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Microplankton dynamics in a perennially ice-covered Antarctic lake – Lake Hoare

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SUMMARY

1. Temporal and spatial variation in planktonic abundance, biomass and composition were determined in Lake Hoare (McMurdo Dry Valleys, Antarctica) over two summer seasons (1996–97 and 1997–98).
2. Phototrophic nanoflagellates (PNAN) dominated planktonic biomass, with a mean monthly biomass ranging between 27.3 and 40.4 μg C L^{-1}. The deep chlorophyll maximum was mainly composed of cryptophytes (>87% of total PNAN biomass) and varied in depth between 6 and 12 m.
3. Maximum bacterial concentration was 11.8×10^5 cells mL^{-1}. Bacterial abundance showed relatively little temporal variation, with the exception of a drop in numbers that occurred in late November of both years studied.
4. Ciliates were the most successful heterotrophic protozoan group, with a mean monthly biomass (1.2–3.2 μg C L^{-1}) being typically at least double that of heterotrophic nanoflagellate (HNAN) biomass (0.1–0.7 μg C L^{-1}).
5. Microbial processes within this lake appear to be dominated by bottom up control. The relative importance of allochthonous inputs into the lake (from the ice-cover and stream flow) and autochthonous recycling (by microzooplankton regeneration) are considered.
6. Results from a horizontal transect indicate that the permanence of the main sample hole may have enhanced planktonic biomass over a relatively small spatial scale.

Keywords: Antarctica, ciliates, cryptophytes, lakes, protozoa

Introduction

The Antarctic continent contains many lakes, most of which are concentrated within areas termed 'ice-free oases' (Simmons, Vestal & Wharton, 1993; Ellis-Evans, 1996). 'Ice-free' is used to indicate the presence of bare ground; glaciers and ice-covered lakes are present within these oases. The majority of Antarctic non-marine biomass can be found concentrated within lakes, being buffered from the low temperatures and low humidity experienced by the terrestrial biota (Simmons *et al.*, 1993). Ice-free oases account for only 2% of the continent's area, the remaining 98% of Antarctic is covered completely by ice. The McMurdo Dry Valleys (76°30′ to 78°30′S, 160° to 164°E) comprise the largest of these oases (approximately 4000 km^2) with a mean annual temperature of −20 °C and precipitation of <10 cm $year^{-1}$.

With the exception of extremely hypersaline lakes, which do not readily freeze, most Antarctic lakes are ice covered for at least 8 months each year (Vincent, 1988). Ice cover has a significant effect on the lake environment, eliminating turbulent mixing by wind-generated currents (Simmons *et al.*, 1993; Spigel & Priscu, 1998), greatly decreasing light penetration to the water column (Howard-Williams, Schwarz & Hawes, 1998) and restricting gas exchange between the atmosphere and the water column (Wharton, Simmons & McKay,

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1989). The McMurdo Dry Valleys possess a number of perennially ice-covered lakes, most of which are meromictic i.e. they are permanently stratified as a result of salinity gradients (Chinn, 1993; Simmons *et al.*, 1993). However, freshwater lakes do exist in the Dry Valleys, including Lake Miers and Lake Hoare.

The ecology of Antarctic lakes is typically dominated by microbial organisms. Plankton in the McMurdo Dry Valleys lakes are comprised of bacteria, cyanobacteria, flagellates and ciliates, the only multicellular organisms present being rotifers and the occasional tardigrade (Spaulding *et al.*, 1994; Roberts *et al.*, 2000, 2004; Lisle & Priscu, in press).

Antarctic lakes are characterised by strong 'bottom-up' control, with light, nutrients and additional physicochemical factors imposing a greater control over microplankton dynamics than 'top-down' influences such as predation and competition (Laybourn-Parry & Bayliss, 1996; Bell & Laybourn-Parry, 1999). As a consequence, organism distribution in Antarctic lakes strongly reflects the physicochemical environment (Roberts *et al.*, 2004).

Formation of the McMurdo Dry Valley lakes began 4.6 million years ago and subsequent geological evolution of the lakes has been complex. Striking physicochemical differences between Lakes Hoare, Fryxell and Bonney, all located within the same valley, can be explained by their geological evolution. Of particular influence was a cold, dry period that persisted between 3000 and 1000 year BP. Lyons *et al.* (1998) used stable isotope data from water of the Taylor Valley lakes to infer that a significant decrease in the depth of the lakes occurred 1000–1200 year BP. During this time Lakes Fryxell lost its ice cover and evaporated to a small hypersaline pond. In contrast, Lake Hoare either evaporated to complete dryness or did not exist prior to 1200 year BP (Lyons *et al.*, 1997, 1998). Either way, Lake Hoare lacks the relict, saline, anoxic pools present in Lake Bonney and Lake Fryxell.

It is now well recognised that environments within the McMurdo Dry Valleys are sensitive to low amplitude climate shifts (Chinn, 1993; Doran *et al.*, 2002). Between 1986 and 2000 the McMurdo Dry Valleys have cooled 0.7 °C per decade (Doran *et al.*, 2002). In response to this cooling, primary productivity within the lakes has decreased (Doran *et al.*, 2002). An accurate representation of seasonal variability in microplankton populations must be obtained if long-term inter-annual changes are to be addressed within these lakes. Here we report the first detailed study of both temporal and spatial variability of microplankton within Lake Hoare, McMurdo Dry Valleys. These results are compared with other geographically distinct Antarctic lakes to determine the role that microplankton have in overall ecosystem structure and function.

Methods

Location and sampling

Lake Hoare is one of four large perennially ice covered lakes situated in the Taylor Valley, Antarctica (Fig. 1). It is 15 km from the sea at 77°38′S 162°55′E (Spigel & Priscu, 1998). The ice cover is approximately 4 m thick and percentage light transmission through the ice to the water column below is on average 1.6% (Howard-Williams *et al.*, 1998). The lake has a surface area of 1.94 km^2 and a maximum depth of 34 m (Spigel & Priscu, 1998). For a few weeks during the year, glacial melt water flows into Lake Hoare from Anderson Creek and directly off the Canada Glacier (Fig. 1). The lake has no out-flow. In contrast to other lakes within the Taylor Valley, Lake Hoare is only anoxic in deep pockets of water, below 28 m.

Water samples were collected from the main sampling hole (H2) in Lake Hoare (Fig. 1) at weekly to fortnightly intervals throughout the two summer seasons (1996–97 and 1997–98) using a 1 L Niskin bottle. All depths are reported with respect to the water level in the sampling hole (piezometric depth), which was approximately 30–50 cm below the surface of the ice (Dore & Priscu, 2001). During the 1996–97 season, water samples were collected at 4.5, 6 and at 2 m intervals down to 20 m whereas, during the 1997–98 season, samples were collected to 18 m, with additional samples at 22 and 28 m.

In order to assess horizontal variability in Lake Hoare, on 12 December 1997 water samples were taken from four different sample sites along a transect (Fig. 1). The distance between each sample site was 200 m. Water samples were taken from 5, 8, 12 and 16 m for chemical and microbial analysis.

Analysis of samples

Biological samples were preserved on return to the shore-side laboratory (within 1 h of collection). All

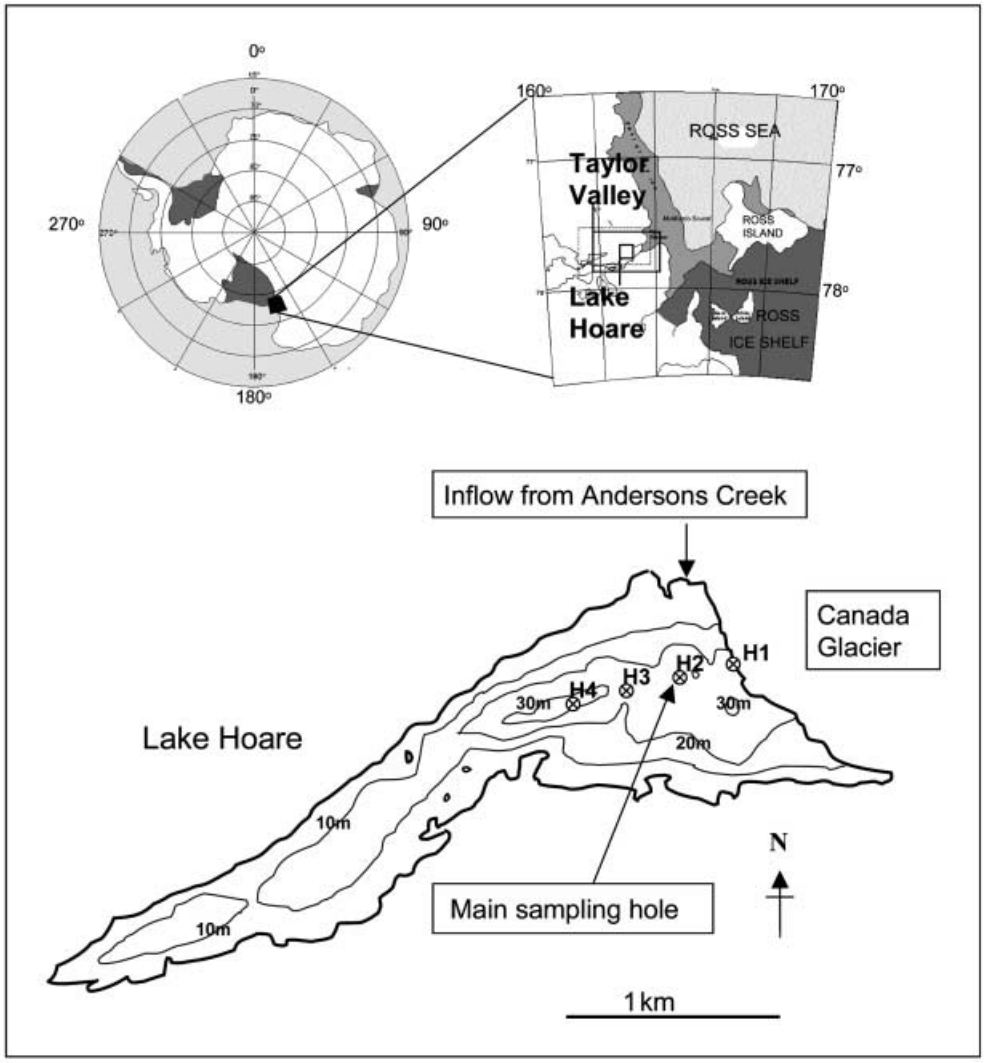

Fig. 1 Map showing location of Lake Hoare (77°38′S 162°55′E) and the four sampling holes. H2 was the main sampling hole.

epifluorescence microscopy was conducted within 1 week of sample collection. For nanoflagellates, 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 prior to analysis. Fifty mL of the sample was stained with 4′, 6-diamidino-2 phenylindole (DAPI) and filtered onto a 2 μm pore Whatman polycarbonate membrane filter. Twenty Whipple grids (Graticules, Edenbridge, Kent, U.K.) were counted at 400× magnification using both UV and blue excitation under epifluorescence microscopy (Zeiss Standard 16 microscope, Carl Zeiss, Welwyn Garden City, Herts., U.K.) in order to distinguish between phototrophic and heterotrophic nanoflagellates (HNAN).

Samples (>50 individuals) of HNAN and phototrophic nanoflagellates (PNAN) were measured using a line graticule (Graticules) at 1000×. Mean cell volume was calculated using the following equation:

$$V = \frac{\pi L W^2}{6}$$

where V = cell volume (μm^3), L = length (μm) and W = width (μm). Biovolume was converted to biomass using a carbon conversion value of 0.22 pg C μm^{-3} (Børsheim & Bratbak, 1987).

For bacterial analysis, 5 mL of 2% glutaraldehyde fixed water was stored in glass vials at 4 °C; 2 mL samples were stained with DAPI and filtered onto a 0.2 μm black Whatman polycarbonate membrane

filter. Filters were viewed under UV epifluorescence microscopy at a magnification of ×1000. Ten randomly selected Whipple grids were counted on each filter. In order to calculate volume, 100 cells were measured at ×1000 using a Patterson Grid (Graticules). Volume of the bacteria was calculated using the following equation:

$$V = \frac{\pi}{4} W^2 \frac{L - W}{3}$$

where V = volume (μm^3), L = length (μm) and W = width (μm). A conversion factor of 0.22 pg C μm^{-3} (Bratbak & Dundas, 1984) was used to convert biovolume to biomass.

For ciliate counts, 500 mL or 1 L samples were concentrated by settling and counted in a Sedgewick–Rafter counting chamber (Graticules). It was not possible to identify ciliates to species using postfixed Bouin's material for protargol staining; therefore, ciliates were identified only to genus. 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 0.19 pg C μm^{-3} (Putt & Stoecker, 1989).

Carbon conversion values of Bratbak & Dundas (1984), Børsheim & Bratbak (1987) and Putt & Stoecker (1989) were used in order to aid comparison between other plankton studies conducted on Antarctic Lakes between 1985 and 2000.

Ciliate ingestion rate was measured using the uptake of fluorescently labelled algae and bacteria (FLA and FLB) according to the methods of Sherr & Sherr (1993). Respectively, FLA and FLB were prepared by labelling cultured *Chlorella vulgaris* (Beijerinck, Culture Collection of Algae and Protozoa, Ambleside, Cumbria, U.K.) and cultured bacteria from Lake Fryxell with DTAF. Ciliates were concentrated by reverse filtration (10 μm mesh) prior to the grazing run. Ingestion rate was measured *in situ* in Lake Hoare using 60 mL acid rinsed Nalgene bottles. Duplicate samples were preserved in 2% ice-cold glutaraldehyde after 1, 2, 4, 6 and 8 h. For each ciliate species, the number of FLB/FLA inside 50 individual ciliates were counted on each preparation.

Untreated water samples were collected for chlorophyll *a*, particulate organic carbon (POC), dissolved organic carbon (DOC) and nutrient analysis. Phaeophytin-corrected chlorophyll *a* was quantified using a Turner Model 10-AU-005 field fluorometer, on Whatman GF/F filtered samples subject to overnight pigment extraction in 90% acetone. POC samples, derived by filtering 300–500 mL of water through combusted GF/F filters, were analysed using a Carlo Erba CHNS elemental analyser. Whatman GF/F filtered water was analysed for dissolved inorganic nitrogen, using a Lachat Quickchem AE Autoanalyser (Strickland & Parsons, 1972). Soluble reactive phosphorus (SRP) was determined with a manual colorimetric method using a 10 cm path length cuvette in the spectrometer (Strickland & Parsons, 1972).

Results

Water temperature within Lake Hoare ranged from 0.15 °C, directly beneath the ice cover, to 0.41 °C at 9 m (Fig. 2). Salinity increased with depth from 0.35 PSU at 4.5 m to 0.70 PSU at 25 m (Fig. 2).

Nutrients concentrations above 10 m were low (Fig. 3), throughout both summer seasons NO_3^- concentration above 14 m remaining close to or below detection limits (<0.04 μM). Ammonium concentration peaked at 14 m during November 1996 and 1997. Highest surface NH_4^+ concentrations were recorded later in the summer season (Fig. 3). The seasonal

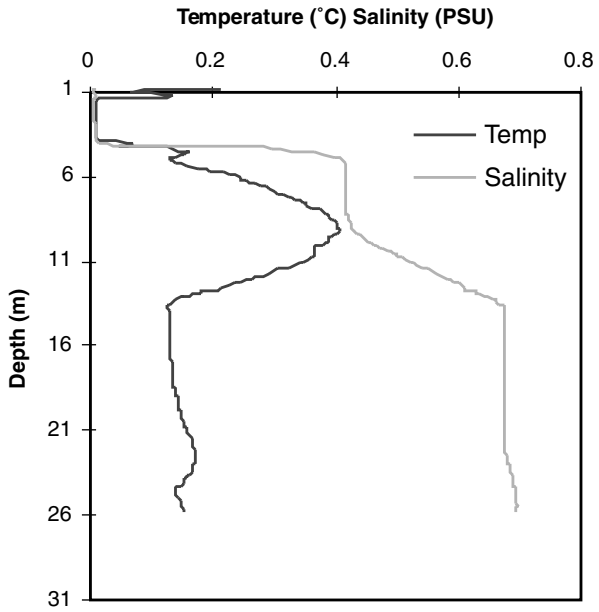

Fig. 2 Temperature (°C) and salinity (PSU) profiles for Lake Hoare, 27 December 1997.

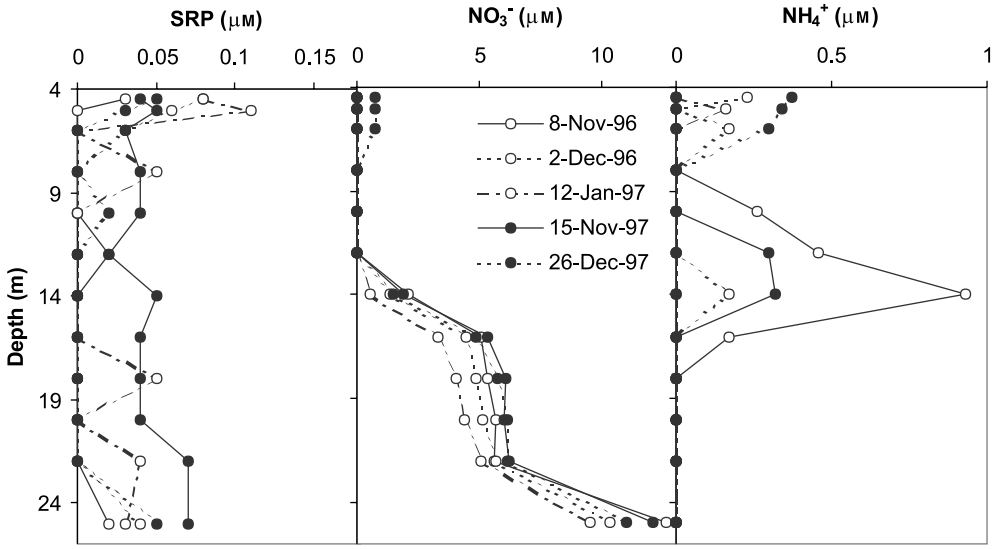

Fig. 3 Nutrient profiles (μM) for Lake Hoare during the 1996–97 and 1997–98 summer seasons.

changes in mid-water and surface NH_4^+ peaks, together with the strong vertical NH_4^+ gradients, indicate nutrient regeneration activities of the protozooplankton.

The highest POC concentration was recorded just below the ice during both the 1996–97 and 1997–98 field seasons (Fig. 4a). At 4.5 m, POC reached 603 μg C L^{-1} on 23 November 1996 and 665 μg C L^{-1} on 10 December 1997. The contribution of living biomass (bacteria, PNAN, HNAN, ciliates and rotifers) to total POC ranged from 0.8 to 53.7%. Highest chlorophyll *a* concentrations were recorded in the upper 18 m, concentration below this depth remaining <1 μg chl *a* L^{-1} (Fig. 4b). Chlorophyll *a* did not peak immediately beneath the ice cover, with a deep chlorophyll maximum (DCM) forming between 8 and 12 m during the 1996–97 season and between 6 and 8 m during the 1997–98 season. Maximum concentrations of 5.5 and 8.1 μg chl *a* L^{-1} were recorded in the first and second summer seasons, respectively. DOC measurements were restricted to five sampling dates over the two summer seasons. Concentration increased with depth, with DOC as low as 0.36 mg C L^{-1} at 4.5 m, reaching 2.57 mg C L^{-1} at 28 m.

During both field seasons, bacterial numbers in Lake Hoare dropped after mid-November, and recovered again by mid-December (Fig. 5a). Highest abundances were recorded at 10 m on 26 January 1997 (11.8×10^5 cells mL^{-1}) during the first season and at 6 m on 17 January 1998 (13.4×10^5 cells mL^{-1}) during the second season. The PNAN community in Lake Hoare was dominated by cryptophytes, accounting for >85% of total PNAN abundance and >87% of the total PNAN biomass. Photosynthetic nanoflagellates occurred deeper in the water column during the first season than in the second (Fig. 5b). Maximum concentrations of 1617 and 2097 cells mL^{-1} were recorded during the first and second season, respectively. HNAN abundance was much lower than that of PNAN, reaching a peak of 338 cells mL^{-1} on 26 December 1996 (Fig. 5c), and were most abundant towards the beginning of the field seasons.

Ciliate abundance in Lake Hoare showed high inter-annual variability (Fig. 5d). Throughout the first season, ciliate abundance remained below 1.4 cells mL^{-1}. A large ciliate bloom occurred during the second summer season, directly beneath the ice, with a maximum abundance of 23.4 cells mL^{-1} at 4.5 m on 10 December 1997. Two ciliate maxima were present towards the end of the 1997–98 season, one between 8 and 10 m and the other at 28 m. High inter-annual variability in ciliate composition occurred in Lake Hoare (Fig. 6). During the 1996–97 field season *Askenasia* was dominant, accounting for >36% of total ciliate numerical abundance above 16 m. Being five times larger than *Askenasia*, *Euplotes* made the largest contribution to biomass during the first season, however. Few ciliate taxa showed stratified relative abundance during the first season, in contrast to the second summer season when the majority of taxa

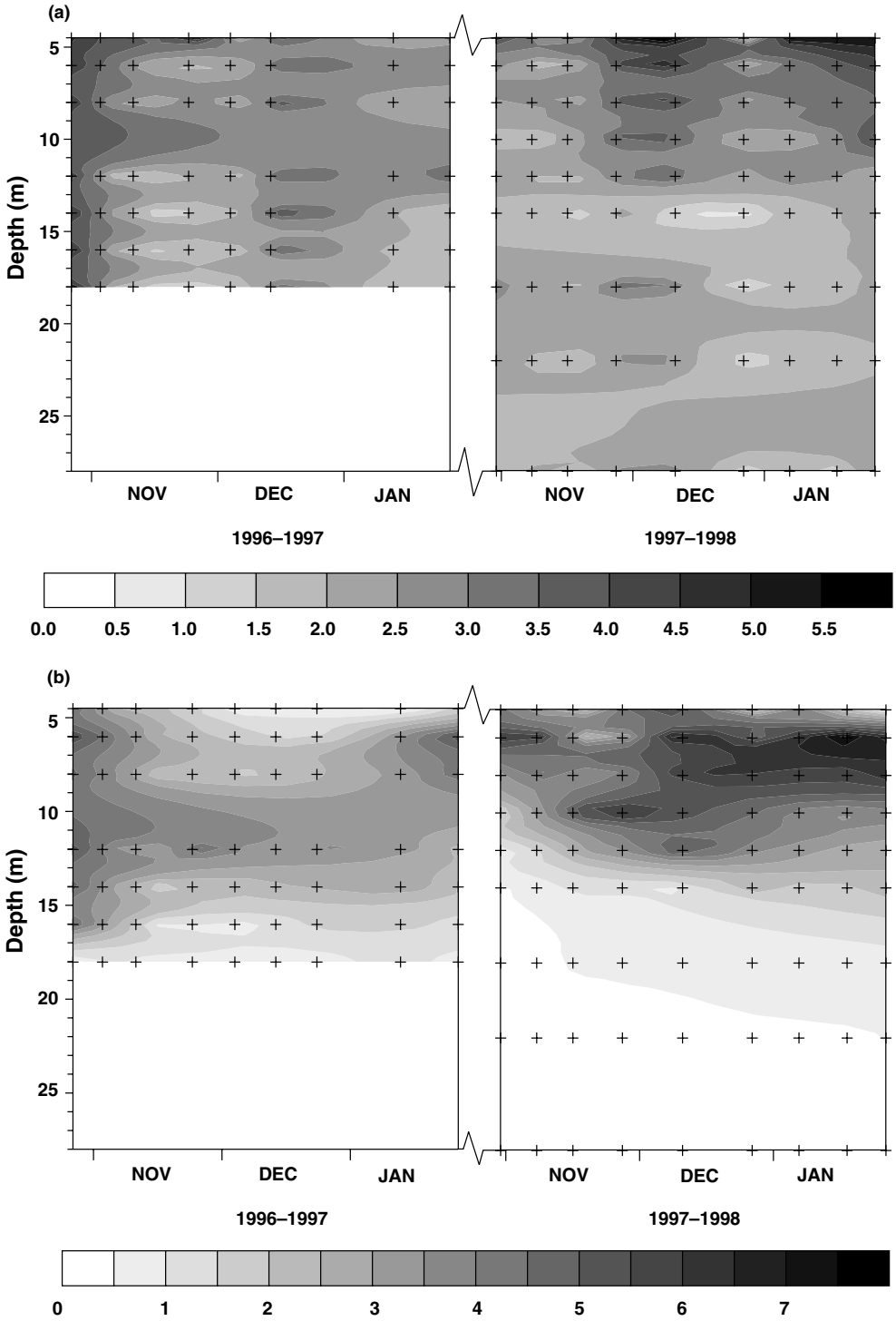

Fig. 4 Spatial and temporal distribution of (a) particulate organic carbon ($\times 10^2$ μg C L^{-1}) and (b) chlorophyll *a* (μg chl *a* L^{-1}) in Lake Hoare during the 1996–97 and 1997–98 summer seasons. '+' denotes the sampling point. Note that during the first summer season the water column was not sampled below 18 m.

occurred in different depth strata (Fig. 6). *Urotricha* dominated abundance just below the ice, comprising 73% of total ciliate numbers at 4.5 m during the 1997–98 summer season. Between 6 and 10 m, *Askenasia* had the highest ciliate abundance and biomass. The relatively large *Blepharisma* (52 451 μm^3) made the

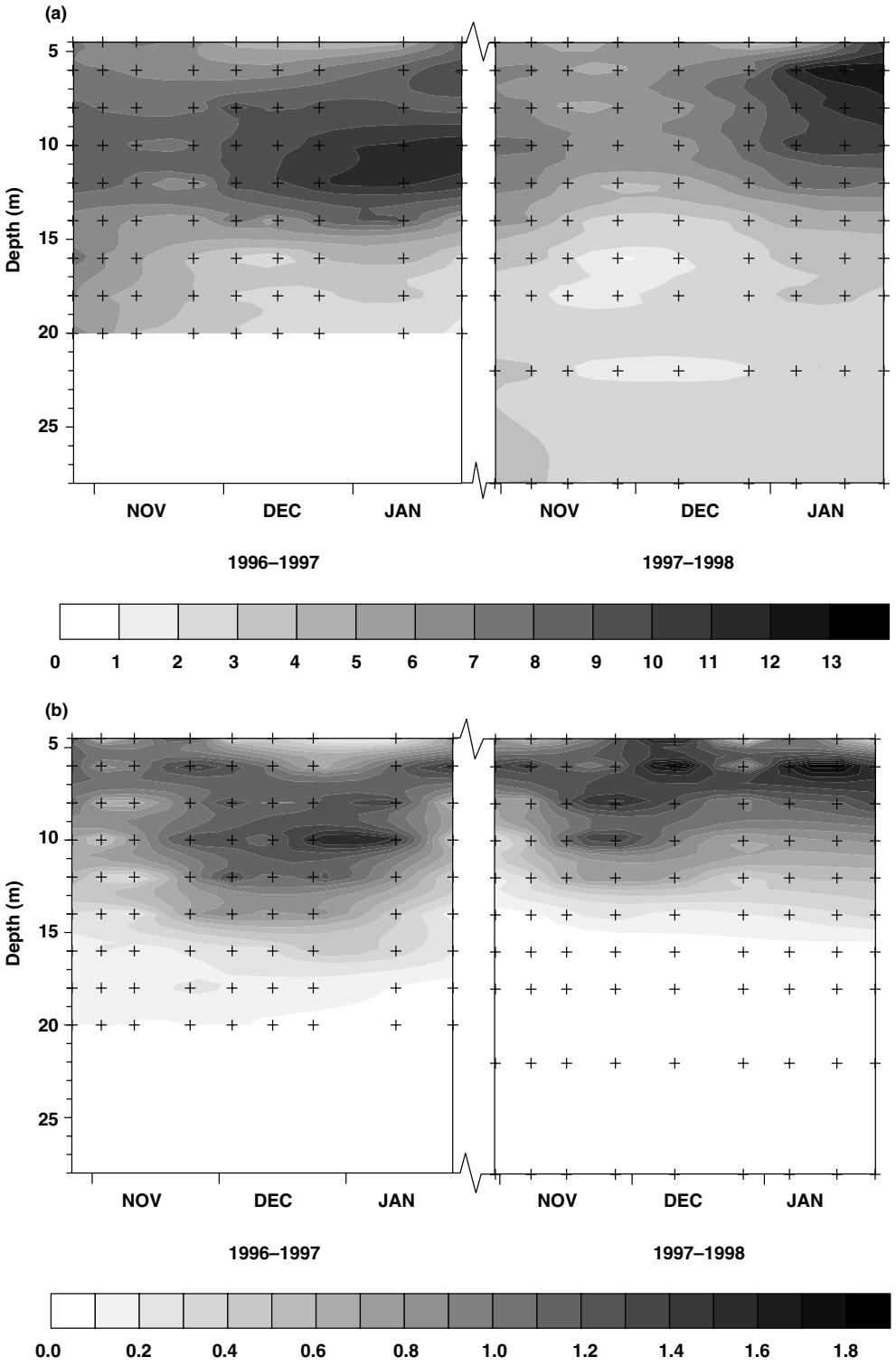

Fig. 5 Spatial and temporal distribution of (a) bacteria ($\times 10^5$ cells mL^{-1}), (b) phototrophic nanoflagellates ($\times 10^3$ cells mL^{-1}), (c) heterotrophic nanoflagellates ($\times 10^2$ cells mL^{-1}) and (d) ciliates (cells mL^{-1}) in Lake Hoare during the 1996–97 and 1997–98 summer seasons. '+' denotes the sampling point. Note that during the first summer season the water column was not sampled below 20 m.

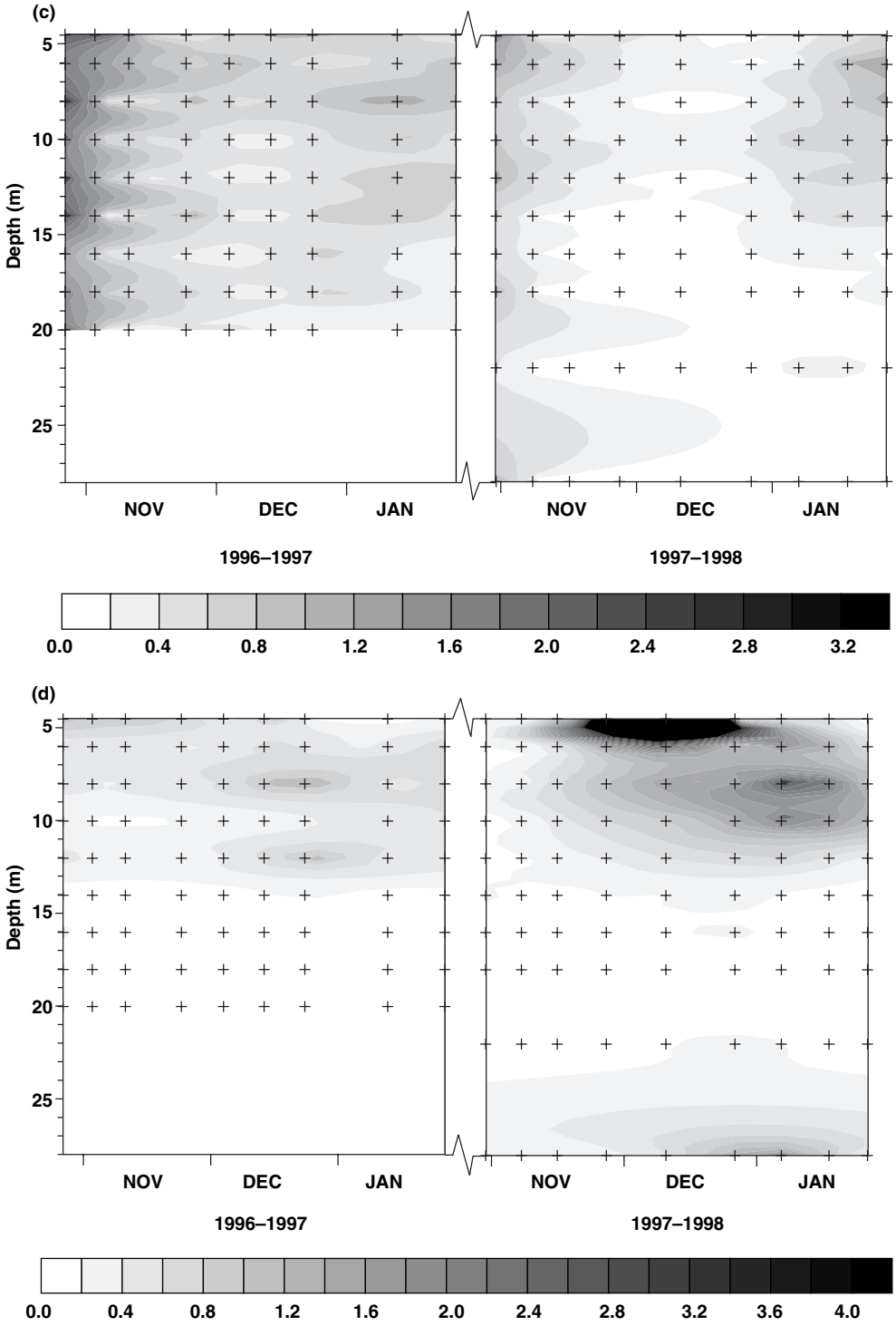

Fig. 5 (*Continued*)

largest contribution to biomass at 14 m (30%). Scuticociliates, absent in the first summer, were the most abundant ciliates below 12 m during the second season (>48%). These small cells (1262 μm^3) made a lower contribution to ciliate biomass, with *Plagiocampa* making up 64% of total biomass at 28 m. *Euplotes* accounted for a much smaller proportion of ciliate biomass during the second summer (<29%).

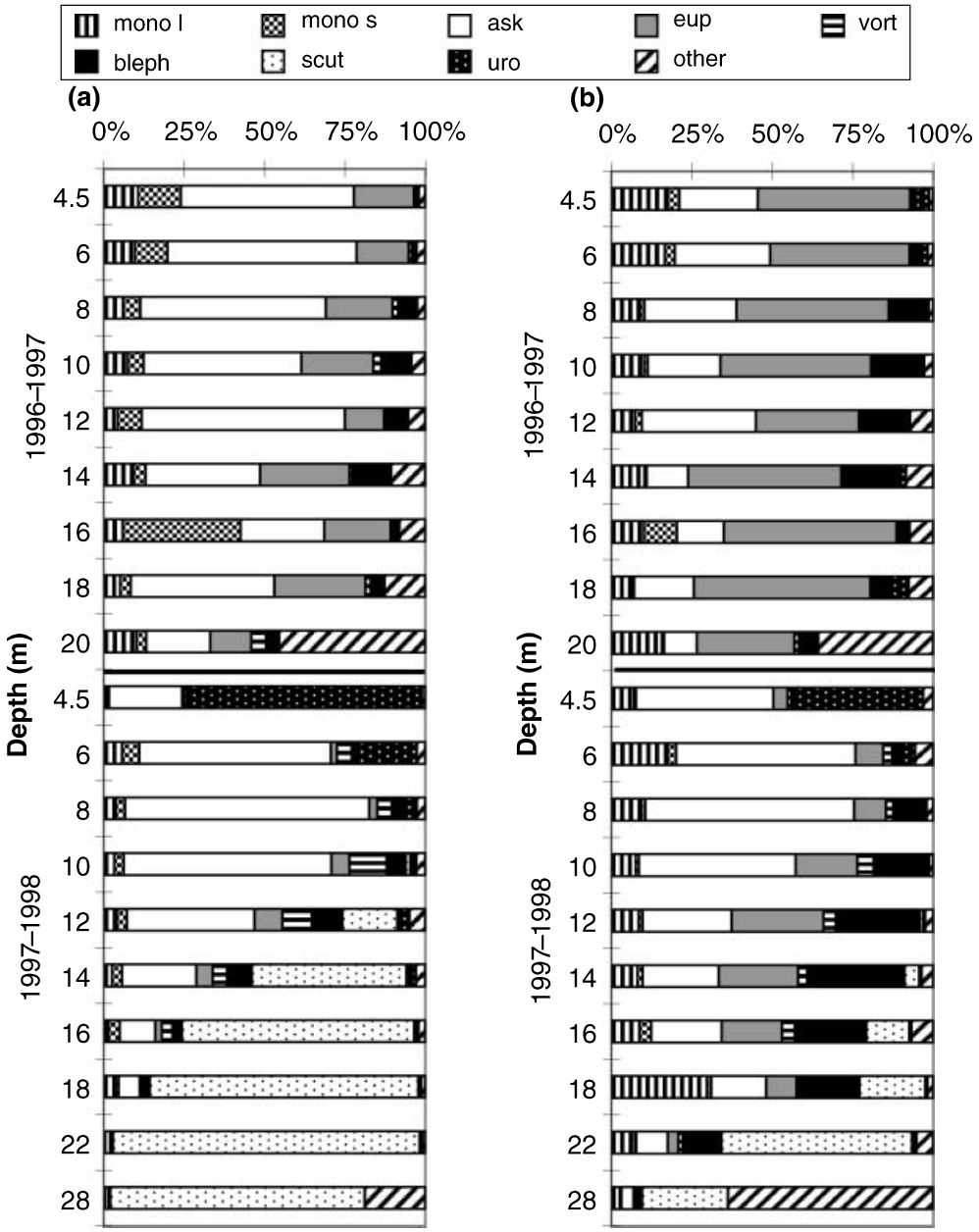

Fig. 6 Relative (a) abundance and (b) biomass of ciliate taxa at selected depths in Lake Hoare during the 1996–97 and 1997–98 field seasons; mono l, *Monodinium* large sp.; mono s, *Monodinium* small sp.; ask, *Askenasia*; eup, *Euplotes*; vort, *Vorticella*; bleph, *Blepharisma*; scut, scuticociliates; uro, *Urotricha*; other, other taxa.

Ingestion rates of the ciliates *Askenasia* and *Vorticella* (measured in Lake Hoare on 7 November 1997) were 0.43 flagellate cell^{-1} h^{-1} and 76.2 bacteria cell^{-1} h^{-1}, respectively.

Microplankton biomass in Lake Hoare was dominated by PNAN, whose biomass was over four times greater than that of bacteria, HNAN or ciliates in all months studied (Fig. 7). Mean, monthly PNAN biomass ranged from 27.3 to 40.4 μg C L^{-1}. Ciliates were most important in terms of heterotrophic protozoan biomass, ciliate mean monthly biomass (ranging from 1.2 to 3.2 μg C L^{-1}) was at least double that of HNAN (ranging between 0.1 and 0.7 μg C L^{-1}).

Variability in microbial abundance along the horizontal transect from sites H1 to H4 on 12 December 1997 can be seen in Fig. 8. From these results it appears

that greatest horizontal variability in planktonic abundance occurred in the upper water column (Fig. 8). With the exception of HNAN, highest microplankton concentrations were recorded at sample hole 2, the permanent sampling hole. In general there was little horizontal variation in protozoan abundance and chlorophyll *a* concentration between sample holes 1, 3 and 4, although ciliate concentration was higher at sample hole 4 compared with holes 1 and 3. The main difference in ciliate composition between holes was related to a greater dominance of *Urotricha* at the main sample site (accounting for 53% of total ciliate abundance at 5 m, H2), relative to the three other holes (<25% total ciliate abundance at 5 m, H1, H3 and H4).

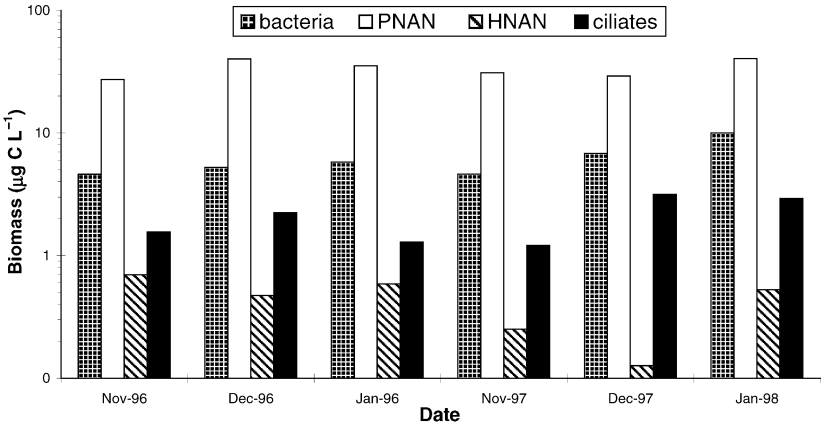

Fig. 7 Mean biomass of different microbial groups in the upper 20 m of Lake Hoare during the 1996–97 and 1997–98 field season. Note the log scale on the *y* axis.

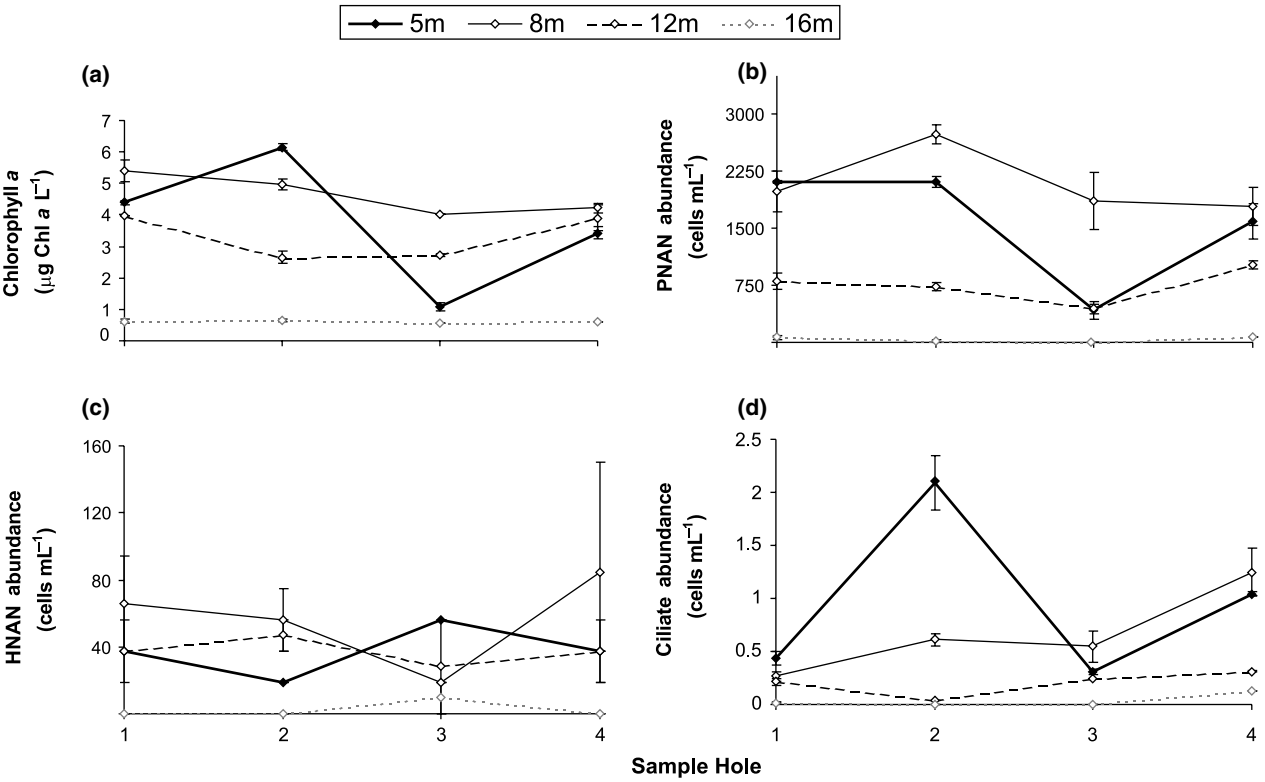

Fig. 8 (a) Chlorophyll *a* (µg chl *a* L^{-1}), (b) phototrophic nanoflagellate abundance (cells mL^{-1}), (c) heterotrophic nanoflagellate abundance (cells mL^{-1}) and (d) ciliate abundance (cells mL^{-1}) at selected depths from four sampling holes in Lake Hoare.

Discussion

There are a number of hydrological and ecological similarities among Antarctic lakes, mainly related to them being ice covered for at least the majority of the year (Table 1). In Antarctica, however, widely differing planktonic distributions can be found within lakes in close proximity to one another (Vincent, 1987; Laybourn-Parry & Marchant, 1992), which coincide with the diversity in physical and chemical conditions found among lakes. Here we compare and contrast the distinct biotic and abiotic features within individual lakes to gain an understanding of the function of ice-covered Antarctic lake ecosystems. In order to highlight key features of these systems, and to gain a broader understanding of Antarctic limnology, our discussion will initially focus on a comparison between Lake Hoare with neighbouring Lake Fryxell. Lake Hoare and Lake Fryxell are both situated within the Taylor Valley, separated only by the Canada

Table 1 A comparison of Lakes Hoare and Fryxell with lakes from the Vestfold Hills and Signy Island, Antarctica

	Lakes Hoare and Fryxell	Vestfold Hills Lakes	Signy Island Lakes
Ice Cover	Perennial (Spigel & Priscu, 1998)	Most lakes ice covered >8 months year^{-1}	Most lakes ice covered >8 months year^{-1}
Plankton community	All lakes dominated by freshwater species (present study)	Meromictic lakes dominated by marine species, as a result of their marine origin. Freshwater lakes dominated by freshwater species (Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999)	Dominated by freshwater species
	PNAN biomass > other planktonic groups (present study; Roberts *et al*., 2000)	Dominant planktonic group is seasonal and lake dependant (Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999)	During summer, PNAN biomass > other planktonic groups in oligotrophic Lake Sombre and eutrophic Lake Heywood (Butler, 1999a,b)
	Cryptophytes dominate phytoplankton (present study; Roberts *et al*., 2000)	Chlorophytes and chrysophytes dominate PNAN (Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999)	Chlorophytes and cryptophytes dominate phytoplankton (Hawes, 1990; Laybourn-Parry, 1997; Butler, 1999b)
	Ciliate biomass > HNAN (present study; Roberts *et al*., 2000)	HNAN biomass > ciliate (Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999)	HNAN biomass > ciliate (Laybourn-Parry, 1997; Butler, 1999a,b)
	No crustacean zooplankton (present study; Roberts *et al*., 2000)	Crustacean zooplankton present e.g. copepod *Paralabidocera antarctica* (Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999)	Crustacean zooplankton present e.g. *Boeckella poppei* (Butler, 1999a) *Branchinecta gaini* (Laybourn-Parry, 1997; Butler, 1999b)
Trophic interactions	Lack of 'top-down' grazing control, except flagellate grazing on bacteria (present study; Roberts & Laybourn-Parry, 1999)	Lack of 'top-down' grazing control	Low 'top-down' grazing control (Laybourn-Parry, 1997; Butler, 1999b)
	Cryptophytes are mixotrophic (Roberts & Laybourn-Parry, 1999; Marshall & Laybourn-Parry, 2002)	*Pyramimonas gelidicola* is mixotrophic (Bell & Laybourn-Parry, 1999)	More grazing experiments required to determine if PNAN are mixotrophic
	Low grazing pressure exerted by ciliates (present study)	Grazing pressure exerted by ciliates, HNAN and metazoan zooplankton is low	Low grazing pressure exerted by ciliates. Potential grazing impact by metazoan zooplankton during summer. At certain times, juvenile stages of crustacean zooplankton can remove up to 10% of PNAN biomass (Butler, 1999b)

PNAN, phototrophic nanoflagellates; HNAN, heterotrophic nanoflagellates.

Glacier. However, these two lakes differ significantly in terms of their physical and chemical structure (Spigel & Priscu, 1998).

Similarities between Lakes Hoare and Fryxell

In common with all continental Antarctic lakes, Lake Hoare is populated mainly by bacteria, phytoflagellates and protozooplankton. These organisms dominate environments where water column stability is high, as they can maintain their position without sinking and recycle nutrients efficiently. Photosynthesis-irradiance response curves imply that phytoplankton photosynthesis within the McMurdo Dry Valley lakes is always light limited (Lizotte & Priscu, 1992). Despite these harsh conditions, PNAN were successful in both Lakes Hoare and Fryxell, always exceeding HNAN abundance and biomass (Laybourn-Parry, Bell & Roberts, 2000; Roberts *et al.*, 2000). This is in contrast to the lakes of the Vestfold Hills, including Lakes Druzhby, Ace and Crooked, where HNAN abundance and biomass was found to be higher or similar to that of PNAN during all seasons studied (Laybourn-Parry & Bayliss, 1996; Bell & Laybourn-Parry, 1999). In oligotrophic Sombre Lake (Signy Island), as in the Dry Valley lakes, PNAN biomass exceeded HNAN biomass during the summer season (Butler, 1999a).

In order to survive in polar lakes, PNAN must be able to commence growth at low radiation fluxes and retain viability over prolonged winter darkness (Hawes, 1990). The success of PNAN in Lakes Hoare and Fryxell can be partially attributed to them exhibiting high levels of photosynthetic efficiency (Vincent, 1981; Morgan *et al.*, 1998; Neale & Priscu, 1998). Neale & Priscu (1998) demonstrated that light saturation of phytoplankton photosynthesis occurs at low irradiance within these lakes. Hawes (1990) reported similar findings for phytoplankton within Sombre Lake, Signy Island, with protein synthesis saturating at a low photon flux density.

Another way in which phytoplankton can survive prolonged periods of darkness is through not being entirely dependent on photosynthesis. Roberts & Laybourn-Parry (1999) and Marshall & Laybourn-Parry (2002) both found cryptophytes (the dominant photosynthetic flagellates in Lake Hoare and Fryxell) to be capable of mixotrophy. Although cryptophytes in Lake Hoare were only able to graze ≤3% of bacterial biomass per day (Roberts & Laybourn-Parry, 1999), previously measured values of bacterial production have been low, commonly ranging between 1 and 0.1 $\mu g\ C\ L^{-1}\ day^{-1}$ (Takacs & Priscu, 1998). Given similar low levels of bacterial production, cryptophytes in Lake Hoare would have been able to cause a significant grazing impact during early summer, potentially accounting for the drop in bacterial abundance recorded in mid-November (Fig. 5a). Mixotrophic PNAN have been reported elsewhere in Antarctic lakes (Table 1). Genera reported as mixotrophic in Antarctic lakes are not typically considered bacterivorous in lower latitude aquatic environments (Sanders & Porter, 1988), indicating that through using mixotrophy, Antarctic PNAN have become well adapted to the extreme shade environments.

Ciliates are relatively successful in both Lakes Hoare and Fryxell, with high biomass compared with HNAN (Fig. 7; Table 1). Lake Hoare possesses a relatively diverse ciliate assemblage compared to other large oligotrophic Antarctic freshwater lakes studied so far. No more than six ciliate species were found in the fresh water lakes of the Vestfold Hills (Laybourn-Parry & Marchant, 1992) compared with the 24 species found in Lake Hoare. Lake Fryxell (McMurdo Dry Valleys), oligotrophic Lake Sombre (Signy Island) and eutrophic Lake Heywood (Signy Island) are three of the few Antarctic lakes to have a comparable diversity to Lake Hoare, with 25, 17 and 23 ciliate morphotypes recorded, respectively (Butler, 1999a,b; Roberts & Laybourn-Parry, 1999).

The possible reasons behind these differences in diversity raise a number of important issues concerning polar biogeography. Possible explanations behind these differences include the age of the lakes, the nutrient status of the lake, the number of suitable niches and the stability of the niches. Laybourn-Parry (1997) consider that, being much older than the Vestfold Hills lakes, the Dry Valley lakes have had a much longer period for colonisation. Lake Hoare, however, either evaporated to complete dryness or did not exist prior to 1200 year BP (Lyons *et al.*, 1998). If the former is the case, ciliates could have formed resistant cysts during cold dry periods, excysting when conditions became more favourable. If the latter is true, ciliates may have colonised Lake Hoare from neighbouring Lake Fryxell. Variation in species diversity between different Antarctic regions may also be related to number and stability of niches. The Dry

Valley lakes have a greater abundance and diversity of prey available to ciliates (Spaulding *et al*., 1994) than lakes of the Vestfold Hills (Laybourn-Parry & Bayliss, 1996; Laybourn-Parry, 1997; Bell & Laybourn-Parry, 1999). Because the Dry Valley lakes are permanently ice covered, plankton are not submitted to wind driven currents and higher ultraviolet radiation experienced by other Antarctic lakes during ice-free periods. The more variable conditions present in the lakes of the Vestfold Hills may be too extreme for certain species of ciliate and ciliate prey to tolerate. Either way, it is evident that further research is required in order to answer important questions regarding Antarctic microbial diversity, biogeography and colonisation. Although we are beginning to understand better the mechanisms behind these processes for freshwater copepod species (Bayly *et al*., 2003), little is still known about the time scale of colonisation for freshwater protozoa.

Ciliates within Lake Hoare appear unable to control nanoflagellates or bacteria by grazing. Measured ingestion rates of *Askenasia* and *Vorticella* were 0.43 flagellate cell^{-1} h^{-1} and 76.2 bacteria cell^{-1} h^{-1}, respectively; these ingestion rates equated to a grazing loss of only 0.25% day^{-1} of flagellate biomass by *Askenasia* and 0.22% day^{-1} of bacterial biomass by *Vorticella*. Even when accounting for a higher abundance of ciliates, a higher ingestion rate with greater prey concentration and low prey production, results indicate that the grazing impact of ciliates would be slight. This absence of top-down control is a general characteristic of lakes throughout Antarctica (Table 1). Ciliated protozoans are particularly poorly represented in some of the Vestfold Hills freshwater lakes, including Crooked Lake (approximately 100 L^{-1}; Laybourn-Parry, Marchant & Brown, 1991). HNAN in Crooked Lake were capable of removing only between 0.1 and 9.7% of bacterial production per day (Laybourn-Parry, Bayliss & Ellis-Evans, 1995). Butler (1999a) (using ingestion rates calculated by Laybourn-Parry, Ellis-Evans & Butler, 1996) reported higher grazing pressures from Sombre Lake, Signy Island, with the protozooplankton removing between about 1 and 45% of daily bacterial production.

Differences between Lakes Hoare and Fryxell

Because Antarctic ecosystems are dominated by bottom-up forces (Priscu *et al*., 1999), differences in hydrology between lakes are reflected in plankton distributions (Vincent, 1987; Laybourn-Parry & Marchant, 1992; Priscu, 1995; Roberts *et al*., 2000, 2004). In meromictic Lakes Fryxell and Bonney, distinct deep chlorophyll maxima form along the chemoclines (Priscu, 1995; Roberts *et al*., 2000, 2004). Photosynthetic nanoflagellates within the chemocline of these lakes use nutrients, transported upwards from the monimolimnion by molecular diffusion (Edwards & Priscu, 1995; Priscu, 1995). The lower depth distribution of the DCM is restricted by irradiance, anoxia, high sulphide and heavy metal concentrations (Ward & Priscu, 1997), whereas the upper depth distribution is effected by nutrient limitation (Priscu, 1995; Dore & Priscu, 2001). In contrast, Lake Hoare lacks the large, low oxygen, deep nutrient pools present within Lakes Fryxell and Bonney. Light alone appears to control the lower depth limit of photosynthetic microplankton within Lake Hoare and, as a result, the depth of the DCM was found to be more variable (Fig. 4) than in meromictic Lake Fryxell and Bonney (Lizotte & Priscu, 1992; Roberts *et al*., 2000).

Autochthonous and allochthonous controls on microplankton dynamics in lake hoare

Studies by Priscu (1995) and Dore & Priscu (2001) indicate that growth of phytoplankton in the upper water column of Lake Hoare is nutrient stressed; additions of P alone, or N plus P, stimulated phytoplankton photosynthesis. Seasonal changes in NH_4^+ concentration and strong vertical NH_4^+ gradients (Fig. 3) indicate that nutrient regeneration by protozoa provides an autochthonous supply of N to the phytoplankton.

In terms of allochthonous supply, there are two ways in which nutrients enter the surface waters of Lake Hoare; through glacial melt water and through organic matter migrating down through the ice cover (Fritsen *et al*., 1998; Lyons *et al*., 1998; Priscu *et al*., 1998). The main sampling site (H2) at Lake Hoare could feasibly be affected by glacial meltwater, because of its close proximity to the Canada Glacier and Anderson Creek (Fig. 1). Both the glacier and the stream have a higher nitrate concentration than the surface waters of Lake Hoare (NO_3^- measured in samples collected from Anderson Creek during the first summer season ranged

between 3.3 and 22.1 μM and Lyons *et al.* (1998) report NO_3^- concentration from the Canada Glacier to be 2.3 μM). Evidence exists from Lake Bonney, indicating that nutrients from stream flow increased photoautotrophic growth (Lizotte, Sharp & Priscu, 1996). However, from the limited data available, no significant correlations were found between surface inorganic nutrient concentrations in Lake Hoare and stream flow from Anderson Creek (SRP, $r = -0.346$, $P = 0.568$, $n = 5$; NO_3^-, $r = -0.276$, $P = 0.653$, $n = 5$; NH_4^+, $r = -0.411$, $P = 0.492$, $n = 5$). The greatest PNAN and ciliate biomass (in November 1996 and December 1997) occurred when stream flow was either low or nonexistent (Fig. 9). This was the case during both field seasons, despite stream flow showing different temporal patterns between years. Surface plankton populations may have been diluted by melt water, although there was no significant correlation between surface PNAN or ciliate biomass with discharge from Anderson Creek (Pearsons correlation coefficients: $r = -0.185$, $P = 0.463$, $n = 18$ and $r = -0.199$, $P = 0.427$, $n = 18$ for PNAN and ciliate biomass, respectively). More research is required in order to determine the relationship between stream flow and plankton in the McMurdo Dry Valley lakes.

In addition to melt-water inflow, the other way in which allochthonous nutrients enter Lake Hoare is through the ice (Fritsen *et al.*, 1998; Priscu *et al.*, 1998, 1999). Exposed soils are eroded and then deposited by the wind onto ice covering the lakes (Fritsen *et al.*, 1998). These sediments, organic matter and associated nutrients are released into the water column via conduits within the ice (Fritsen *et al.*, 1998; Priscu *et al.*, 1998, 1999). Such an influx of organic matter into Lake Hoare appears to have occurred during mid-December 1997 (Fig. 4a), with living microplankton biomass at 4.5 m accounting for only 17% of total POC. The influx of POC was associated with a peak in PNAN abundance on 10 December 1997 (Fig. 5b), whose community growth may have been stimulated by allochthonous nutrient input. Increased surface NO_3^- and NH_4^+ concentrations were still evident by the 26 December 1997.

Unusually high ciliate abundance was also recorded at 4.5 m on 10 December 1997 (Fig. 5d). *Urotricha*, a ciliate not typical of the water column of Lake Hoare, accounted for over 80% of ciliate numbers at 4.5 m on this particular date. The rapid accumulation and disappearance of this *Urotricha* population was unlikely to have been because of *in situ* growth alone (Laybourn-Parry *et al.*, 2000). More likely, the upper waters were inoculated with large numbers of *Urotricha* from the ice cover. Although there has been no research to date into ciliates living within the ice cover of the McMurdo Dry Valley lakes, micro-autoradiography and physiological studies have indicated that morphologically and metabolically diverse microbial communities exist within the ice covering these lakes (Paerl & Priscu, 1998; Gordon, Priscu & Giovannoni, 2000).

Microbial data from the horizontal transect (Fig. 8) further indicate the potential influence of allochthonous inputs from the ice cover on the planktonic community below. Although horizontal variability in Lake Hoare may be considered minor relative to non-polar aquatic environments, highest surface abundances of PNAN and ciliates were recorded at the main sampling hole (sample hole 2, Fig. 8). It is therefore likely that the permanence of this hole altered the environment below sufficiently to cause enhanced biomass over a relatively small spatial scale (an observation also made in Lake Bonney, Priscu & Neale, 1995). The main sampling hole was

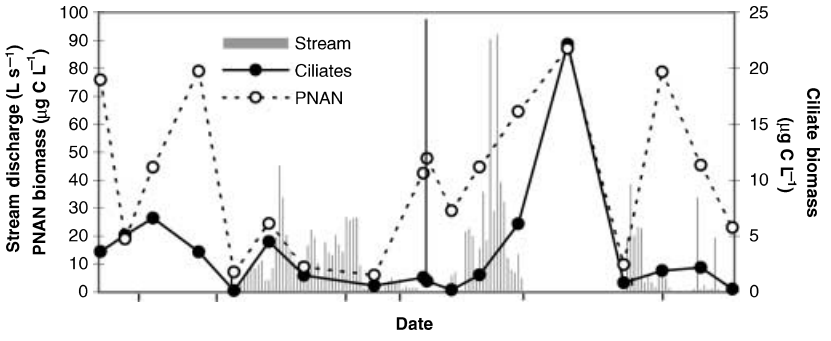

Fig. 9 The effect of stream discharge from Anderson Creek (L s^{-1}) on phototrophic nanoflagellate (PNAN) and ciliate biomass (μg C L^{-1}) immediately beneath the ice cover (4.5 m) in Lake Hoare. Stream data courtesy of Diane McKnight.

permanently covered, preventing wind blown organic matter entering the lake. However, the sample hole would have provided a means whereby sediment, associated nutrients and microbial communities contained within the ice could be rapidly transported down into the water column. The fact that *Urotricha* was more dominant at the main sample site, H2, relative to the less permanent holes, H1, H3 and H4, further indicates that this ciliate species may have been transported down into the lake through the ice. Although environmental and logistical constraints make taking horizontal transects through the ice covers of Antarctic lakes extremely difficult, they are essential in assessing horizontal variability and anomalous results brought about by the presence of a permanent sampling hole.

McMurdo Dry Valley lakes as climate change indicators

Because of Antarctic lake ecology being dominated by bottom up forces, communities within the lakes are likely to respond rapidly to changes in physicochemical parameters effected by climate change. Doran *et al.* (2002) indicate that climate cooling within the McMurdo Dry Valleys has induced increases in lake ice thickness, reducing underwater irradiance. They suggest this decrease in irradiance has suppressed mean annual primary production in the west lobe of Lake Bonney by 9%.

It is expected that because of differences in geological evolution between McMurdo Dry Valley lakes (Lyons *et al*., 1997), each lake may respond differently to climate change. In Lakes Bonney and Fryxell, phytoplankton appear more dependent on internally cycled nutrients relative to allochthonous inputs (Dore & Priscu, 2001). This is because nutrient profiles within Lakes Bonney and Fryxell reflect past events, both containing deep, anoxic, nutrient rich pools that have remained unchanged for thousands of years (Lyons *et al*., 1998; Spigel & Priscu, 1998). In Lake Hoare, although nutrient regeneration by protozooplankton provides phytoplankton with a recycled source of nutrients, this lake lacks the nutrient rich bottom waters found in Lakes Fryxell and Bonney. As a consequence, phytoplankton in Lake Hoare are more reliant on present day exogenous nutrients from stream flow and from the ice cover. For this reason it may be argued that planktonic communities within Lake Hoare may be potentially more sensitive to climate related nutrient variation than either Lakes Bonney or Fryxell.

Despite extreme light limitation (Lizotte & Priscu, 1992), planktonic biomass in Lake Hoare is dominated by photo-autotrophs (Fig. 7). The success of these phytoplankton in such a dark environment is because of a combination of factors, including being able to photosynthesise efficiently at low irradiance (Lizotte & Priscu, 1992; Neale & Priscu, 1998), being mixotrophic (Roberts & Laybourn-Parry, 1999; Marshall & Laybourn-Parry, 2002) and being subject to very low grazing pressure (present paper). The population dynamics of PNAN in Lake Hoare is determined by light (affected by ice cover thickness/condition) and nutrients (obtained from the ice cover, stream flow and from regeneration). All of the aforementioned physicochemical factors are affected by meteorological events, making the Lake Hoare planktonic community a potentially sensitive indicator of climate change. This paper provides the first detailed study of seasonal variation in plankton population dynamics in Lake Hoare. Such data are essential if long-term inter-annual changes are to be assessed. It is apparent that, if the response of plankton populations to climate change within the McMurdo Dry Valley lakes is to be fully understood, more research is required to determine the exact coupling between physicochemical controls and plankton dynamics. It is also essential that researchers avoid disrupting the water column below.

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