0	4519	0	18599.6
C. lacustrus	0	0	0	0	0	0	0	22126.7	0	0	0
Ochromonas	10030	17874	0	13740	43702.2	2342.2	679.7	0	0	15090.9	10030
Chrysophyta											
Aphanotheca	0	0	0	0	0	0	0	0	0	0	0
Miscellaneous diatoms	0	0	303.1	0	0	36.7	0	36.7	0	0	0
Unidentified	0	64.3	0	0	0	0	0	0	0	1267.5	0
No. taxa	6	4	9	3	6	6	3	3	4	4	5
Protozoa											
Phylum Ciliophora											
Postciliodesmatophora											
Class Spirotrichea											
Subclass Choreotrichia											
Strombidium	0	0	0	0	0	0	0	0	0	0	0
Halteria	0	0	10633	0	0	0	1200	0	30	967	0
Small oligotrichs	0	0	0	0	0	450	9000	0	0	133	0
Subclass Stichotrichia											
Stichotrichs < 80 µm	550	0	167	650	1733	117	0	33	17	100	167
Stichotrichs > 80 µm	33	0	0	100	1333	133	0	200	0	100	567
Rhabdophora											
Class Prostomatea											
Urotricha	0	0	17	33	0	0	100	0	0	133	0
Bursellopsis	0	0	0	0	0	0	0	0	0	100	0
Class Litostomatea											
Subclass Haptorida											
Trachelophyllum	67	0	0	133	0	50	0	0	33	0	0
Didinium	0	0	0	0	0	0	400	0	550	167	0
Didinidae	0	0	0	383	0	0	0	0	0	2500	0
Actinobolina	0	0	0	0	0	0	0	0	0	0	0
Spathidium	0	0	0	0	0	0	0	0	0	0	0
Class Nassophorea											
Subclass Nassophorea											
Chilodonella	3650	167	283	383	0	117	0	0	67	0	300
Nassula	750	33	0	233	0	83	0	0	17	33	0
Subclass Hypotrichea											
Euplotes	2400	233	1250	1317	0	483	0	167	50	367	67
Class Oligohymenophorea											
Subclass Hymenostomia											
Cinetochilum	750	0	267	0	17933	200	0	0	0	0	233
Scuticociliates	3450	700	767	217	10000	250	0	0	0	367	1433
Subclass Peritrichia											
Vorticella	2300	2167	333	12367	0	650	3367	300	967	9800	1233
Miscellaneous ciliates < 20 µm	0	8367	33	28067	0	0	4833	98400	67564	24733	19233
Miscellaneous ciliates > 20 µm	766	567	367	1016	600	300	300	283	200	233	233
Total Ciliophora	14717	12233	14117	44900	31600	2833	19200	99417	69514	39733	23467
Rotifera	0	67	50	50	0	83	133	50	117	267	0

Table 2 (Contd.)

Hayden2	Bay	AX	P701	P702	Ribbon	Legin	Bambi	Galore	Skua	Lunch	Casten1	Casten2	IRP	KO81	KO82
0	0	27.6	9.2	0	18.4	0	0	55.1	*	45.9	64.3	211.3	*	0	82.7
0	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	0	0	0	0	0	0	0	*	0	36.7	0	*	0	0
119.4	321.5	1203.2	27.7	0	55.1	128.6	450.1	18.4	*	0	1882.9	2186	*	1129.8	918.6
0	0	0	0	0	0	0	64.3	0	*	0	0	0	*	0	0
0	0	18.4	0	0	0	0	0	0	*	0	0	0	*	18.4	0
0	0	0	0	0	0	0	0	18.4	*	0	0	0	*	0	0
0	0	45.9	9.2	0	0	45.9	0	0	*	64.3	9.2	9.2	*	0	0
0	0	0	0	0	0	0	0	863.4	*	1478.8	0	0	*	0	0
0	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	146.9	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	587.8	0	0	55.1	0	0	266.4	*	165.3	0	64.3	*	0	55.1
64.3	0	0	597	0	0	0	0	0	*	0	0	229.6	*	0	0
0	0	0	0	18.4	0	0	0	0	*	0	0	0	*	0	0
12151.8	6916.3	0	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0
0	0	0	0	3967.9	0	0	0	0	*	0	0	0	*	0	0
0	0	0	0	0	0	569.5	0	0	*	0	0	0	*	0	0
0	0	0	101	27.6	137.8	0	0	73.5	*	73.4	0	0	*	0	36.7
808.2	146.9	0	0	0	0	0	0	0	*	0	321.5	0	*	0	0
4	3	7	8	3	4	4	2	9	*	6	5	5	*	3	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1750	0	0	0	683	950	133
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	167
0	0	67	0	0	33	0	0	0	0	0	0	0	0	0	0
0	100	33	0	0	0	0	0	0	0	0	0	0	0	0	0
0	467	0	0	0	33	0	0	0	0	0	0	900	0	0	0
0	0	0	0	0	0	33	16	0	633	133	916	283	0	600	250
0	33	0	17	0	0	0	0	0	0	0	0	0	0	17	0
350	267	100	33	0	0	0	0	17	0	0	500	133	0	0	0
0	0	0	0	0	0	17	50	0	0	0	0	6050	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	67	900	8833	116	133	200	167	0	133	17	33	17	33	50
0	0	33	50	267	17	0	50	0	100	0	33	0	0	167	33
0	267	333	17	0	67	83	0	433	0	83	17	0	0	0	0
700	67	433	0	0	0	0	0	0	0	0	0	0	150	0	0
0	600	167	150	0	17	50	17	0	0	0	0	0	0	0	0
6000	1066	300	2167	117	417	633	150	650	600	917	233	883	150	2667	4283
1666	15233	9233	49725	0	4150	7433	1500	2583	2200	1000	46980	74102	1333	1450	150
433	300	267	233	367	283	433	133	183	13950	2917	7234	333	150	650	200
9167	18400	11033	53291	9583	5133	8733	2117	4033	19233	5183	55930	82719	2483	6533	5267
800	33	0	117	133	17	33	33	0	17	33	100	217	33	33	216

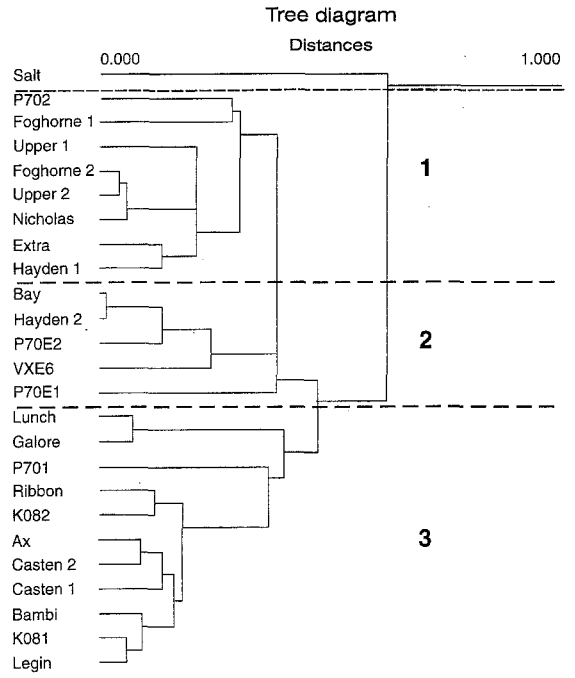

Fig. 2 Hierarchical clustering of ponds based on log-transformed phytoplankton abundance and species diversity. *Numbers* refer to clusters identified in the text

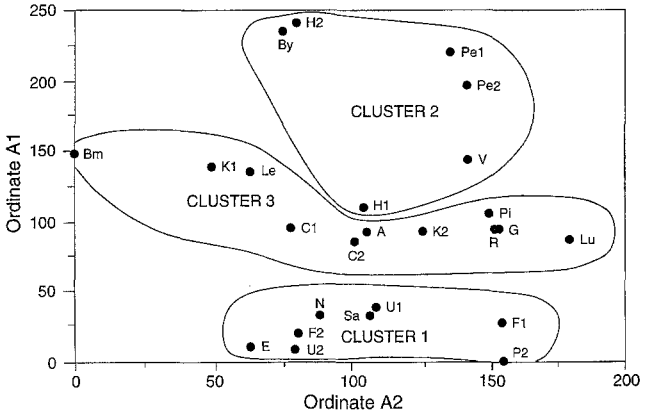

Fig. 3 Clustering of ponds by DECORANA, based on phytoplankton species diversity and abundance. *Symbols* represent the first letter of the pond name, *Sa* Salt, *Sk* Skua, *Pe* P70E, *Lu* Lunch, *Le* Legin, *By* Bay, *Bm* Bambi. *Numbers* refer to first and second surveys

Time courses of bead uptake by bacterial-sized particles (0.5 μm) for *Vorticella* and *Euplotes* are shown in Fig. 5. Reported uptake rates are generally linear for the first 20–30 min (Pace and Bailiff 1987; Sherr et al. 1987) and then the rate of ingestion slows. A similar response curve was observed for *Euplotes* but the uptake rate remained linear for at least 60 min for *Vorticella*. Investigations were run at a temperature of 5°C but whether this response was temperature related cannot be determined from these limited experiments. Uptake rates converted to clearance rates (μl cleared per animal per hour) for major taxa are given in Table 4. *Vorticella* was very efficient at removing bacteria and picoplankton-sized particles, and *Euplotes*, scuticociliates and oligotrichs removed bacterial-sized particles. No 1.0 or 5.0 μm beads were found in *Euplotes*, scuticociliates or oligotrichs, and *Urotricha*, *Chilodonella*, *Nassula*, *Bursellopsis* and the Didinidae did not ingest any of the particles offered.

Grazing rates for the major ciliate taxa were then combined with abundance to assess the grazing impact on bacteria. Ciliate grazing generally removed $< 5\%$ of the bacterial standing stock per day except for Extra (13.6%) and Nicholas (10.7%) Ponds. Grazing impact was closely correlated with abundance of *Vorticella* ($r = 0.976$, $n = 27$).

Grazing impact was also determined with selectively filtered pond water from Nicholas Pond. Phytoplankton biomass (chlorophyll *a*) and bacterial abundance were not significantly different between incubations without grazers (< 2 μm) and incubations with grazers < 10 μm and < 200 μm, over the 5 days (Fig. 6). Apparently grazers were not having a measurable impact on either phytoplankton or bacterial abundance in Nicholas Pond despite the moderate abundance of heterotrophic flagellates ($15{,}090\ \mathrm{ml}^{-1}$) and ciliates ($39{,}700\ \mathrm{l}^{-1}$).

Discussion

The melt ponds on the McMurdo Ice Shelf contained a surprisingly varied planktonic community. Samples were taken only from the pelagic zone but because of the shallow nature of these ponds and the extensive benthic mats, taxa more characteristic of 'benthic' communities were also commonly encountered. We did not identify the ciliated protozoa below genus level, but it has generally been accepted that the majority of species found in Antarctica are cosmopolitan, with very few endemics (Armitage and House 1962; Hawthorn and Ellis-Evans 1984). Broady (1989) suggested that a large proportion of the algal flora in ponds of Victoria Land are ubiquitous in continental Antarctica. This would also apply to the phytoplankton community in ponds on the McMurdo Ice Shelf, where the majority of the dominant, truly 'planktonic' taxa, like *Ochromonas*, *Chroomonas lacustrus* and *Chlamydomonas* have also been recorded in a number of ponds on Ross Island (Goldman et al. 1972; Broady 1989), northern Victoria Land (Broady 1989) and lakes of southern Victoria Land (Parker et al. 1982) and the Vestfold Hills in eastern Antarctica (Laybourn-Parry and Marchant 1992). Confirmation, however, of ubiquity needs further rigorous taxonomic characterisation of algae in Antarctic freshwaters. The cyanobacteria flora found in the water column of the ponds was dominated by *Oscillatoria deflexa*, *Anabaena* sp., *Phormidium autumnale* and *P. angustissimum*. The first three taxa also

Table 3 Spearman rank correlation coefficients for phytoplankton taxa (*A*) and ciliate taxa (*B*) with environmental variables for melt ponds on the McMurdo Ice Shelf

Taxa	Bacteria	Chl*a*	Conductivity	Depth	Size	DRP	NO_3–N	NH_4–N	Mat cover	Ice cover
A Phytoplankton										
Diatoms	–	–				– 0.508		–	–	–
Chlamydomonas			–	–	–	–	–	–	–	–
Chroomonas	–	–	–	–	– 0.531			–		–
Ochromonas	–		0.549	– 0.488	– 0.498	–	–	0.610	–	–
Phormidium		–	–	–			–	–		–
Oscillatoria	–	–	–	–	–	0.752[a]	–	–		–
Anabaena	–	–	–	–	–	–			– 0.634[a]	–
Synechococcus	–		–	–	–	–	–	–	–	
Chl *a*	–		–	–	–	0.671[a]	–	–		– 0.565
B Ciliate taxa										
Bursaria	–	–	– 0.475	–	–			–		–
Chilodonella	–	–	–	–	–	–	–			–
Cinetochilum	–	–	0.579	–	–	0.479	0.475		– 0.471	–
Didinidum	–	–	–	–	–	–	–	–	–	–
Euplotes	–	–	–	–	– 0.552	–	–	0.558	–	–
Halteria	–	–		–		–		–	–	
Hymenostomes	0.497		0.629[a]		– 0.618[a]	–	–	0.593	–	–
Stichotrichs < 80 μm	–	–	0.636[a]	–	– 0.653[a]	–		0.736[a]		–
Stichotrichs > 80 μm	–		0.535	– 0.546	– 0.634[a]		–	–	–	–
Nassula	–	–	–		–		–	–	–	–
Small oligotrichs	–	–	–	–	–	–	–	–		–
Urotricha	–	–	–	–	–		–		–	–
Vorticella	–	–	–	–	–	–	–	–	–	–
Total ciliates	0.626[a]	–	–	–	–	–			0.512	

[a] $P < 0.01$, all other correlations presented are $P < 0.05$

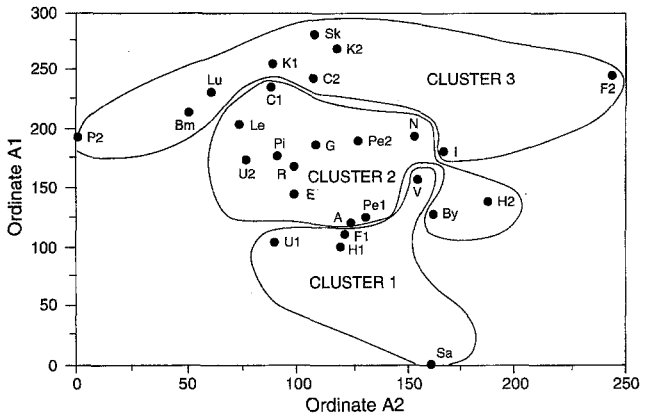

Fig. 4 Clustering of ponds by DECORANA, based on ciliate species diversity and abundance. *Symbols* represent the first letter of the pond name, *Sa* Salt, *Sk* Skua, *Pe* P70E, *Lu* Lunch, *Le* Legin, *By* Bay, *Bm* Bambi. *Numbers* refer to first and second surveys

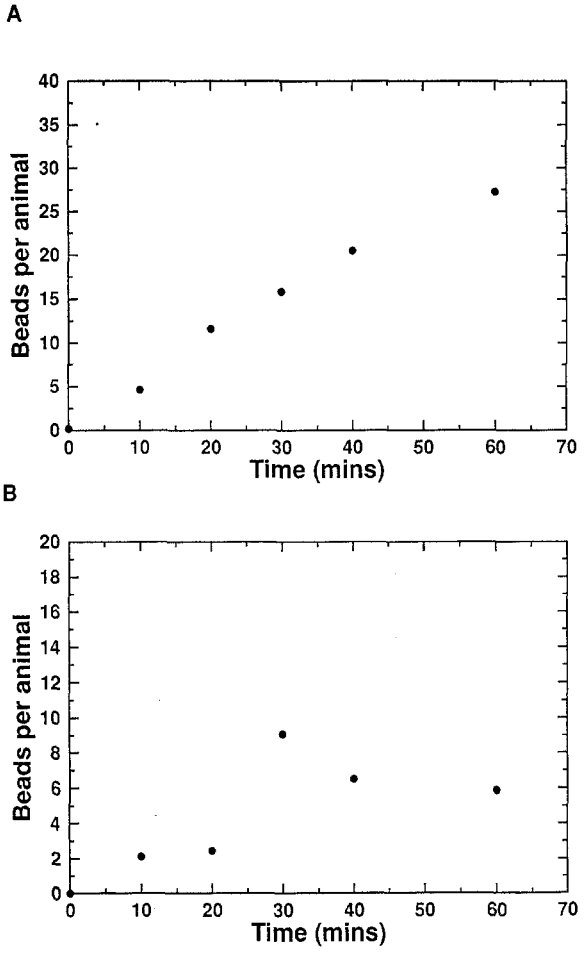

Fig. 5A, B Time course for uptake of 0.5-μm fluorescent beads by *Vorticella* (**A**) and *Euplotes* (**B**) in Antarctic ponds

dominated the benthic mats and were probably mixed into the water column through wind-generated turbulence or breakage of mats (Howard-Williams et al. 1990). *Phormidium angustissimum*, which was very

Table 4 Clearance rates (μl animal^{-1} h^{-1}) for microzooplankton in Antarctic melt ponds (*ns* not significant)

Ciliate taxa	Bead size		
	0.5 μm	1.0 μm	5.0 μm
Euplotes	0.09	ns	0
Vorticella	0.42	1.9	0
Scuticociliates	< 0.01	ns	0
Small oligotrichs	0.05	ns	0

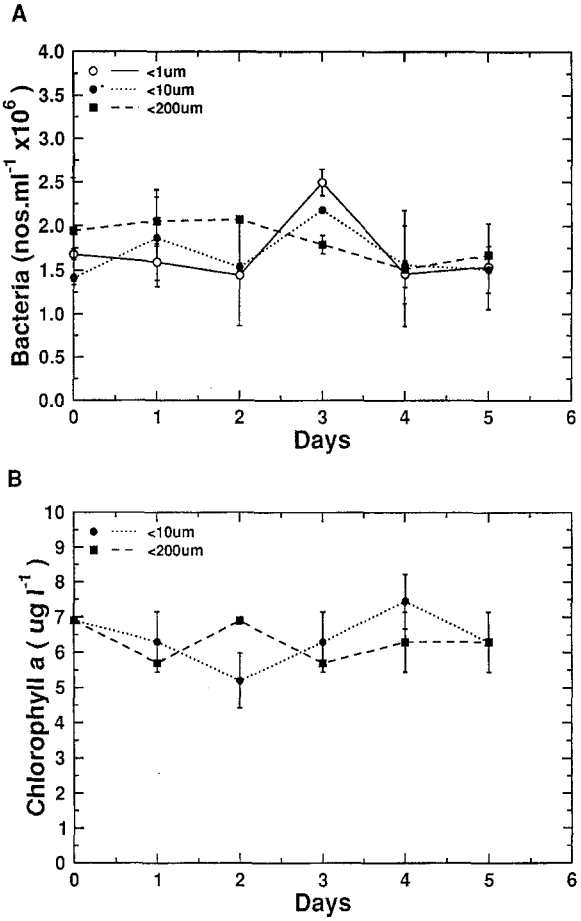

Fig. 6A, B Changes in **A** bacterial concentrations, and **B** chlorophyll *a* over 5 days in size-fractionated water from a McMurdo Ice Shelf pond, Antarctica. *Bars* represent 1 SD for duplicate incubations

abundant in two of the larger ponds, Galore and Lunch, has not been previously recorded in the benthos of ponds.

'Benthic' cyanobacteria were ubiquitous in the 20 ponds surveyed but it was the presence or absence of flagellates that demarcated ponds in the multivariate phytoplankton analysis. Cryptophytes dominate the phytoplankton in most freshwater communities of Antarctica (Goldman et al. 1972; Parker et al. 1982; Laybourn-Parry and Marchant 1992) but in the ponds of the McMurdo Ice Shelf they were common in the small

ponds and rarely found in the larger, less saline ponds. Cryptophytes were totally absent in eight of these ponds but *Chlamydomonas* was present. Goldman et al. (1972) failed to demonstrate any allelopathic effect of cyanobacteria mats on phytoplankton carbon uptake and there was no clear relationship between planktonic abundance and mat cover in this study of the McMurdo Ice Shelf ponds. The only correlations between cryptophytes and environmental variables were size of pond and conductivity with *Ochromonas*. The relationship between cryptophytes and bacteria was not significant at $P < 0.05$, but there was a trend for greater abundance of *Chroomonas* and *Ochromonas* at higher bacterial concentrations ($P < 0.2$). Most of these flagellates were weakly pigmented, and Salonen and Jokinen (1988) demonstrated that *Ochromonas* is an efficient mixotroph, capable of obtaining a substantial part of its energy from uptake of bacteria as well as from photosynthesis. Bacterial concentrations were $< 10^6$ ml^{-1} in the eight ponds without cryptophytes (with the exception of Casten, 1.2×10^6 ml^{-1}), which is potentially too low to support bactivorous planktonic protozoa (Fenchel 1980).

The ability to move to layers of high nutrients and bacterial concentrations and relatively fast growth rates in response to higher concentrations of resources is an advantage in the large, stable ice-covered lakes of Antarctica. This advantage does not appear to apply to large shallow ponds on the McMurdo Ice Shelf, which are ice free for 2–3 months and subject to greater wind-driven mixing. Smaller ponds in troughs, on the other hand, are likely to be less affected by wind mixing, have higher nutrient levels and higher bacterial populations. These ponds were dominated by cryptophytes that in some cases formed bands visible near the bottom of ponds. The dynamic nature of these small ponds was reflected in a reduced phytoplankton species diversity and abundance over the 4 weeks as nutrients were depleted, particularly NO_3-N, which was undetectable in most of the ponds when resurveyed at the end of January. The changes in the larger ponds, however, were relatively small. Similar patterns were observed in the ciliate community where the change was more dramatic for P70 and Foghorne Ponds than the larger KO81 and Casten Ponds. This limited data set suggests species succession may only occur in the smaller, productive ponds during the short Antarctic growing period.

Of the 22 taxa of protozoan ciliates recorded in the ponds, at least 15 are commonly found in the plankton. Some groups like scuticociliates were not classified to genus level but the number of genera identified was comparable with studies of protozoan ciliates in ponds on Ross Island (Armitage and House 1962) and Signy Island (Hawthorn and Ellis-Evans 1984). Seven genera were recorded by Armitage and House (1962) but they used #20-mesh plankton nets to concentrate the organisms and thus will have missed many of the small nano-ciliates recorded for ponds on the McMurdo Ice Shelf. Dillon and Bierle (1980) recorded 48 species from Coast Lake and Thompson and Croom (1976) reported a total freshwater ciliate fauna of 40 species from King George Island. These studies, however, focused on ciliate taxonomy and included many strictly 'benthic' species. The number of pelagic species found in ponds on the McMurdo Ice Shelf was an order of magnitude lower than in 2 Michigan ponds where 176 and 202 species were recorded (Cathey et al. 1981).

Ciliate species diversity in Antarctic freshwaters is constrained mainly by the requirement to form resistant cysts when ponds and lakes freeze for 9–10 months. In the ponds of the McMurdo Ice Shelf, the majority of species also displayed broad ecological tolerances with most taxa found in ponds with a range of conductivity. It was only in Salt Pond that physicochemical conditions appeared to limit species diversity.

Most of the studies to date on Antarctic freshwater ponds have focused on quantitative analysis of benthic rather than planktonic fauna. Abundance in the ponds with low phytoplankton biomass and bacterial populations was comparable to mesotrophic temperate lakes, but significantly higher than in Antarctic continental lakes, which are regarded as ultra-oligotrophic (Laybourn-Parry 1992). In the more eutrophic ponds like Hayden, ciliate abundance was significantly lower than in temperate eutrophic lakes where densities can reach 200,000 l^{-1} (Pace 1982).

The most striking difference between the ciliate community of the ponds on the McMurdo Ice Shelf and Antarctic lakes is the absence of larger choreotrichs like *Strombidium*. This group of organisms often forms the highest trophic level in the absence of grazing copepods, functioning as the major herbivore group in Antarctic lakes. The ciliate community in small- and medium-sized ponds (clusters 1, 2; Fig. 7) was dominated by bacterivores like *Vorticella*, *Euplotes* and small hymenostomes. The only strict herbivores were *Chilodonella* and *Nassula* (Dillon and Bierle 1980), which are both typical 'benthic' taxa. These organisms feed on filamentous cyanobacteria and diatoms (Patterson and Hedley 1992) and were observed to have orange pigmentation derived from the orange mats on the base of the ponds. *Vorticella* requires filamentous algae for attachment and in the ponds probably relies on the filamentous cyanobacteria.

In most freshwater habitats the primary grazers of flagellates are tintinnids, prostomes, *Bursaria* and metazoan rotifers and copepods. The only potential grazers on flagellates in the McMurdo Ice Shelf ponds were the prostomes *Bursellopsis* and *Prorodon* (cf. Curds 1982) but, surprisingly, these genera were only found in significant numbers in the large ponds where cryptophytes were absent (cluster 3; Fig. 7). No 5.0-μm beads of similar size to small cryptophytes were ingested by ciliates in our grazing experiments but this does

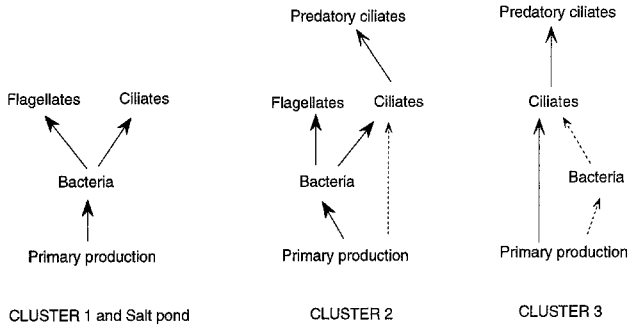

Fig. 7 Food web diagrams for different clusters identified in the text. *Solid lines* show dominant pathways and *dashed lines* less important pathways

not necessarily mean no grazing takes place because of potential selectivity against beads (Sherr et al. 1991).

The results of grazing experiments using beads and size selective filtration combined with ciliate abundance suggest grazing pressure by ciliates is unlikely to control phytoplankton populations. Based on known feeding strategies (Dillon and Bierle 1980; Curds 1982; Curds et al. 1983; Patterson and Hedley 1992), only 12% of the ciliates in the ponds were herbivores, 4% were potential detritivores, $< 1\%$ were carnivores (*Trachelophyllum*, *Didinium* and *Spathidium*) and 83% were bacterivores. This contrasts with the study of microbiocoenoses in the benthic mat community of Coast Lake on Ross Island where Dillon and Bierle (1980) found nearly 60% of the ciliates were strictly herbivores and 35% were variable feeders. Bacteria appeared to be the major source of energy for planktonic ciliates in the ponds but feeding experiments indicate ciliates were not controlling the bacterial population. Based on these feeding rates and ciliate abundance the only ponds where $> 10\%$ of the bacterial biomass was removed per day were Extra (13.6%) and Nicholas (10.7%). *Vorticella* was very abundant in these ponds. The mixotrophic cryptophytes, however, with densities of 10–30,000 ml^{-1} and feeding rates of 0.4 nl $flagellate^{-1}\ h^{-1}$ (Bloem 1989) could potentially remove up to 30% of the bacterial population per day. At the low ambient temperatures in Antarctic ponds, this impact is likely to be greater than in temperate or tropical waters where bacterial production would be faster. Primary production in these ponds is dominated by the benthic community (Hawes et al. 1993) and this is a major source of organic carbon supporting the bacteria and higher trophic levels.

In summary, there was clearly a distinction between small, productive ponds dominated by the bacterivorous small ciliates, hymenostomes and heterotrophic cryptophytes, and the larger, less productive ponds where these taxa are less abundant or, in the case of cryptophytes, may be absent. There was no clear relationship between planktonic abundance and mat cover, suggesting that allelopathy is not a controlling factor. The mats of cyanobacteria and diatoms may be a source of food for some ciliate species and offer greater niche diversity but the majority of ciliates were bacterivores. The lack of large herbivorous ciliates, the heterotrophic capabilities of cryptophytes, their broad ecological tolerances and their ability to rapidly respond to a changing light regime and temperature would all contribute to a planktonic community dominated by cryptophytes. Relatively low phytoplankton biomass in most ponds, competition for the same resources and the constraints of encystment during freezing result in a low species diversity and abundance of ciliates, features typical of other Antarctic freshwater systems.

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