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ORIGINAL PAPER

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The distribution of microplankton in the McMurdo Dry Valley Lakes, Antarctica: response to ecosystem legacy or present-day climatic controls?

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Abstract Plankton abundance and biomass were investigated in five lakes of the McMurdo Dry Valleys, Antarctica: Lakes Bonney, Fryxell, Joyce, Hoare and Miers. Despite plankton communities being dominated by organisms <100 μm in length, there were striking differences between the lakes, including large variations in plankton vertical distribution and differences in total plankton biomass. Bacterial biomass was highest in the anoxic monimolimnia of the meromictic lakes, reaching 191 μg C l^{-1} in Lake Fryxell. Photosynthetic nanoflagellates dominated phytoplankton in the five lakes studied. Highest chlorophyll *a* concentrations were recorded at the chemocline of Lake Fryxell (21 μg chl *a* l^{-1}). Heterotrophic nanoflagellate concentrations were low, ranging from 2 cells ml^{-1} in Hoare to 237 cells ml^{-1} in Bonney. By Antarctic standards, ciliates were relatively successful in terms of biomass and diversity in Lakes Fryxell and Hoare. In contrast, Lake Miers possessed extremely low ciliate abundance (<0.04 cells ml^{-1}). On both sampling occasions, copepod nauplii were observed in Lake Joyce. This is the first recording of crustacean zooplankton within the McMurdo Dry Valley Lakes. Because the foodwebs of these lakes are structured by "bottom-up" forces, differences in plankton distributions could be related to the physicochemical characteristics of each lake. The effect of lake evolution (legacy) and present-day climate change on planktonic dynamics is discussed.

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Introduction

The lakes of the McMurdo Dry Valleys, Antarctica, possess plankton communities dominated by single-celled eukaryotes and prokaryotes (Parker et al. 1982; Priscu et al. 1999; Roberts et al. 2000). This is a characteristic of all continental Antarctic lakes so far described (Laybourn-Parry et al. 1991, 2001; Laybourn-Parry and Bayliss 1996). Antarctic lakes typically lack metazoan plankton, but may contain sparse populations of rotifers, as observed in the McMurdo Dry Valley lakes, or a single crustacean, as in the lakes of the Vestfold Hills (Laybourn-Parry et al. 1995, 1997; Bell and Laybourn-Parry 1999). The McMurdo Dry Valley lakes consistently maintain a thick perennial ice cover (Fritsen and Priscu 1999). In this respect they differ from the lakes of the Antarctic coastal oases, where many of the lakes lose their ice for a few weeks each summer (Heywood 1972; Vincent 1988). Permanent ice cover greatly reduces wind-driven turbulence of the water column, resulting in persistent physical and chemical gradients (Spigel and Priscu 1998). The McMurdo Dry Valley lakes can be considered amongst the most hydrologically stable aquatic environments on earth. This lack of mixing creates a conducive environment for flagellates, cyanobacteria and ciliates that are able to maintain their position in the water column and effectively recycle nutrients.

Detailed studies of plankton temporal and spatial variability over the austral summer have been undertaken in a number of individual lakes within the McMurdo Dry Valleys (in Lake Fryxell by Roberts et al. 2000; Marshall and Laybourn-Parry 2002, and in Lake Hoare by E.C. Roberts and J. Laybourn-Parry, unpublished work). A comparative study of plankton ecology between McMurdo Dry Valley lakes does exist (Parker et al. 1982); however, it lacks detail with respect to depth profiles and microbial analysis. The investigation reported here provides a detailed survey of plankton populations within five McMurdo Dry Valley lakes (Lakes Bonney, Fryxell, Joyce, Hoare and Miers).

Meteorological data demonstrated that a net cooling of the Antarctic continent occurred between 1986 and 2000 (Doran et al. 2002). The McMurdo Dry Valleys, for example, cooled by 0.7°C per decade between 1986 and 2000, with greater rates of cooling in the austral summer and autumn. Because environments within the McMurdo Dry Valleys are sensitive to low amplitude climate shifts, it has been suggested that meteorological change may be reflected in planktonic communities within these lakes (Doran et al. 2002). The influence of present and past climate change is discussed in relation to planktonic community structure.

Materials and methods

Sampling and study sites

Hydrographic parameters and locations of the lakes are shown in Table 1 and Fig. 1, respectively. For more detailed physicochemical data on the lakes, refer to the reviews of Green and Friedmann (1993) and Priscu (1998). Water samples and profiles were taken from the deepest point in each lake between one and three times during each of the austral summers of 1996 and 1997. All depths are reported with respect to the water level in the sampling hole (piezometric depth), which was ~30–50 cm below the surface of the ice (Dore and Priscu 2001). Lake Bonney has two lobes, which are separated by a shallow sill (13 m) that effectively eliminates interchange of deep waters between the lobes (Spigel and Priscu 1998). Both lobes were sampled, as each lobe has distinct physicochemical characteristics (Priscu 1997). During each sampling date, vertical profiles of conductance, temperature and photosynthetically active radiation (PAR) were recorded, using an SBE 25 Sealogger CTD (Sea-Bird Electronics) and Licor LI-193SA spherical quantum sensor, respectively. Water samples were collected with a 5-l Niskin bottle from a range of depths, as part of a U.S. NSF-funded Long Term Ecological Research (LTER) project (see http://huey.colorado.edu/LTER for detailed information on depths and dates).

Analysis of samples

Water samples were collected for dissolved inorganic nutrients (soluble reactive phosphate, NO_3^-, NH_4^+), particulate organic carbon (POC), dissolved organic carbon (DOC) and chlorophyll *a* analysis. Briefly, Whatman GF/F filtered samples were subject to overnight pigment extraction in 90% acetone prior to phaeophytin-corrected chlorophyll *a* analysis, which was quantified using a

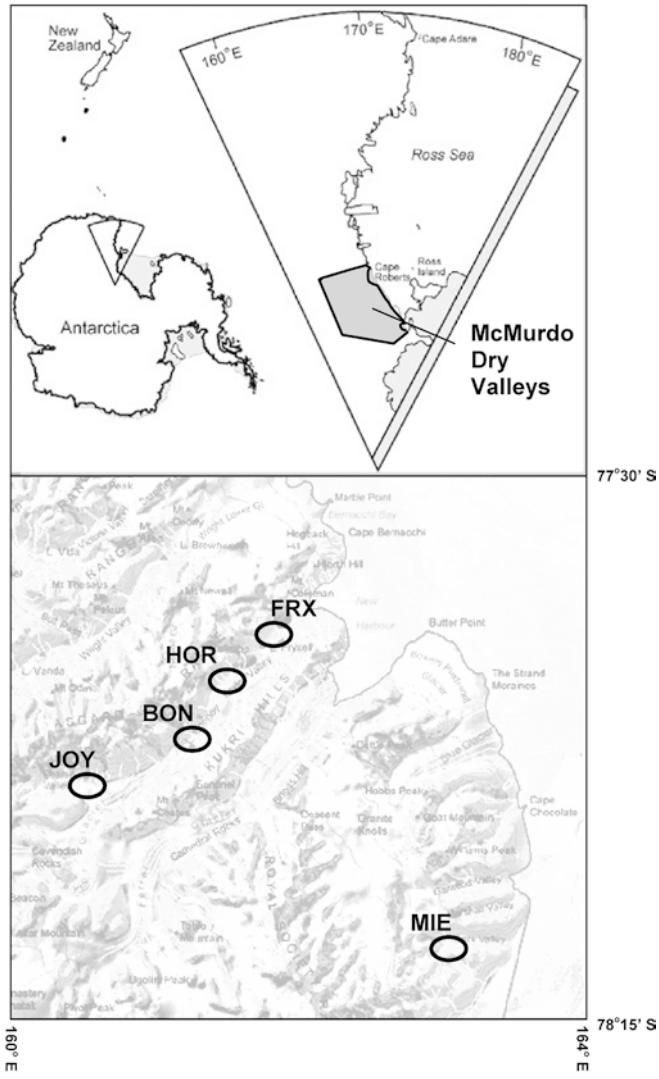

Fig. 1 Map showing locations of Lakes Bonney (*BON*), Fryxell (*FRX*), Joyce (*JOY*), Hoare (*HOR*) and Miers (*MIE*) within the McMurdo Dry Valleys, Antarctica

Table 1 Hydrographic parameters of the McMurdo Dry Valley lakes. Modified from Priscu and Spigel and Priscu (1998)

	Bonney East Lobe	Bonney West Lobe	Joyce	Miers	Fryxell	Hoare
Max. depth (m)	37	40	35	21	20	34
Surface area (km^2)	3.32	0.99	0.83	1.3	7.08	1.94
Ice thickness (m)	4.0–4.5	3.8–4.1	5.0–5.6	4.0–5.0	3.7–4.9	4.5–5.5
Max. salinity (PSU)	150	125	3.5	< 0.1	6.2	0.7
Temperature (°C)	−2.8 to 7.9	−5.4 to 3.2	0–2.5	0–5.5	0–3.5	0–1.2
% Transmission through the ice	2.7	2.8	1.2	0.3	1.3	1.6
Depth of chemocline/oxycline (m)	15	13	26	17	9.5	28

Turner Designs Model 10-AU-005 field fluorometer. POC samples, derived by filtering 300–500 ml water through combusted GF/F filters, were analysed using a Carlo Erba model 1500 elemental analyser. Whatman GF/F filtered water was analysed for dissolved inorganic nitrogen and soluble reactive phosphorous (SRP) using a Lachat Quickchem AE Autoanalyser and a manual colorimetric method, respectively (Strickland and Parsons 1972). For DOC samples, lake water was filtered through precombusted Whatman GF/F filters into precombusted 125-ml amber glass bottles and acidified with 1 ml concentrated phosphoric acid. Samples were analysed using a TOC UV oxidation analyser.

Biological samples were fixed upon immediate return to the shore-side laboratories until further analysis. All epifluorescent microscopy was performed in the field, within a few days of sample collection. Duplicate 5-ml bacteria samples for enumeration and biomass estimations were preserved with 2% glutaraldehyde and stored in glass vials at 4°C. Samples (2 ml) were stained with 4′, 6-diamidino-2 phenylindole (DAPI, 5 μg DAPI ml^{-1}) and filtered onto a 0.2-μm black Nuclepore polycarbonate membrane filter. Filters were viewed under UV illumination at a magnification of ×1,000 using a Ziess Axioskop epifluorescent microscope. Ten randomly selected Whipple grids (Graticules, UK) were counted on each filter. In order to calculate bacterial biovolume, 100 cells were measured from each lake at ×1,000 using a Pattersons Grid (Graticules, UK). Biovolume was converted to carbon-biomass using a conversion factor of 0.22 pg C μm^3 (Bratbak and Dundas 1984).

For cyanobacteria, picophytoplankton, heterotrophic and phototrophic nanoflagellate analysis, duplicate 54-ml water samples from each depth were fixed in buffered glutaraldehyde to a final concentration of 2%. Samples were stored in 60-ml Nalgene bottles at 4°C in darkness before analysis. Fifty millilitres of the sample was stained with DAPI (5 μg DAPI ml^{-1}) and filtered onto a 2-μm pore-size Nuclepore polycarbonate membrane filter. Twenty randomly selected Whipple grids (Graticules, UK) were counted at ×400 magnification using both UV and blue excitation under epifluorescence microscopy (Ziess Standard 16 microscope) to distinguish between phototrophic and heterotrophic nanoflagellates (PNAN and HNAN, respectively). The phytoplankton community was considered as consisting of three main groups: PNAN (without small chlorophytes), small chlorophytes and cyanobacteria. When reference is made to PNAN, this should be considered as PNAN excluding small chlorophytes. Over 50 individual HNAN and PNAN were measured in samples taken from each lake using a line graticule (Graticules, UK) at ×1,000 (Ziess Axioskop microscope). Mean cell volumes (MCV) were calculated using an appropriate geometric shape. Biovolume was converted to carbon-biomass using a carbon conversion figure of 0.22 pg C μm^{-3} (Børsheim and Bratbak 1987).

For ciliate counts, 500 mL or 1-l samples were concentrated by settling, and counted in a Sedgewick-Rafter counting chamber (Graticules, UK). It was not possible to identify ciliates to species level using post-fixed Bouin's material for protargol staining; therefore, ciliates were identified only to genus level. Ciliate MCV was obtained by measuring 50 cells of each taxon and using the nearest appropriate geometric shape to calculate volume. MCV was converted to biomass using a carbon conversion figure of 0.22 pg C μm^{-3} (Putt and Stoecker 1989).

The carbon conversion figures of Børsheim and Bratbak (1987), Bratbak and Dundas (1984) and Putt and Stoecker (1989) have been used in order to aid comparison between other plankton studies conducted in Antarctic Lakes between 1985 and 2000.

Results

Lake Bonney

Lake Bonney had the strongest thermohaline stratification of all the lakes studied (Fig. 2). A strong chemocline was present at 15 m in the east lobe and 13 m in the west lobe. Temperatures ranged between −5.4°C in the monimolimnion to 7.9°C above the chemocline (Table 1). Priscu (1995) and Dore and Priscu (2001) demonstrated that SRP was the inorganic nutrient limiting photoautotrophic production in Lake Bonney. SRP remained below 0.2 μM above the chemocline and increased within the monimolimnion. Concentrations of NH_4^+ and NO_3^- were low in surface waters, increasing with depth (Table 2). Chlorophyll *a* formed both surface and deep maxima in Lake Bonney (Fig. 3). The deep chlorophyll maximum (DCM) was particularly well defined in the west lobe, reaching a concentration of 7.2 μg chl *a* l^{-1} at the chemocline on 22/12/97. The phytoplankton community in Lake Bonney consisted mainly of PNAN and small (< 3 μm) chlorophyte species (Fig. 4). Different PNAN species occupied different depths, with the upper peak consisting mainly of cryptophytes, and the DCM being composed of *Chlamydomonas* and *Ochromonas*.

Highest DOC and bacterial biomass were found in the anoxic water below the chemocline in both lobes (Table 2, Fig. 5). Heterotrophic protozoa were dominated by HNAN and were evenly distributed throughout the water column (Table 3 and Fig. 6). Ciliates were very sparse and were only observed in surface samples (Fig. 6).

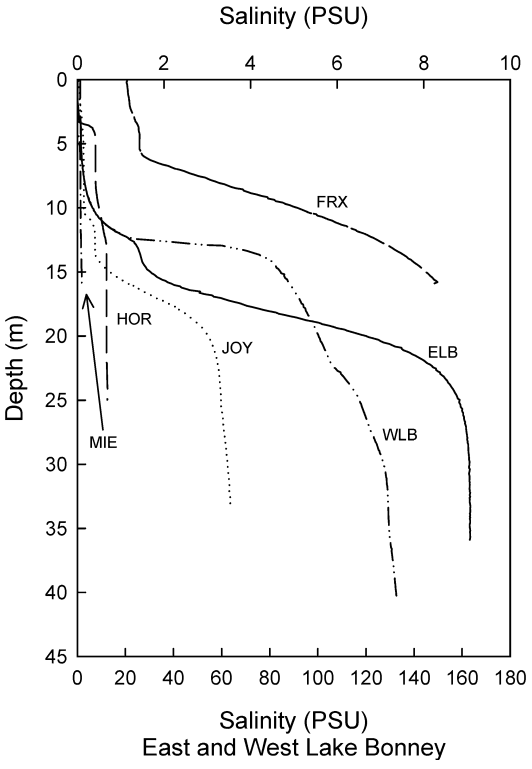

Fig. 2 Salinity profiles (PSU) for Lakes East and West Bonney (*ELB*, 21 December 1997; *WLB*, 23 December 1997), Fryxell (*FRX*, 19 November 1997), Hoare (*HOR*, 27 December 1997), Joyce (*JOY*, 9 December 1997) and Miers (*MIE*, 5 December 1997). Note that East and West Lake Bonney are plotted on the secondary *x-axis*. The UNESCO salinity equations of state are valid between the ranges of 2 and 42 PSU and −2 and 35°C

Table 2 Integrated mean (and standard error) inorganic nutrients (μM) and organic carbon (mg lL^{-1}) concentrations in the water columns of the McMurdo Dry Valley lakes during summers 1996–1997 and 1997–1998. For the meromictic lakes, values for the mixolimnion (*Mixo*) and the monimolimnion (*Mono*) are given separately. In this instance the chemocline (*Chemo*) is included within the monimolimnion. Lake Miers is not salinity stratified (*Nd* not detectable)

Parameter	Section of water column	Bonney east lobe	Bonney west lobe	Joyce	Miers	Fryxell	Hoare
SRP (μM)	Mixo	Nd (nd)	0.05 (0.01)	0.05 (0.02)	0.05 (0.01)	0.08 (0.01)	0.02 (0.02)
	Mono and Chemo	0.20 (0.18)	0.27 (0.19)	1.59 (1.49)	- (-)	13.27 (13.02)	1.31 (-)
NO_3^- (μM)	Mixo	13.40 (9.50)	9.92 (3.73)	36.05 (0.19)	Nd (nd)	Nd (nd)	2.63 (3.45)
	Mono and Chemo	125.53 (50.45)	12.02 (10.63)	30.55 (0.39)	- (-)	Nd (nd)	7.82 (-)
NH_4^+ (μM)	Mixo	1.89 (3.28)	1.89 (3.67)	0.39 (0.26)	0.14 (0.16)	0.05 (0.08)	0.07 (0.11)
	Mono and Chemo	112.22 (64.78)	191.28 (87.89)	104.11 (109.39)	- (-)	227.44 (232.39)	7.56 (-)
DOC (mg l^{-1})	Mixo	1.5 (0.6)	1.2 (0.6)	2.2 (1.7)	1.1 (0.5)	4.4 (1.6)	1.9 (0.5)
	Mono and Chemo	18.1 (8.7)	11.4 (6.1)	3.7 (0.8)	- (-)	14.7 (4.9)	2.5 (0.1)
POC (mg l^{-1})	Mixo	0.17 (0.03)	0.23 (0.13)	0.30 (0.15)	0.19 (0.08)	0.47 (0.29)	0.13 (0.05)
	Mono and Chemo	0.25 (0.11)	0.23 (0.11)	0.24 (0.03)	- (-)	0.67 (0.22)	0.12 (0.02)

Lake Fryxell

The deep water of Lake Fryxell is less saline than that of Lake Bonney but possesses haline stratification nonetheless (Fig. 2). Nutrient concentrations were low/undetectable within the upper oxic layer, increasing sharply below the chemocline (Table 2). Lake Fryxell possesses a pronounced DCM just above the chemocline, with concentrations reaching 22 μg chl *a* l^{-1} on 29/12/97 (Fig. 3). The PNAN component of the phytoplankton was dominated by three species of cryptophytes, with fewer numbers of *Pyramimonas* and *Chlamydomonas*. Filamentous cyanobacteria contributed minimally to the phytoplankton biomass within this lake (Fig. 4).

Bacterial abundance in Lake Fryxell was higher than in the other lakes studied (Table 3). Similar to the meromictic Lakes Bonney and Joyce, the highest bacterial biomass occurred in the anoxic monimolimnion (Table 3, Fig. 5). HNAN contribution to heterotrophic protozoan biomass was relatively low, with maximum abundance reaching 649 cells ml^{-1} (Fig. 5). In Lake Fryxell, a large population of the ciliate *Plagiocampa* sp. was associated with the DCM, and extended below the chemocline into the anoxic waters of the monimolimnion. They were observed feeding on cryptophytes which were clearly visible inside the cells. Concentrations of *Plagiocampa* sp. reached 30 cells ml^{-1} in the DCM. Ciliate numbers in Lake Fryxell were 5 times higher than in any of the other lakes. Lake Fryxell also possessed the greatest number of ciliate species (25 species, Table 4).

Lake Joyce

Lake Joyce has weaker salinity stratification than Lakes Bonney or Fryxell, with salinity not exceeding 4 PSU. The oxic-anoxic interface occurred at 26 m and highest bacterial biomass was found below this depth, reaching 76 μg C l^{-1} (Fig. 5). In contrast to Lakes Bonney and Fryxell, there was no distinct DCM, with chlorophyll *a* fluctuating throughout the water column and showing considerable variation between sampling dates (Fig. 3). PNAN abundance (>200 cells ml^{-1}) was the lowest of the five lakes studied (Table 3). Phytoplankton was composed of a combination of PNAN, small chlorophytes and filamentous cyanobacteria, these populations showing little stratification with depth (Fig. 3). Heterotrophic protozoan abundance and biomass were low (Table 3, Fig. 6). Ciliate and HNAN biomass were evenly distributed throughout the water column, with the exception of a ciliate peak that occurred at 26 m, composed of *Plagiocampa* (Fig. 6, Table 4).

Copepod nauplii were found in samples collected from 26 m on 5/12/96 and 9/12/97.

Lake Hoare

The water column of Lake Hoare is composed of fresh water, with salinities never exceeding 0.7 PSU. Pockets of anoxic water were encountered below 28 m, but there was no distinct chemocline, as seen in Lakes Bonney and Fryxell (Fig. 2). Nutrient concentrations within the upper 28 m were low, remaining close to detection limits (Table 2). The DCM occurred between 6 and 12 m, forming a less distinct peak than measured in Lakes Fryxell and Bonney (Figs. 3, 4). In common with neighbouring Lake Fryxell, cryptophytes dominated phytoplankton biomass. Here too, ciliates were the most successful heterotrophic protozoan group, possessing a high species diversity and greater biomass than HNAN (Table 4, Fig. 6).

Lake Miers

Lake Miers was the least saline (>0.1 PSU) of all the lakes studied and showed no evidence of chemical stratification (Fig. 2). This lack of water-column stability was reflected in the plankton distributions, with

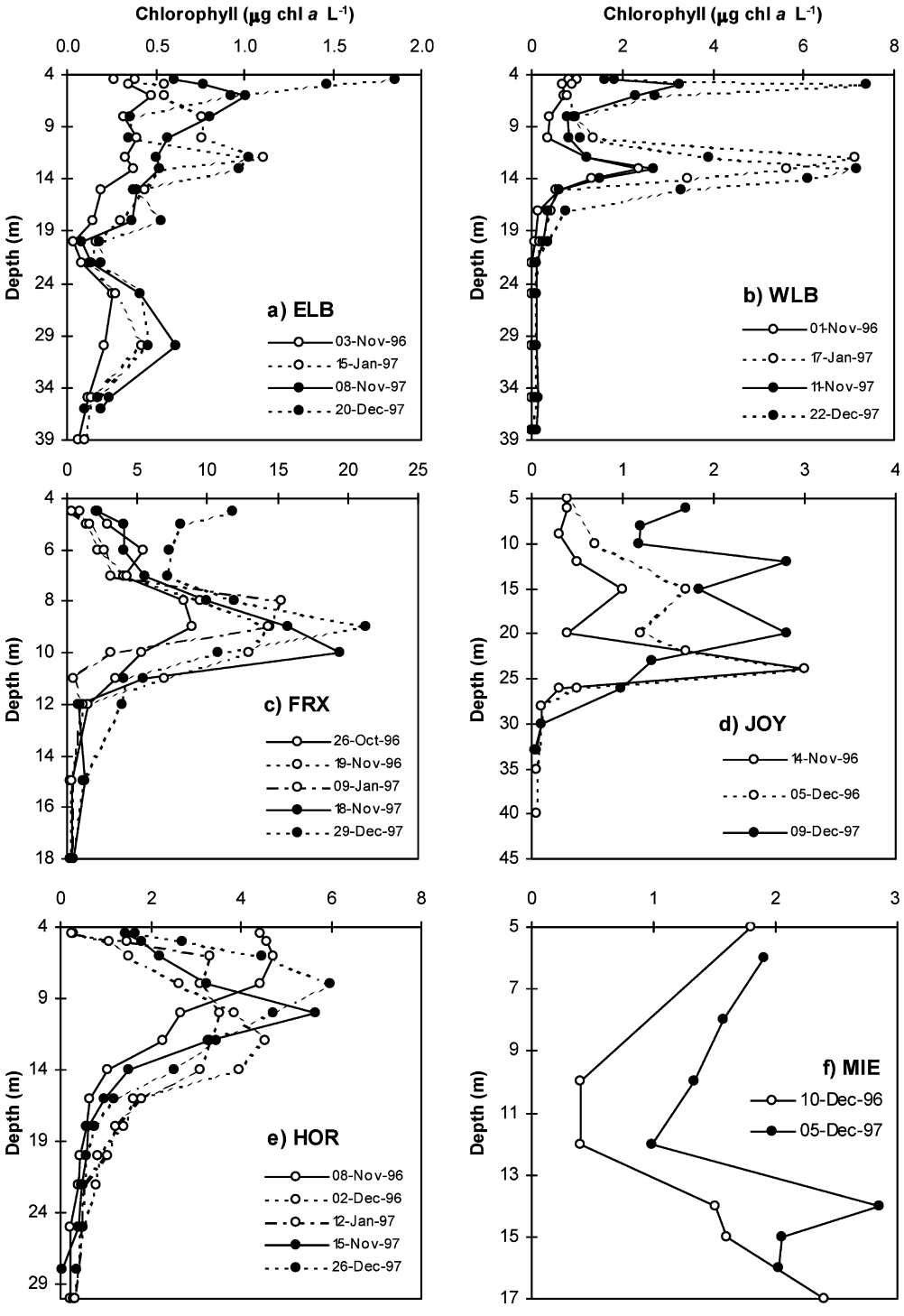

Fig. 3a–f Chlorophyll *a* concentration (µg chl *a* l^{-1}) in Lakes **a** Bonney east lobe (*ELB*), **b** Bonney west lobe (*WLB*), **c** Fryxell (*FRX*), **d** Joyce (*JOY*), **e** Hoare (*HOR*) and **f** Miers (*MIE*). Note different *scales* on axes

bacterial, phytoplankton and heterotrophic protozoan biomass all being relatively evenly distributed throughout the water column (Figs. 4, 5, 6). The exception was a small chlorophyte species, which increased with depth, reaching highest numbers and biomass close to the lake bottom (Fig. 4). Heterotrophic protozoan biomass in this lake was extremely low, typically remaining below 1 µg C l^{-1} (Fig. 6).

Discussion

In common with lakes of the Vestfold Hills region, Antarctica, plankton < 100 µm dominates McMurdo Dry Valley lakes (Laybourn-Parry and Bayliss 1996; Bell and Laybourn-Parry 1999). Despite this similarity, there are striking biological differences that occur between the

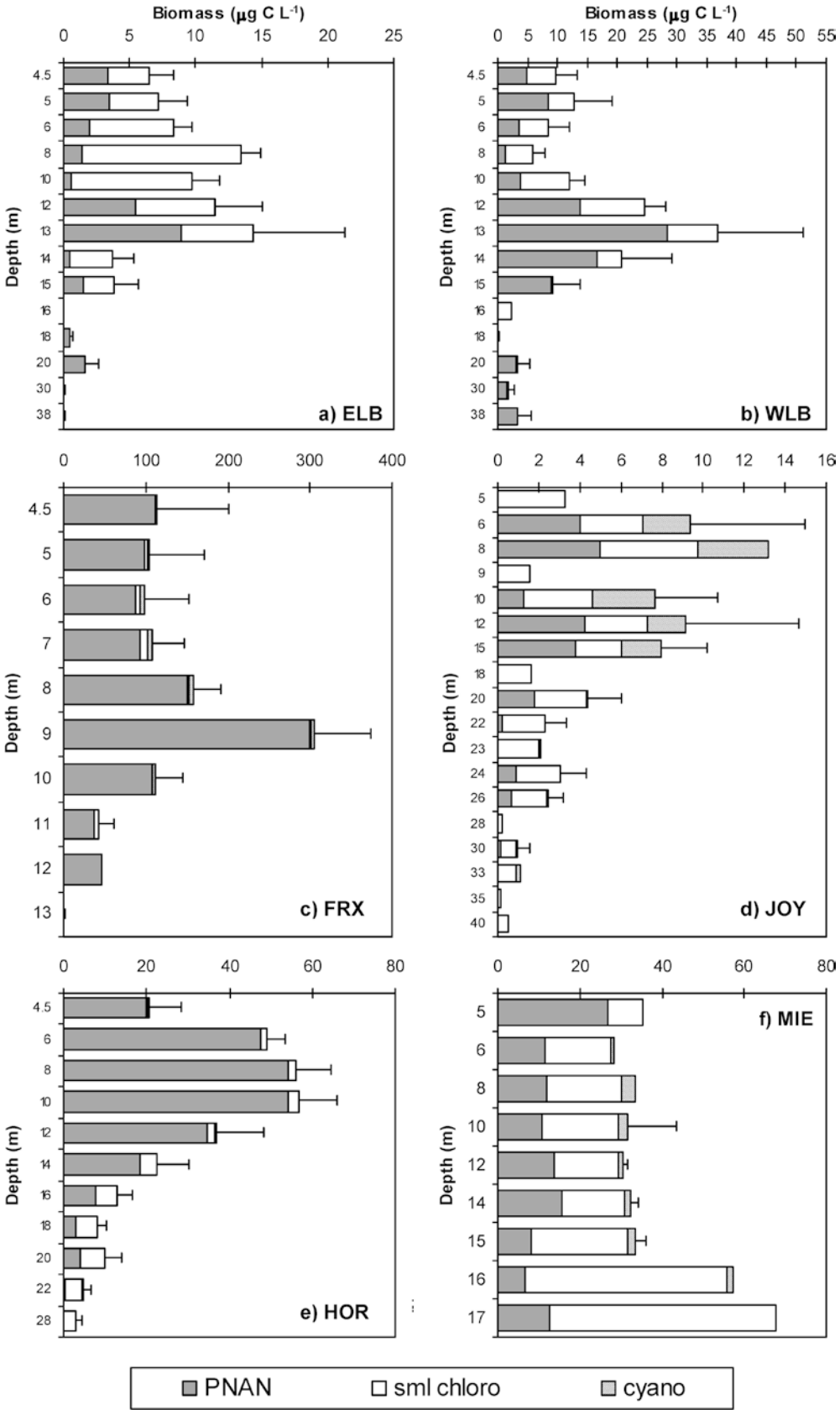

Fig. 4a–f Mean (+SEM) phytoplankton biomass (µg C l^{-1}) in Lakes **a** Bonney east lobe (*ELB*), **b** Bonney west lobe (*WLB*), **c** Fryxell (*FRX*), **d** Joyce (*JOY*), **e** Hoare (*HOR*) and **f** Miers (*MIE*) (*PNAN* photosynthetic nanoflagellates excluding small chlorophytes, *sml chloro* small chlorophytes (< 3 µm), *cyano* cyanobacteria). For sample dates refer to Fig. 3. Note different *scales* on axes

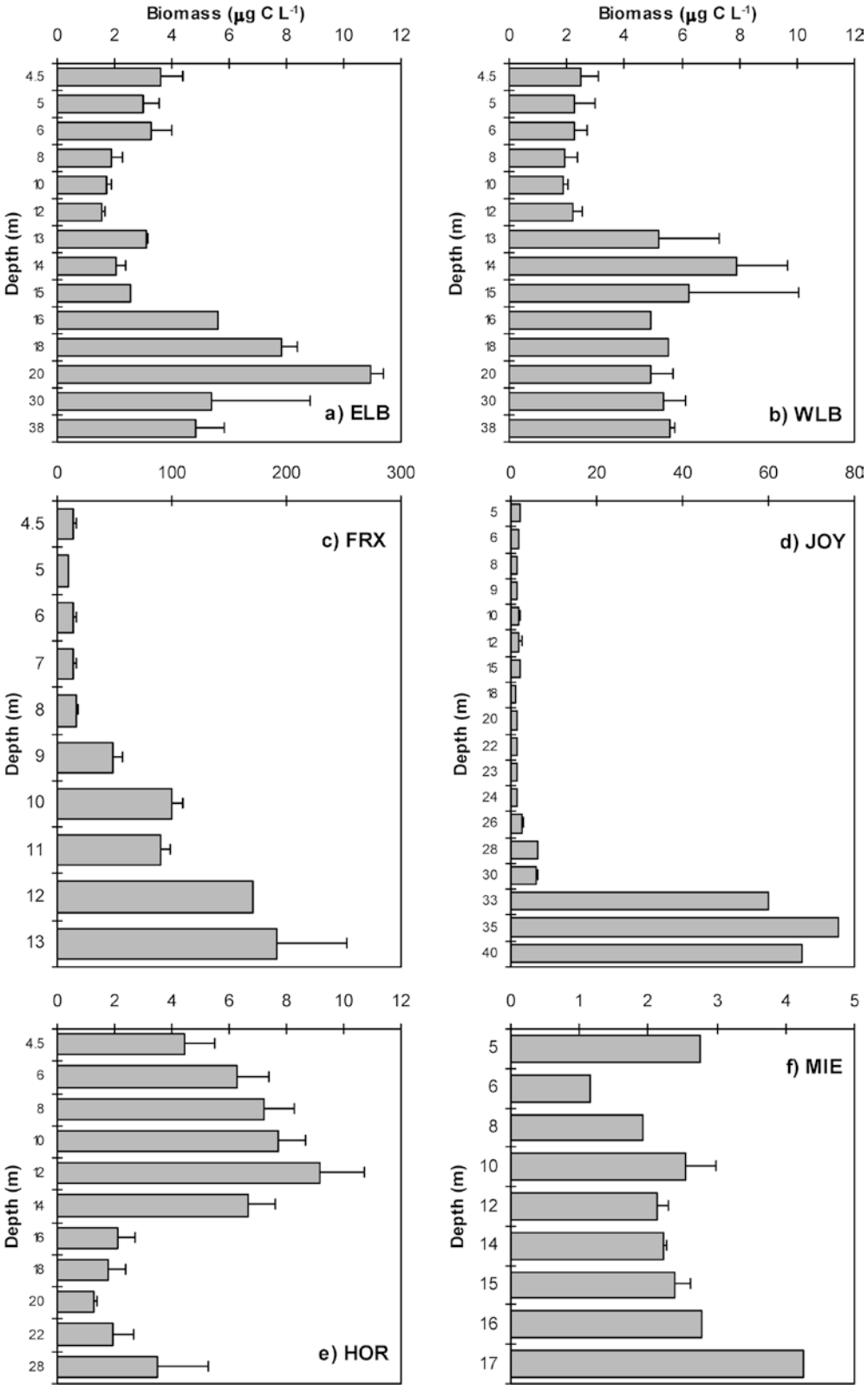

Fig. 5a–f Mean (+SEM) bacterial biomass (µg C l^{-1}) in Lakes **a** Bonney east lobe (*ELB*), **b** Bonney west lobe (*WLB*), **c** Fryxell (*FRX*), **d** Joyce (*JOY*), **e** Hoare (*HOR*) and **f** Miers (*MIE*). For sample dates refer to Fig. 3. Note different *scales* on axes

lakes of the McMurdo Dry Valleys. These include large differences in plankton vertical distribution, variation in total plankton biomass and differences in relative species composition and diversity.

Studies by Roberts and Laybourn-Parry (1999 and unpublished work) indicate the McMurdo Dry Valley lakes lack ''top-down'' grazing control, with the exception of flagellates grazing on bacteria. Consequentially,

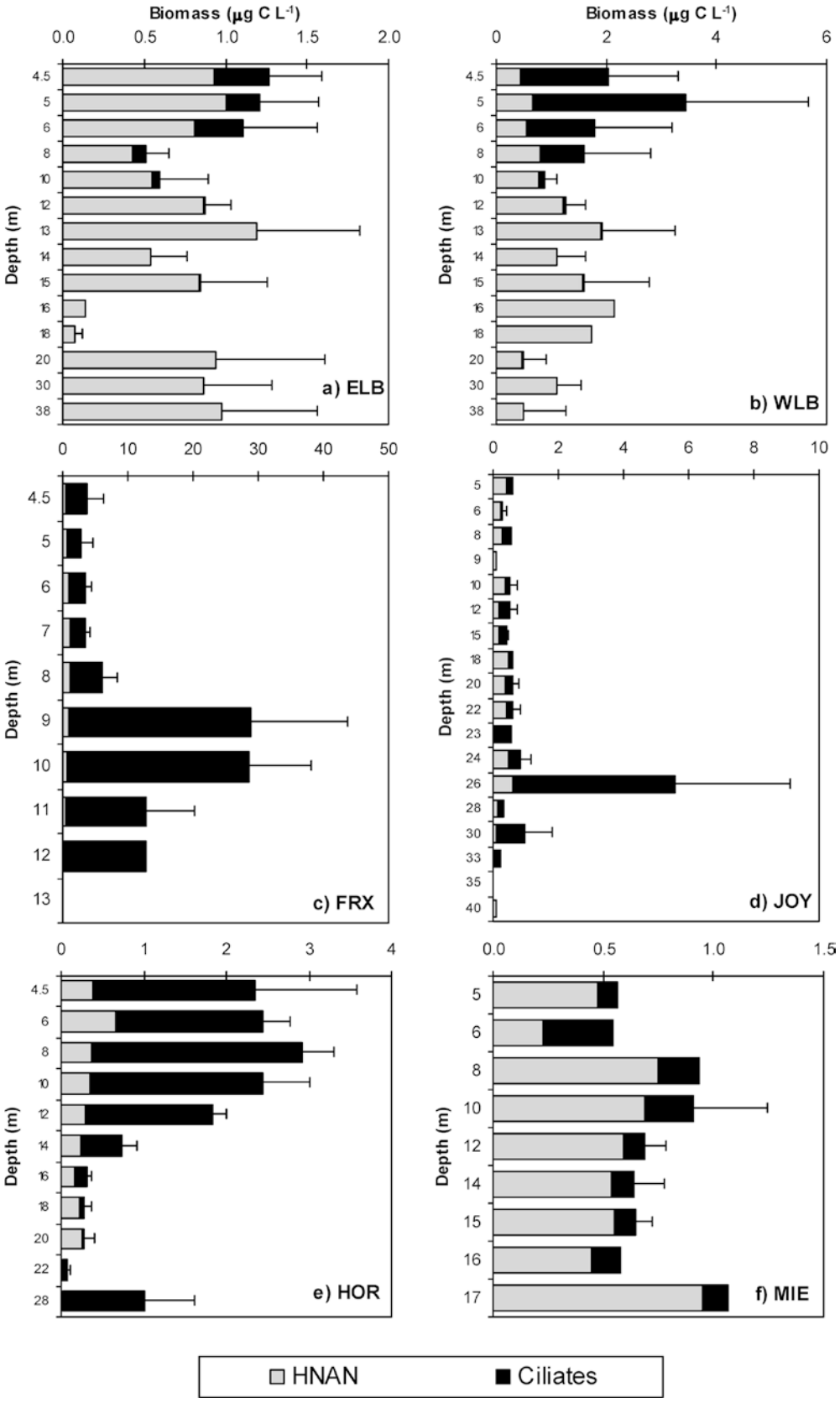

Fig. 6a–f Mean (+SEM) heterotrophic protozoan biomass (µg C l^{-1}) in Lakes **a** Bonney east lobe (*ELB*), **b** Bonney west lobe (*WLB*), **c** Fryxell (*FRX*), **d** Joyce (*JOY*), **e** Hoare (*HOR*) and **f** Miers (*MIE*) (*HNAN* heterotrophic nanoflagellates). For sample dates refer to Fig. 3. Note different *scales* on axes

Table 3 Integrated mean (and standard error) plankton abundance in the water columns of the McMurdo Dry Valley lakes during summers 1996–1997 and 1997–1998. Plankton includes bacteria ($\times 10^5$ cells ml^{-1}), PNAN (photosynthetic nanoflagellates, cells ml^{-1}), small chloro (chlorophytes < 3 μm, cells ml^{-1}), cyano (cyanobacteria, cells ml^{-1}), HNAN (heterotrophic nanoflagellates, cells ml^{-1}), ciliates (cells ml^{-1}) and rotifers ($\times 10^{-3}$ individuals ml^{-1}) (*Mixo* mixolimnion, *Chemo* chemocline, *Mono* monimolimnion)

Parameter	Section of water column	Bonney east lobe	Bonney west lobe	Joyce	Miers	Fryxell	Hoare
Bacteria ($\times 10^5$ cells ml^{-1})	Mixo	1.77 (0.75)	1.96 (0.75)	1.92 (0.43)	2.57 (0.85)	9.63 (3.50)	59.7 (2.71)
	Chemo	1.79 (0.19)	4.08 (2.72)	2.40 (0.25)	- (-)	30.75 (11.49)	2.97 (0.79)
	Mono	5.77 (2.21)	4.72 (2.02)	53.76 (22.5)	- (-)	54.45 (18.69)	- (-)
PNAN (cells ml^{-1})	Mixo	71.1 (114.6)	113.3 (167.6)	38.5 (53.3)	259.9 (110.0)	2279.6 (2647.6)	565.4 (518.7)
	Chemo	31.0 (39.2)	821.6 (1039.4)	18.0 (26.6)	- (-)	4085.4 (3093.6)	0 (0)
	Mono	7.5 (12.8)	71.0 (170.8)	1.3 (3.5)	- (-)	481.1 (675.7)	- (-)
Sml chloro (cells ml^{-1})	Mixo	2533 (1477)	2483 (1411)	1030 (379)	8860 (5519)	307 (232)	1202 (999)
	Chemo	1459 (144)	3326 (981)	672 (477)	- (-)	332 (441)	1203 (63)
	Mono	19 (24)	107 (246)	225 (209)	- (-)	117 (124)	- (-)
Cyano (cells ml^{-1})	Mixo	- (-)	- (-)	757 (549)	728 (368)	1595 (1218)	43 (28)
	Chemo	- (-)	- (-)	9 (-)	- (-)	1408 (979)	9 (13)
	Mono	- (-)	- (-)	56 (40)	- (-)	152 (294)	- (-)
HNAN (cells ml^{-1})	Mixo	98.3 (71.2)	93.4 (81.7)	37.4 (30.3)	72.9 (25.7)	109.3 (102.0)	39.4 (33.4)
	Chemo	105.3 (89.3)	237.4 (310.6)	73.6 (75.5)	- (-)	105.3 (96.9)	2.3 (3.3)
	Mono	87.7 (114.8)	125.7 (146.6)	7.5 (7.7)	- (-)	23.2 (38.4)	- (-)
Ciliates (cells ml^{-1})	Mixo	0.024 (0.044)	0.199 (0.330)	0.093 (0.103)	0.038 (0.027)	0.738 (0.783)	0.331 (0.347)
	Chemo	0.001 (0.001)	0.013 (0.015)	2.053 (2.714)	- (-)	11.085 (10.599)	0.792 (0.904)
	Mono	0.000 (0.000)	0.000 (0.001)	0.190 (0.390)	- (-)	2.980 (4.838)	- (-)
Rotifers ($\times 10^{-3}$ individuals ml^{-1})	Mixo	1.0 (1.7)	0.6 (1.2)	0.8 (1.0)	9.7 (8.0)	4.3 (9.1)	11.5 (23.2)
	Chemo	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	- (-)	0.0 (0.0)	0.5 (0.7)
	Mono	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	- (-)	0.1 (0.3)	- (-)

biomass profiles for McMurdo Dry Valley lakes are largely dictated by their physicochemical properties, resulting from each lake's respective geographic location, geochemical evolution and present-day hydrologic processes (Lyons et al. 1997, 1998, 2000). For Lakes Bonney and Fryxell, the evolution of the saline pools is the key to understanding present-day biological distributions (Priscu 1995; Lyons et al. 2000).

Lakes Fryxell and Bonney

Among the McMurdo Dry Valley meromictic lakes, Fryxell and Bonney posses the most strongly developed stratification (Spigel and Priscu 1998). The salinity profiles in Lakes Bonney and Fryxell have been heavily influenced by draw-down events, the last one completed ~1,000 years BP (Lyons et al. 1998). During the cool dry period, prior to 1,000 years BP, there was a dramatic reduction in the depth of these lakes. The east lobe of Lake Bonney lost its ice cover and evaporated to a small hypersaline pond. Since ~1,000 years BP, the climate has become warmer and wetter, resulting in refilling of the lakes by fresh-water inflow (Lyons et al. 1998).

Lake Fryxell and the west lobe of Lake Bonney both exhibited a well-developed DCM. The depth at which the DCM occurred is dictated by the present-day position of the chemocline, a factor heavily influenced by past climatic events (Lyons et al. 1998). These chemocline phytoplankton populations are dependent on nutrients that diffused upwards across the chemocline (Priscu 1995). Below this depth, phytoplankton growth does not occur due to anoxia, high sulphide concentrations and high salinity (Ward and Priscu 1997). Above the chemocline, phytoplankton growth is limited by P and N in Lakes Bonney and Fryxell, respectively (Priscu 1995; Dore and Priscu 2001). The reason for the differences in nutrient composition between lakes is determined in part by ancient geochemical variations in the mixolimnion, as opposed to present-day biochemical or physical processes (Priscu 1995; Lyons et al. 2000). Upper phytoplankton populations in Lakes Fryxell and Bonney are more directly affected by present-day events, being dependent on nutrients from intermittent stream flow and from the perennial ice cover (Priscu 1995; Howard-Williams et al. 1998).

Lake Joyce

Lake Joyce is meromictic, possessing a nutrient-rich monimolimnion, although plankton biomass is much lower than in Lakes Fryxell or Bonney. The absence of a well-defined DCM in Lake Joyce was most likely related to the depth of the chemocline (26 m). Although PAR profiles for Lake Joyce were absent, underwater PAR at 25 m is estimated to be $< 0.1\%$ of ambient PAR. This indicates the chemocline in Lake Joyce lies below the compensation depth. Hence, no phytoplankton growth would have occurred at this depth and phytoplankton would have been unable to directly utilise nutrients diffusing up from the monimolimnion. There is no data on stream flow in the Pearse Valley; the only inputs would be meltwater directly from the Taylor Glacier. Phytoplankton distribution was highly variable

Table 4 Ciliate taxa present in the plankton of the McMurdo Dry Valley lakes. (• indicates present)

Taxa	Bonney west lobe	Bonney east lobe	Fryxell	Joyce	Hoare	Miers
Prostomatida						
Plagiocampa sp.			•	•	•	
Urotricha sp.			•		•	
Oligotrichida						
Halteria sp.	•	•	•	•	•	•
Strombidium sp.	•	•	•	•	•	
Pelagiostrombilidium sp.					•	
Haptorida						
Didinium sp.	•		•		•	
Monodinium sp. 1 (large)	•	•	•	•	•	•
Monodinium sp. 2 (small)	•	•	•	•	•	•
Mesodinium sp.			•		•	
Askenasia sp.	•	•	•	•	•	•
Lacrymaria sp.			•			
Spathidium sp.					•	
Pleurostomatida						
Pleurostomatid sp. 1		•	•			
Nassulida						
Nassula sp.			•		•	
Hymenostomatida						
Frontonia sp.			•			
Heterotrichida						
Blepharisma			•	•	•	•
Hypotrichida						
Euplotes sp. 1 (large)	•	•	•	•	•	
Euplotes sp. 2 (small)	•	•			•	•
Exogenida						
Sphaerophrya sp.	•	•	•	•	•	
Suctorian sp. 2					•	
Peritrichida						
Vorticella sp. (small)	•	•	•	•	•	•
Voticella sp. (large)			•		•	
Bursariomorphida						
Bursaria sp.	•	•	•		•	•
Hymenostomata						
Scuticociliate			•	•	•	
Unidentified						
Sp. 1			•	•		
Sp. 2			•			
Sp. 3	•	•	•	•	•	•
Sp. 4			•			
Sp. 5			•		•	
Sp. 6					•	

throughout the water column. In contrast, a species of prostomatid ciliate formed a sharp peak at the chemocline. The preferred prey for this population was not obvious as POC, phytoplankton and bacterial concentration were all low at this depth. In both years sampled, copepod nauplii were found to be present at the chemocline. This is the first observation of crustacean presence within the McMurdo Dry Valley lakes. It is possible the nauplii were migrants from a benthic copepod community, similar to those in the lakes of the Vestfold Hills. The high concentrations of *Plagiocampa*, present at 26 m, could have provided a useful food source for these nauplii.

Lake Hoare

Lake Hoare differs from Lakes Fryxell and Bonney, in that it lacks a large relict saline pool. Anoxic, nutrient-rich pockets of water are present only in the very deepest portions of the lake (>28 m). This is because either Lake Hoare evaporated to complete dryness between 1,000 and 1,200 years BP or it did not exist prior to 1,200 years BP (Lyons et al. 1997, 1998). As a consequence, phytoplankton within Lake Hoare is reliant on allochthonous nutrient input from the ice cover and from stream/glacial melt-water flow (Priscu 1995; E.C. Roberts and J. Laybourn-Parry, unpublished work). Recent findings by E.C. Roberts and J. Laybourn-Parry (unpublished work) indicate that surface plankton populations within close proximity to glaciers or streams tend to be diluted once melt-water flow commences and, hence, nutrient injection from the ice cover may be more influential in boosting microbial abundance in these regions. Because nutrient input is variable and light determines the lower depth limit of autotrophs in Lake Hoare, the DCM forms a less distinct peak in this lake than in Lakes Fryxell or Bonney (E.C. Roberts and J. Laybourn-Parry, unpublished work).

Lake Miers

Lake Miers is the only lake included in this study to have a stream outlet. The steam outlet has a large influence on the lake hydrology, creating a through-flow of melt water that flushes the lake of salts during the austral summer. As a consequence, Lake Miers had the lowest salinity (Fig. 2), and the lack of salinity gradient resulted in thermohaline convection. Spigel and Priscu (1998) found Lake Miers to be the most mixed of all the McMurdo Dry Valley lakes, with a turbulent region existing above 6.5 m (corresponding with stream through-flow) and thermohaline convection cells mixing below 8.5 m. Physical mixing in the lake influenced plankton distributions, Lake Miers having the most uniform distribution of PNAN, HNAN and ciliates within the McMurdo Dry Valleys (Figs. 4, 6). Similarly low biomass and uniform depth distribution of plankton has also been recorded in the ultra-oligotrophic fresh-water lakes of the Vestfold Hills (Crooked Lake and Lake Druzhby, Laybourn-Parry et al. 1991; Laybourn-Parry and Bayliss 1996). Parker et al. (1982) recorded an absence of ciliates in the 1-l samples collected from Lake Miers, suggesting that the low ciliate abundance recorded in the present study is not unrepresentative of this lake. Only 2% of reported fresh-water planktonic environments have ciliate abundance of < 0.1 cells ml^{-1} (Finlay and Fenchel 1996).

Modern-day climate change versus legacy

The McMurdo Dry Valley lakes are ecologically simple systems, being dominated by microbial organisms and receiving minimal terrestrial organic-carbon input. Low allochthonous inputs, combined with lack of ''top-down'' grazing pressure on phytoplankton and ciliates, ultimately leads to a plankton community largely controlled by physicochemical drivers (Doran et al. 2002). Both light levels and amount of allochthonous nutrient input into the lakes are influenced by temperature. Doran et al. (2002) indicated that climate cooling within the McMurdo Dry Valleys has induced increases in ice-cover thickness, reducing underwater irradiance. This decrease in PAR is thought to have suppressed primary production in the west lobe of Lake Bonney by 9% annually (Doran et al. 2002).

However, ecological conditions within the McMurdo Dry Valley lakes are also strongly affected by past climatic conditions. This has been referred to as ''legacy'', implying that carryover ''memory'' has great influence over current lacustrine ecosystems (Lyons et al. 2000). The interplay between legacy and present-day physicochemical forcing differs among lakes, indicating planktonic communities within each lake will respond differently to changes in climate.

In Lakes Fryxell and Bonney, the main nutrient supply is from upward diffusion from the monimolimnion (Priscu 1995; Dore and Priscu 2001). Present-day stream flow and ice-cover melt has little influence over the lakes' nutrient composition. Planktonic distributions in these lakes are therefore strongly determined by past geological and geochemical modifications. Response of these communities to present-day meteorological events is likely to arise through changes in the light climate within the lakes, affected by ice-cover thickness (Doran et al. 2002). The effect of legacy is also strongly imprinted on nutrient biogeochemistry within Lake Joyce. However, past hydrological evolution of this lake has resulted in the chemocline occurring below the compensation depth, and hence phytoplankton biomass is low. Due to low phytoplankton biomass, low stream flow and the strong influence of legacy, the response of the plankton community to present-day climate change may not be immediately obvious within Lake Joyce.

In contrast to meromictic lakes within the McMurdo Dry Valleys, plankton distribution within Lake Hoare is controlled by current physicochemical factors (E.C. Roberts and J. Laybourn-Parry, unpublished work). Phytoplankton population dynamics within this lake are determined by allochthonous nutrient input (from stream flow, glacial melt-water and the ice cover) and PAR (influenced by ice-cover thickness and condition). All of these controls respond relatively rapidly to changes in climate. Because ciliate and phytoplankton biomass in Lake Hoare are high enough to detect population changes, the response of the ecosystem to metereological fluctuation may be more evident and immediate in Lake Hoare than in other McMurdo Dry Valley lakes (E.C. Roberts and J. Laybourn-Parry, unpublished work).

Of the five lakes studied, the influence of legacy is weakest in Lake Miers, because it is an open system containing an outflow to McMurdo Sound. Hydrological retention times within this lake are relatively low compared to other McMurdo Dry Valley lakes, and light penetration through the ice (Table 1) and water-column stability are particularly low (Spigel and Priscu 1998). Planktonic biomass within this lake was found to be less than in other McMurdo Dry Valley lakes. Because this lake possesses a stream outflow, the impact of climate change on planktonic distribution may not be easily detectable.

The McMurdo Dry Valley lakes provide model environments in which to study the effects of climate change and legacy on microplankton variability. In order to be able to model and predict the potential influence of climate on McMurdo Dry Valley lake pelagic ecosystems, it is important to understand the exact relationship between plankton communities and their physicochemical controls. Exploring the relationship between plankton communities and their physicochemical controls will enhance our understanding of past and present-day climatic influence on ecosystem function.

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