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Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in maritime Antarctica

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Abstract A limnological survey of 15 lakes and 6 streams was carried out on Byers Peninsula (Livingston Island, South Shetland Islands, Antarctica) during austral summer 2001–2002. Most of the surface waters had low conductivities (20–105 $\mu S\ cm^{-1}$) and nutrients (total phosphorus 0.01–0.24 μM), but some coastal lakes were enriched by nutrient inputs from seal colonies and marine inputs. Plankton communities in the lakes contained picocyanobacteria (10^2–10^4 cells ml^{-1}), diatoms, chrysophytes and chlorophytes, and a large fraction of the total biomass was bacterioplankton. Zooplankton communities were dominated by *Boeckella poppei* and *Branchinecta gainii*; the benthic cladoceran *Macrothrix ciliata* was also recorded, for the first time in Antarctica. The chironomids *Belgica antarctica* and *Parochlus steinenii*, and the oligochaete *Lumbricillus* sp., occurred in stream and lake benthos. The phytobenthos included cyanobacterial mats, epilithic diatoms and the aquatic moss *Drepanocladus longifolius*. These observations underscore the limnological richness of this seasonally ice-free region in maritime Antarctica and its value as a long-term reference site for monitoring environmental change.

Keywords Antarctica · Limnology · Plankton · Benthos · Biodiversity · Lakes

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Introduction

Most of the Antarctic continent is permanently ice-covered because of its extreme meteorological conditions, with continuous sub-zero temperatures throughout the year. However, the maritime Antarctic region, comprising the western side of the Antarctic Peninsula and nearby islands, is characterized by a less extreme climatic regime, with higher mean temperatures and precipitation than elsewhere in Antarctica. These climatic conditions result in the presence of a large number of freshwater ecosystems that melt out and become ice-free in summer. Byers Peninsula, located on Livingston Island (South Shetland Islands), is one such area containing abundant lakes and streams.

Byers Peninsula has been designed as an Antarctic Specially Protected Area (ASPA No. 126: Byers Peninsula, Livingston Island, South Shetland Islands) under the Antarctic Protected Areas System because of its geological, archaeological, natural and biological values. Among the latter are many inland lakes with an aquatic biota that includes aquatic mosses, cyanobacterial mats and the populations of chironomids *Parochlus steinenii* and *Belgica antarctica*. However, from a limnological point of view, only two studies, one on lake benthic diatom communities (Jones et al. 1993) and a second on stream algal mats (Davey 1993), together with a general description of freshwater ecosystems (Ellis-Evans 1996), have been performed in Byers Peninsula, one of the most important limnological areas in maritime Antarctica.

The relationships between biological communities and limnological features have been examined in several other parts of Antarctica containing lakes and streams. These include extensive studies in the McMurdo Dry Valleys area (Vincent 1988; Howard-Williams et al. 1990; Hawes et al. 1993; Priscu 1998), Signy Island (Heywood 1967; Caulket and Ellis-Evans 1997) and the Vestfold Hills (Roberts and McMinn 1996; Bell and Laybourn-Parry 1999; Gibson 1999).

Some limnological studies have also been carried out in South Shetland Islands and Antarctic Peninsula lakes focused on various biological communities: diatoms and the periphytic flora (Hansson and Håkansson 1992; Jones et al. 1993), microbial communities (Tell et al. 1995; Vinocur and Pizarro 2000), crustaceans (Paggi 1996) and phytoplankton (Vinocur and Izaguirre 1994; Izaguirre et al. 1998; Vinocur and Unrein 2000). Additional work has been undertaken on the algal communities of maritime Antarctic streams on Signy Island (Hawes 1989), James Ross Island (Hawes and Brazier 1991), King George Island (Pizarro and Vinocur 2000) and the Antarctic Peninsula (Vinocur and Pizarro 1995; Pizarro et al. 1996; Izaguirre and Pizarro 1998, 2000).

The aim of the present study was to provide a detailed regional description of the freshwater ecosystems of Byers Peninsula. We surveyed the biological communities of 15 lakes and 6 streams to assess their biodiversity, and to describe the physical and chemical properties of these aquatic ecosystems. The onset of accelerated climate change in the maritime Antarctic region (the most rapid in the Southern Hemisphere, Meredith and King 2005) highlights the need for an improved understanding of current baseline ecological conditions. As a protected ASPA, Byers Peninsula will be a critical site for future monitoring.

This research forms part of the LIMNOPOLAR Project, an interdisciplinary project to investigate the environmental controls on aquatic ecosystems at polar latitudes.

Materials and methods

Study area

Byers Peninsula lies at the western end of Livingston Island (latitudes 62°34′35″ to 62°40′35″S and longitudes 60°54′14″ to 61°13′07″W), the second largest island in the South Shetland Islands, in maritime Antarctica (Fig. 1). The peninsula has a surface area of 60.6 km^2 and a maximum altitude of 265 m (Cerro Start). The central area comprises a plateau of gentle undulating relief around 105 m a.s.l. The geology is mainly dominated by Upper Jurassic to Lower Cretaceous marine sedimentary, volcanic and volcaniclastic rocks. These rocks have been shattered by periglacial processes, and long term weathering and erosion have generated debris, gravel and sand throughout the area (López-Martínez et al. 1996a). The active lithosol soil layer of shattered rocks extends to about 30 cm depth and overlays permafrost. Water can flow underground over this permanently frozen underlayer (Serrano et al. 1996). The importance of such groundwater flows in permafrost soils for catchment hydrology and streamflow generation is well known from other polar latitudes (Woo and Carey 1998).

The climate at Livingston Island is maritime and less extreme than in continental Antarctica, with mean summer temperatures in the range 1–3°C, daily maxima up to 10°C and daily minima to −10°C. In winter, minimum temperatures can reach −35°C and maxima are always below 0°C. Precipitation is much higher than in most of continental Antarctica, with annual

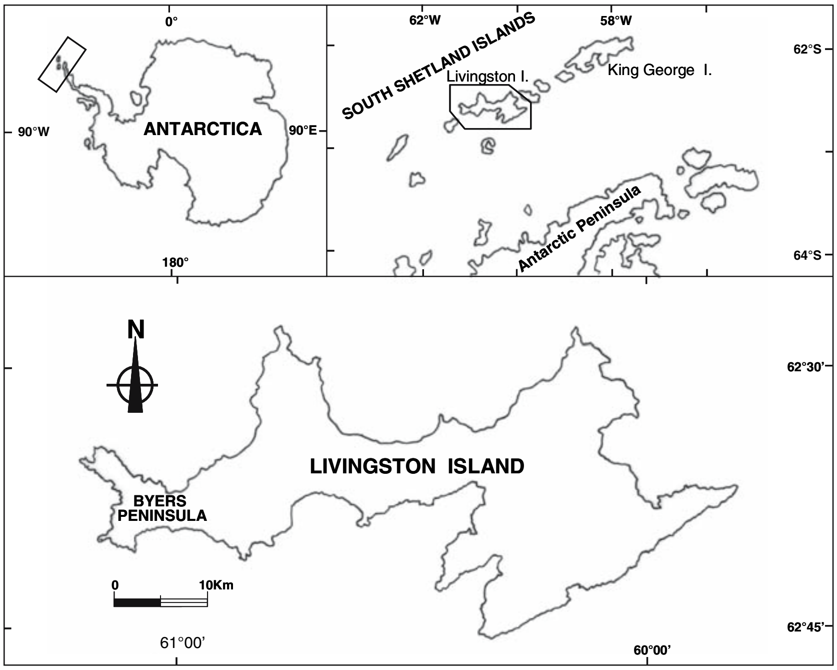


Fig. 1 Location of Byers Peninsula (Livingston Island), in the Antarctic Peninsula area

mean values of 700–1,000 mm (Bañón 2001). Livingston Island is mostly covered by glaciers, except for some coastal areas and the Byers Peninsula, the largest ice-free area in the South Shetlands Islands. The region is snow covered during at least 7–8 months per year, and snow packs can persist throughout summer in some accumulation areas. The deglaciation chronology of Byers Peninsula has been inferred from lake sediments (Björck et al. 1996) and shows rapid deglaciation from around 4,500 BP, with most areas of Byers Peninsula ice-free by 4,000 BP. Some lakes situated in shady areas were deglaciated as recently as 400–500 BP, particularly those located close to the edge of Rotch Dome (Björck et al. 1996).

There are three hydrographic systems on Byers Peninsula, with streams that discharge at South Beaches, Robbery Beaches (North) and President Beaches (West) respectively. The streams are shallow (5–20 cm mean depth) in the central plateau, becoming deeper in lower reaches close to the beaches (up to 50 cm). Flow regime in the streams follows a pluvio-nival pattern, with maximum flows during summer months. The relatively flat relief of the plateau and the presence of over-deepened basins produced by glacial erosion have favoured water retention in more than 110 lakes and ponds of variable sizes, covering a total surface area of about 1.5% of Byers Peninsula, with a complex drainage system and diffuse catchments boundaries (López-Martínez et al. 1996a, b). Midge Lake is the deepest and the largest lake, with a maximum depth of 9 m and a surface area of 5 ha. Most of the studied lakes are located in the central plateau of Byers Peninsula, although some (Maderos, Refugio, Diablo and Limícolas) are situated in the vicinity of the sea (South and Western beaches). Those located on the plateau had a well-defined surface outlet, with the exception of Lake Cerro Negro, whose outflow infiltrates under a boulder area to flow out in a cascade at the edge of Cerro Negro Mountain; Lake Escondido, which is found in a land depression between three basaltic hills; and Lake Maderos which receives water from Lake Limícolas.

The terrestrial vegetation in Byers Peninsula is sparse although it is one of the most diverse floristic areas in the maritime Antarctica region. It is mainly composed of lichens (more than 50 species) and mosses (over 29 species) (Sancho et al. 1999), which form extensive carpets in some coastal areas, and by the vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunt) Bartl. on the beaches and lowlands. On coastal areas of Byers Peninsula there are breeding colonies of penguins and other sea birds, as well as of southern elephant seals (*Mirounga leonina*). Such breeding areas are known to be an important source of nutrients for lakes and streams elsewhere in the maritime Antarctica (Smith 1988; Ellis-Evans 1990). However, most lakes on Livingston Island are located inland, and so nutrient inputs from these sources are likely to be less important relative to other areas such as Signy Island in South Orkney Islands with its higher percentage of coastal lakes (Jones et al. 1993).

Physical and chemical analyses

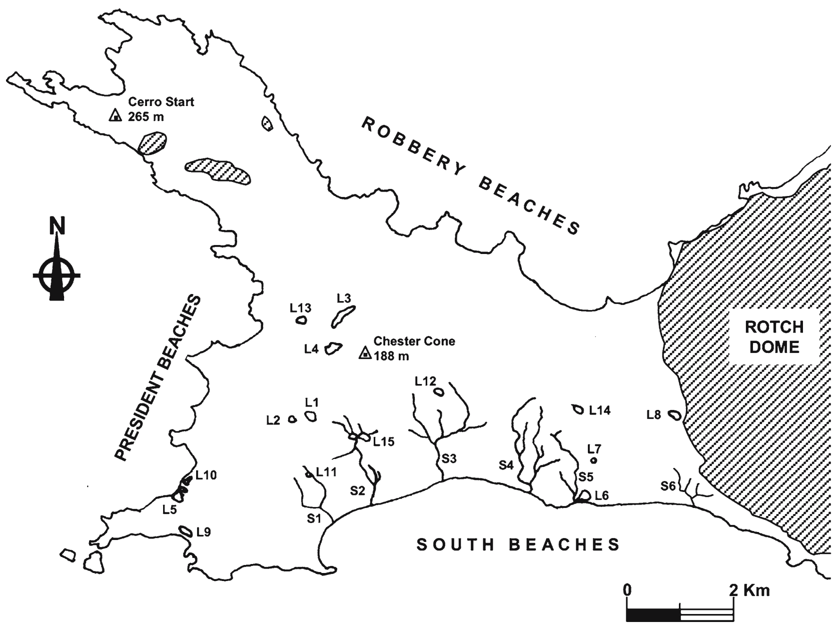
Limnological field work was carried out in Byers Peninsula from December 2001 to February 2002. To cover the full range of freshwater ecosystems in the area, 6 streams (flowing into South Beaches), and 15 lakes along a North–South and West–East gradient, were sampled (Fig. 2). With the exception of Midge Lake, the names of the lakes and streams are not official, and follow, when possible, the nomenclature used by previous researchers in the area.

Meteorological data were obtained from the Spanish Antarctic Base Juan Carlos I (Bañón 2001) on Livingston Island, 35 km to the East of Byers Peninsula. To define the local climate, an automatic meteorological station (AMS) equipped with a Campbell CR10X logging unit, two gel batteries (90 A h) and one 10 W (0.57 A) solar panel for recharging the batteries, was installed on 10 December 2001 on the south-western central plateau of Byers Peninsula. The AMS was located between two lakes (Limnopolar and Somero lakes) at about 65 m a.s.l. and 2 km from the coast. It provided continuous data, except during the period from 11–28 January 2002. This station registered air temperature, global and PAR radiation, wind speed and direction, relative humidity and soil temperature, and also conductivity in the shallow waters of Lake Somero. Rainfall was recorded daily during the fieldwork periods in summer.

Stream flows were estimated on specific dates of sampling with an acoustic Doppler current velocity meter (Sigma model PVM 3872). Velocity was measured at different depths across a transverse section of the channel.

Surface (streams and lakes) and deeper (2–3 depths down to the bottom) samples were collected and stored in acid washed bottles for water chemistry. A Kemmerer water sampler bottle was used to collect the samples down the water column of the lakes.

Vertical profiles of dissolved oxygen, temperature, conductivity and pH were obtained in each lake at its estimated deepest point using an YSI 556 MPS Water Logger System. In streams, these variables were registered over the centre of the riverbed.



LAKES				STREAMS			
Code	Name	X-UTM	Y-UTM	Code	Name	X-UTM (outlet)	Y-UTM (outlet)
L1	Limnopolar	597.100,0	3.052.200,0	S1	Petreles	597.515,0	3.050.100,0
L2	Somero	596.800,0	3.052.150,0	S2	Ballenas	598.175,0	3.050.400,0
L3	Midge Lake	597.700,0	3.054.150,0	S3	Tres Cerros	599.540,0	3.050.900,0
L4	Chester Cone	597.500,0	3.053.550,0	S4	Bélgica	601.135,0	3.050.650,0
L5	Maderos	594.650,0	3.050.650,0	S5	Negro	601.975,0	3.050.430,0
L6	Refugio	602.200,0	3.050.550,0	S6	Rotch	604.260,0	3.050.350,0
L7	Cerro Negro	602.425,0	3.051.275,0				
L8	Domo	603.850,0	3.052.175,0				
L9	Diablo	594.800,0	3.049.950,0				
L10	Limícolas	594.825,0	3.050.900,0				
L11	Chica	597.100,0	3.051.050,0				
L12	Escondido	599.475,0	3.052.650,0				
L13	Asa	596.975,0	3.054.100,0				
L14	Las Palmas	602.050,0	3.052.300,0				
L15	Turbio	598.000,0	3.051.800,0				

Fig. 2 Location of streams and lakes sampled during 2001–2002 summer period in Byers Peninsula (Livingston Island). Names are not official, except Midge Lake, and are named according to past usage and current conventions (U.T.M. Coordinates WGS-84 IMW Sheet SP20)

Water samples for chemical analyses of dissolved compounds were filtered through pre-combusted Whatman GF/F filters within 2 h of collection. The samples were frozen immediately and stored at −20°C until analysis. Inorganic nitrogen and phosphorus were measured according to Golterman et al. (1978) and Huiskes and Quesada (2005), using spectrophotometric measurements with a 5-cm pathlength cuvette. All glassware and plastic bottles used in the inorganic nutrient determinations were acid-washed and then rinsed with the filtered sample. Nitrate plus nitrite was measured after reduction of nitrate to nitrite with cadmium, and then nitrite was measured after reaction with sulphanilamide and *N*-(1-naphthyl) ethylenediamine dihydrochloride in a strong acid medium. Ammonium concentrations were determined by the phenol–hypochlorite method. Soluble orthophosphate was measured with the phosphomolybdic acid–ascorbic method, and total phosphorus following the same procedure after persulphatic-acid digestion and subsequent neutralization prior to analysis. Soluble reactive silica concentrations were determined by the silicomolybdic acid method. The concentrations of major ions (calcium, magnesium, sodium, potassium, sulphate and chloride) were determined by a Waters Capillary Ion Analyzer. Alkalinity was measured after titration with HCl using a pH shift indicator (phenolphtalein) of the equivalence end point pH.

Pigment analyses were performed by HPLC as described by Vincent et al. (1993). Samples were filtered through glass fibre filters (Whatman GF/F) in the field and kept frozen until extraction with 90% acetone in the lab. The solvent was evaporated and then pigments were redissolved in a smaller volume of acetone in order to concentrate the samples prior to injection into a C18 Spherisorb HPLC column. Chlorophyll-a (Chl-a) concentration was used as an indicator of the trophic status and presence of nutrients in the lakes.

Plankton

To sample zooplankton, vertical hauls from the lake bottom and horizontal trawls were taken at the estimated deepest area of the lakes using a 50 μm mesh net. Samples were preserved by adding formalin solution to a final concentration of 4% (v/v). Samples for phytoplankton were taken from surface, bottom and middle of each water column and preserved in glass bottles with acidified Lugol's iodine for microscopic examination.

Bacterial counts were done by epifluorescence on a Zeiss-III phase contrast microscope on DAPI-stained samples concentrated on black polycarbonate filters (0.2 μm). Samples were preserved at 4°C with buffered formalin until counting at the laboratory. Autotrophic picoplankton were counted on Isopore GTBP filters (Millipore), and autotrophs were identified by the autofluorescence of chlorophyll-a and phycobiliproteins (MacIsaac and Stockner 1993). Algal species were determined with an inverted microscope at 400× and 1,000× using the Utermöhl (1958) sedimentation method.

Benthos

Epilithic diatoms samples were taken from lakes and streams by collecting stones from permanently water-covered zones along representative shorelines. The surface diatom communities were detached from the stones by using a toothbrush and washing with a distilled water bottle through a funnel into a polythene bottle. Samples from shoreline epipsammon or epipelon diatoms were taken with a plastic pipette or syringe to remove the surface layer (to 1 mm depth) of a 25 cm^2 area. Aquatic mosses that had been detached and washed into the shallow littoral zone were collected by hand and washed with distilled water to remove epiphytic diatoms. Samples were preserved with formaldehyde.

Samples of benthic invertebrates were collected with a hand net (200 μm mesh size) by kick or sweep sampling the bottom substrata of lakes and streams and with a Surber sampler (same mesh size).

Samples from microbial mat communities were taken with metal corers (11–17 mm internal diameter) from homogeneous areas of the mats. Live mat material was teased out and examined at the site by light and epifluorescence microscopy. The classification system of Anagnostidis and Komarek (1988) and Komarek and Anagnostidis (1989) was used throughout. Some cores were preserved in formaldehyde 4% and then stored refrigerated until subsequent analysis.

Results and discussion

Meteorology

During the period December 2001 to February 2003 (date of data-logger recordings), air temperatures ranged from a minimum of −21.7°C (October 2002) to a maximum of +5.6°C (January 2003), with mean daily values over 0°C (mean minimum temperatures over 0°C were recorded only in January–February). These values are similar to other meteorological stations located along the coast of the Antarctic Peninsula for the period 1977–2005 (BAS 2005). Monthly total rainfall ranged from 15 to 72 mm from December to February (2001–2002 and 2002–2003), with a mean value of 53 mm month^{-1}, and over 200 mm for the whole summer period. This range of values is also similar to those reported for coastal western Antarctic Peninsula (28–47 mm for the period 1956–1993 in Rothera and Faraday stations; Turner et al. 1997), although total summer rainfall was higher than at Rothera and Faraday (85 and 107 mm), suggesting a greater maritime influence in Byers Peninsula. The maximum rainfall recorded over a 24 h period was 15.2 mm in February 2002.

Maximum global radiation was recorded in November (less cloudy than December), with a mean value of 16,500 kJ m^{-2} per day, and maximum daily values of 29,000 kJ m^{-2}.

Wind direction showed a general predominance along the SW–NE axis. The NE and ENE components had the strongest gusts. Mean wind speed ranged from 20 to 30 km h^{-1}, with maximum daily mean values exceeding 50 km h^{-1} in several months (68 km h^{-1} in October 2002). Maximum speeds over 100 km h^{-1} are frequent during the whole year (139 km h^{-1} in December 2002 was the highest recorded value).

Hydrology

Lake outlets and stream flows are conditioned by several factors during summer period, such as snowmelt, rainfall events, surface water evaporation and permafrost melting. The permafrost active layer is about 40 cm deep in summer time, and it is an important feature controlling local hydrology (Lopez-Martinez et al. 1996a). We have observed that for systems where the lake outlet was located in a narrow gorge, the lake level could increase substantially (2–3 m) during thaw behind ice/snow dams that had formed during winter. These ice dams usually ruptured as catastrophic events during summer melting. This resulted in a sudden decrease in lake level by several meters in a few hours, and substantial floods downstream. Such an event was recorded at Lake Turbio the night of December 18th, 2001. Some lakes became completely dry after the sudden break-up of the ice and snow dam, as observed in a lake basin located 0.5 km north of Lake Limnopolar. A similar process has been reported by Drago (1983) in King George Island.

Petreles Stream, representative of the many streams on Byers Peninsula, showed flow values ranging from 0.036 to 0.276 m^3 s^{-1} near its outlet in South Beaches, and water velocities 0.4–1.0 m s^{-1} from December 2001 to February 2002. Maximum flows and water velocities were reached during snow melt (December–January), with wide daily fluctuations during sunny days with higher temperatures. Flow values for other streams in Byers Peninsula were similar in magnitude. The mean width of studied streams was about 5 m with a mean depth of 5–15 cm. In episodes of high flows some stream depths could reach over 30–50 cm, and more than 10 m width near the outlet in South Beaches (Ballenas and Belgica streams), with water velocities higher than 2.0 m s^{-1} and water flows over 0.9 m^3 s^{-1} (Tres Cerros and Belgica streams).

Physical and chemical properties

Ice break-up in the lakes was observed to start in December near the lake outlets or inlets, however ice blocks or thin ice layers could persist until the first weeks of February. Similar ice break-up dates have been reported for other areas in the maritime Antarctic zone (Signy Island) (Priddle 1980) or Antarctic Peninsula (Cierva Point) (Mataloni et al. 1998). Shallow lakes or ponds, with maximum depths less than 0.5 m, were almost frozen solid during winter and early summer. For example, Lake Somero (max. depth 0.5 m) was mostly frozen at the beginning of December 2001, when most of the lakes located at the central plateau area were totally ice-covered, with variable ice thicknesses (Limnopolar, 45 cm; Somero, 30 cm; Midge Lake, 65 cm; Chester Cone, 60 cm).

Our conductivity sensor placed at the bottom of Lake Somero demonstrated that throughout winter the bottom layer was frozen solid only for a brief period of time (15 days in July) and during the rest of the winter this bottom layer was below 0°C but still liquid, probably due to salt exclusion during the ice formation process. Similar results have been described for ponds in Bratina Island Ice Shelf (McMurdo Sound) by Hawes et al. (1999) and are also known from the Arctic (Mueller and Vincent 2006).

At the end of December 2001, lake ice covers were reduced to about 10–20% of the surface, with complete melt-out observed in many of the lakes by the beginning of January 2002. The lakes located close to the sea had a 1–2 week shorter ice-cover period than the plateau lakes, likely due to their lower altitude, shallow depths and higher salt content causing a delay in freezing and earlier melt-out.

All the lakes that we profiled on Livingston Island were cold monomictic. This is likely the result of their relative shallowness, cold climate and exposure to frequent strong winds. Inverse thermal water stratification occurred during their long period (>8 months) of ice-cover. During this winter period, the maximum temperature of the bottom water layers varied between 3.0 and 3.9°C. After the ice break-up, water temperatures increased through summer, and in the deepest lakes sometimes varied down the water column by 2°C during calm periods. Over summer, the temperature ranged from 0.5–2°C in December to a maximum of 5–6°C in February, although higher values were occasionally recorded in the shallower lakes (up to 9.5°C in Somero or 9.8°C in Refugio). The lakes of this region lie on the border between cold and temperate thereimictic lakes, according to Bayly and Williams (1973) classification. This thermal regime is similar to that reported for other lakes from the maritime Antarctic region including Deception Island (Drago 1989), South Orkney Islands (Heywood 1968) and King George Island (Drago 1980).

During the present study, no oxygen depletion was recorded at the end of the winter period in the bottom waters of the lakes. However, Ellis-Evans (1996), noted evidence of anoxia in the bottom of Midge Lake at the end of winter 1990–1991 before the ice break-up. The bottom of this lake is covered by mosses (see below), and interannual differences in the balance between production and respiration by these communities might account for the differences in oxygen depletion. Lakes from Byers Peninsula usually had dissolved oxygen concentrations close to saturation or slightly below saturation, with typical values near 12 mg l^{-1}. Lake Refugio was a notable exception with lower oxygen saturation values (around 75%) likely due to the continuous input and decomposition of organic matter from marine animals (seals and penguins).

Stream temperatures ranged from 2.1 to 11.6°C from mid January to mid February. An extreme value of 13.3°C was recorded in the most frequently monitored Petreles Stream at a downstream site on 9 January; at this time the stream flow was low (0.035–0.06 $m^3 s^{-1}$), maximum day air temperature was 8–9°C, winds were calm, and irradiance was high (daily total radiation of 20,930 kJ m^{-2}). Dissolved oxygen values in streams were typically 90–100% of saturation.

The main physical and chemical features of the studied lakes and streams are shown in Table 1. Stream pH was circumneutral or slightly alkaline during the summer period, except in Rotch Stream, located in the eastern part of South Beaches, where pH was as high as 9.18. This anomalously high value was subsequently confirmed in the 2003 and 2004 seasons. The lakewater pH values ranged from slightly acidic to slightly alkaline, as elsewhere in the maritime zone (Vinocur and Unrein 2000). Highest values were recorded in Lakes Refugio and Limícolas (7.7 and 7.8, respectively) associated with their higher primary productivity and relatively low buffering capacity due to relatively low dissolved inorganic carbon content. Jones et al. (1993) also found some of the highest pH values (up to 8.02) in coastal lakes in Byers Peninsula.

Conductivities were mostly in the range 30–100 μS cm^{-1}, with three groups of waters that could be differentiated based on solute content. Lakes located far from the sea and at higher altitudes, had lowest salt concentrations (mean conductivity values below 50 μS cm^{-1}). This group included Lake Domo, close to the ice cap; Lake Las Palmas, which has a small catchment area and is located at a relative long distance from the sea; and Lakes Chester Cone, Cerro Negro and Chica, which had the smallest catchment sizes. The second group of lakes had intermediate conductivities between 50 and 100 μS cm^{-1}, most of them located in the central plateau of the Peninsula. The last group comprised lakes close to the sea such as Lakes Maderos, Refugio, Diablo and Limícolas. These had conductivities over 100 μS cm^{-1}, due to the influence of sea spray and animal inputs. By comparison with a previous study carried out by Jones et al. (1993) in some of these lakes in the summer 1990–1991, we found much lower conductivities. This was especially evident in Lake Maderos, with a value of 2,960 μS cm^{-1} in 1991 (Jones et al. 1993) and 189 μS cm^{-1} in 2001. Rainfall recorded by the meteorological station located in Base Juan Carlos I (Livingston Island) show similar values for the summer period of both years, which are among the highest recorded for the period 1987–2003, with rainfall of 222 mm during the 1990–1991 summer and 215 mm for the 2001–2002 summer (Bañón 2001, and unpublished data from the Spanish National Meteorology Institute). Thus, no differences in weathering rates and ions inflows should be expected between these two studies. In the case of Lake Maderos, because of its proximity to the sea shore, a possible occasional inflow of sea water into the lake prior to Jones' et al. sampling, or an occasional connection to the sea at a high tide (Ellis-Evans 1996) could explain the difference.

Conductivity in the lakes and streams increased progressively from the onset of snow melt until the end of the summer (see minimum and maximum in Table 1). This is likely due to the reduced flows, and to the interaction with rock and mineral substrates (Cuchí et al. 2004).

Sodium was the main cation in these waters, and was especially high in lakes close to the sea (Refugio and Maderos with 35 and 107 mg l^{-1}, respectively). The rest

Table 1 Range of values of chemical variables of lakes (L) and streams (S) sampled during 2001–2002 summer period in Byers Peninsula

Code	Name	Catchment size (km^2)	Max depth (m)	Conductivity (μS cm^{-1} 25°C)	pH	Chl-a (μg l^{-1})	$NO_3 + NO_2$ (μM)	NH_3 (μM)	PO_4 (μM)	SiO_2 (μM)	SO_4^{2-} (mg l^{-1})	Cl^- (mg l^{-1})	Na^+ (mg l^{-1})	K^+ (mg l^{-1})	Mg^{2+} (mg l^{-1})	Ca^{2+} (mg l^{-1})	Alk (meq l^{-1})
L1	Limnopolar	0.58	5.5	51–80	6.54–7.76	0.13–0.18	0.11–0.32	1.00–3.44	0.03–0.09	25.2–64.87	8.29–16.01	15.11–16.09	9.37–11.05	0.28–0.38	1.97–2.97	5.04–9.49	0.89–1.02
L2	Somero	0.06	0.5	35–105	6.60–7.82	0.75–2.22	0.08–0.20	0.50–1.42	0.03–0.07	62.67–85.29	3.12–5.61	24.79–25.42	13.47–17.60	0.38–0.61	2.89–4.04	4.66–6.98	0.54–1.32
L3	Midge Lake	0.27	8.2	63–73	6.48–7.28	0.07–0.15	0.15–2.80	<0.25–1.18	<0.01–0.14	38.67–51.71	5.67–8.96	12.98–18.29	13.76–16.94	0.43–0.47	2.41–2.68	4.49–4.86	0.45–0.77
L4	Chester Cone	0.09	5.0	35–68	6.69–7.03	0.06	0.26–1.16	<0.25–1.20	0.02–0.03	21.13–41–74	8.53	13.36	8.87	0.36	1.70	3.51	0.49
L5	Maderos	2.41	0.5	189	7.18	1.44	14.96	0.78	0.24	21.27	31.03	143.0	107.20	–	11.95	16.62	0.60
L6	Refugio	0.12	0.5	128–134	7.60–7.70	17.0–40.5	3.83–48.02	1.02–1.06	2.70–3.11	71.6	7.95–8.30	24.88–26.52	19.09–35.00	1.69–1.73	0.32–0.51	0.31–0.40	0.94–1.47
L7	Cerro Negro	0.01	2.2	51	6.65	–	–	–	–	–	–	–	–	–	–	–	–
L8	Domo	0.18[a]	4.5	28–31	6.26–6.60	0.07	0.35–0.45	0.68–1.56	0.05–0.13	4.31–13.47	1.54–1.59	7.29–9.14	6.57–7.21	0.21	0.82–0.94	0.68–0.99	<0.01–0.97
L9	Diablo	0.29	–	90	6.99	–	–	–	–	–	–	–	–	–	–	–	–
L10	Limícolas	2.24	0.2	125	7.79	–	–	–	–	–	–	–	–	–	–	–	–
L11	Chica	0.01	–	20–60	6.84–7.10	0.85	0.12	1.11	0.04	46	–	–	–	–	–	–	–
L12	Escondido	0.08	4.5	50–69	6.31–7.00	0.25	0.44–9.38	0.62–0.81	0.18–0.21	2.80–3.99	2.66–6.15	17.82–32.65	10.52–17.79	–	1.24–2.43	1.06–1.77	<0.01–0.22
L13	Asa	0.07	0.8	73	6.93	1.27	1.81	0.29	0.10	32.24	6.48	15.39	11.00	0.43	1.91	3.89	<0.01
L14	Las Palmas	0.12	2.2	31–32	6.24–6.60	0.07	0.52	0.98	0.05	4.46	2.38	13.45	9.72	–	1.18	1.39	0.65
L15	Turbio	0.58	7.8	35–81	6.04–7.23	0.46–0.57	0.36–0.98	<0.25–0.55	0.04–0.07	12.16–35.57	0.39–4.01	0.65–17.03	2.53–10.29	2.53–10.29	0.38–1.68	0.83–5.05	<0.01–0.43
S1	Petreles	0.71	–	75	6.77	–	18.71	0.34	0.91	76.24	51.19	14.43	31.95	–	4.84	26.63	0.74
S2	Ballenas	1.10	–	90	7.45	–	1.53	176	0.47	67.16	12.49	6.65	18.69	0.44	2.94	7.97	0.81
S3	Tres Cerros	1.41	–	48	7.59	–	4.07	0.04	0.91	52.6	2.14	10.62	15.60	0.17	1.00	1.66	0.68
S4	Belgica	1.45	–	64	7.61	–	3.14	0.31	2.09	78.46	2.10	9.90	21.13	–	0.79	1.08	0.41
S5	Negro	1.14	–	49	7.42	–	2.80	<0.25	0.83	72.67	2.71	10.68	15.16	0.22	1.04	1.63	<0.01
S6	Rotch	0.73[a]	–	64	9.18	–	4.33	0.62	2.52	73.17	3.26	15.82	26.16	–	0.50	0.67	0.65

[a] Ice cap Rotch Dome area is not included in catchment size

of the lakes usually had concentrations of 6–18 mg l^{-1} sodium, 1–5 mg l^{-1} calcium, 0.5–3 mg l^{-1} magnesium, and 0.2–0.5 mg l^{-1} potassium. Among anions, chloride was the most abundant, both in lakes close to the sea (26 and 143 mg l^{-1} in Refugio and Maderos, respectively) as well as on the plateau (7–25 mg l^{-1}), with a lower abundance of sulphate (usually 2–9 mg l^{-1}) and bicarbonate (0.6–60 mg l^{-1}). Streams showed similar chemical features, with the exception of much higher values of SO_4^{2-} and Ca^{2+} in the Petreles Stream.

Inorganic nutrients and chlorophyll *a*

The lakes ranged in trophic status from ultra-oligotrophic to oligotrophic, with the exception of some of them located close to the coast such as lakes Maderos and Refugio. These latter lakes were frequented by marine animals, especially elephant seals, which enriched the waters with organic and inorganic nutrients as described elsewhere in maritime Antarctica (Hansson et al. 1996; Butler 1999; Vinocur and Unrein 2000). These coastal lakes had the highest concentrations of inorganic nitrogen compounds (especially nitrate), soluble reactive phosphorus (SRP) and Chl-a (Table 1). Lake Refugio had values of Chl-a ranging from 17 to 40 µg l^{-1}, and also the highest recorded abundance of bacterioplankton (>6 × 10^6 cells ml^{-1}) (Table 2). These hypereutrophic conditions are caused by the proximity of the lake to one of the largest elephant seal colonies on Byers Peninsula, and these animals frequently transit close to and into the lake.

Ammonium concentrations were low and for most lakes ranged from undetectable values (<0.25 µM) to 1.5 µM. An exception was Ballenas Stream with a value of 176 µM, likely due to dead elephant seals located upstream. Nitrate concentrations were also low, from 0.3 to about 1 µM. Higher concentrations were occasionally measured in Midge Lake (2.8 µM), Lakes Maderos (14.9 µM) and Lake Escondido (9.4 µM). An unusually high value of 48 µM of nitrate was found in Lake Refugio, likely the result of the elephant seals colony and nitrification of excreted ammonium. SRP concentrations were also low in the waters of most lakes, usually <0.05 µM. Hypereutrophic Lake Refugio was again an exception, with values over 2.7 µM. Soluble reactive silica was mostly in the range 20–70 µM (Table 1) probably due to the high weathering rate of rocks materials in the catchments and the presence of tephra deposits (Ellis-Evans 1996). Jones et al. (1993) also reported higher values of silica in Livingston Island lakes relative to Signy Island sites, implying differences in catchment geochemistry.

Most lakes had low Chl-a concentrations, typically below 1 µg l^{-1}. The lowest values (0.06 µg l^{-1}) were recorded in ultraoligotrophic Lakes Chester Cone and Las Palmas. Such low Chl-a concentrations have been recorded in oligotrophic lakes from elsewhere in maritime Antarctica such as the nearby King George Island (Vinocur and Unrein 2000). In Lake Refugio, because of the higher input of nutrients due to the elephant seal colony, Chl-a reached concentrations from 17 to 40 µg l^{-1}, similar to other maritime Antarctic lakes influenced by marine mammals (Butler 1999). In this lake, excess of both N and P was recorded, and nutrient supply was unlikely to limit phytoplankton growth. Similar levels of enrichment have been recorded in the shallow ponds of Ross Island that receive nutrient inputs from penguins (Vincent and Vincent 1982a).

Ammonium concentrations were also low in the streams of the Byers Peninsula, ranging from 0.1 to about 2 µM. Nitrate was usually more abundant, although the concentrations were also relatively low

Table 2 Bacterioplankton and autotrophic picoplankton (APP) abundances in lakes of Byers Peninsula during the 2001–2002 summer period (higher and lower values along lakes' water column, except for APP which corresponds to the upper half of the water column of each lake)

Code	Lake name	Maximum depth (m)	Bacterioplankton (10^6 cells ml^{-1})	APP (cells ml^{-1})
L1	Limnopolar	5.5	1.229–2.167	29–129
L2	Somero	0.5	1.891–4.067	27–98
L3	Midge Lake	8.2	0.808–1.426	16–188
L4	Chester Cone	5.0	0.826–3.358	153–1,227
L5	Maderos	0.5	3.718	245
L6	Refugio	0.5	6.039–6.583	204–299
L7	Cerro Negro	2.2	–	–
L8	Domo	4.5	1.078–1.378	27–143
L9	Diablo	–	–	–
L10	Limícolas	0.2	–	–
L11	Chica	–	1.673	69
L12	Escondido	4.5	1.090–2.052	113–288
L13	Asa	0.8	1.239	75
L14	Las Palmas	2.2	0.700–1.443	34–61
L15	Turbio	7.8	0.588–1.714	12–65

– No data

(1.5–4.3 μM). An exception was Petreles Stream, where nitrate was in the range 18–27 μM. SRP concentrations were much higher in streams relative to the lakes, usually around 1–2 μM, and soluble silica showed consistently high concentrations (50–80 μM).

Plankton

Bacterioplankton abundance in lakes (Table 2) was in the range 0.5–6.5 × 10^6 cells ml^{-1}. Some lakes exhibited high abundances, such shallow Lake Somero and Lake Maderos, and eutrophic Lake Refugio. Bacterioplankton often account for a large fraction of total planktonic biomass in oligotrophic lakes in general and Antarctic lakes specifically (Takacs and Priscu 1998), and the abundances found in Byers lakes are of a similar range to other lakes from continental (Laybourn-Parry et al. 1995; Takacs and Priscu 1998) and maritime Antarctica (Butler 1999; Izaguirre et al. 2003) of similar trophic status.

Autotrophic picocyanobacteria in surface lake waters were typically in the range 100–200 cells ml^{-1}. A maximum of 1.2 × 10^3 cells ml^{-1} was recorded in Chester Cone Lake (Table 2). Much higher concentrations were sometimes recorded in deeper waters, for example 2 × 10^4 cells ml^{-1} in the bottom waters of Lake Limnopolar. Even these values, however, are well below the high concentrations found elsewhere in Antarctica, for example in the deep chlorophyll maximum (DCM) of Lake Vanda in continental Antarctica (Vincent and Vincent 1982b). In saline lakes of the Vestfold Hills, picocyanobacteria reach concentrations as high as 8 × 10^6 cells ml^{-1} (Vincent et al. 2000), and in Lake Boeckella, a relatively shallow (4 m max depth) mesotrophic freshwater lake located in the Antarctic Peninsula (Izaguirre et al. 2003), picocyanobacteria attain concentrations of 3.6 × 10^5 cells ml^{-1} and represent up to 80% of phytoplankton biomass (Allende and Izaguirre 2003). In Antarctic continental lakes, strong water column stability could favor the development of phycoerythrin-rich picocyanobacterial populations, such as has been found in lakes from temperate areas (Camacho et al. 2003). The low stability of Byers lakes in combination with their relatively shallow lake depths and low nutrient status likely represents unfavorable conditions for the formation of picocyanobacteria-rich DCM layers.

The larger cell fraction of lake phytoplankton was dominated by a variety of diatom species, chrysophytes (*Chrysococcus* ssp., *Pseudokephyrion* sp., *Ochromonas* sp.) and chlorophytes (*Chlamydomonas* sp.). The diatoms were dominated by pennate species, in particular the genera *Navicula*, *Fragilaria*, *Achnanthes*, *Pinnularia*, *Gomphonema* and *Nitzschia*. Many of these are likely to have been of benthic origin. Diatoms, chrysophytes and chlorophytes (e.g. *Chlamydomonas* sp., Mataloni et al. 1998, 2000) have also been recorded as the main components of the phytoplankton in other maritime Antarctic lakes (Unrein and Vinocur 1999; Vinocur and Unrein 2000; Izaguirre et al. 2003).

The macrozooplankton community in most of the lakes was composed of the copepod *Boeckella poppei* and the fairy shrimp *Branchinecta gainii*. *B. poppei* is a calanoid copepod distributed along many freshwater lakes of the maritime Antarctica and South America (Bayly et al. 2003). *B. gainii* was relatively abundant in some lakes as Limnopolar and Somero. It is the largest lake freshwater animal in Antarctica (Peck 2004), and can play an important role in aquatic food webs, as has been reported by Paggi (1996) in South Shetland Islands. Cladocera were also represented in two of the lakes, Limnopolar and Chester Cone, specifically by *Macrothrix ciliata.* This is a nekto-benthic species associated with the aquatic moss *Drepanocladus longifolius* and is the first record of this species in Antarctica, and the second freshwater cladoceran to be found in the south-polar region. The other cladoceran species, *Daphniopsis studeri*, is known only from East Antarctica (Akatova 1966).

Small but unidentified rotifers were also found in many of the lakes. Ciliated protozoa were specifically sampled for in Lake Limnopolar. *Balanion planctonicum* was the only euplanktonic species, although many other species were associated with the benthic environment (Petz et al. 2005).

Benthic invertebrates

The benthic invertebrate communities of lakes in Byers Peninsula had a relatively low diversity compared to temperate systems, although the number of taxa and functional groups was higher by comparison with other Antarctic locations. In Lake Limnopolar, the community contained two macroinvertebrates, the oligochaete *Lumbricillus* sp. and the chironomid *Parochlus steinenii*. Both *Lumbricillus* and *Parochlus* were also found in several streams situated along South Beaches area from Sealer Hill to nearby Roth Dome ice cap. *Parochlus* was also present in other lakes where the aquatic moss *Drepanocladus longifolius* occurred over part of the lake bottom, such as Midge Lake and Chester Cone Lake.

Our identification of aquatic Oligochaeta is the first record for Livingston Island. Previous data in Antarctica are from the Schirmacher Oasis in moss-associated sediments of a lake (Ingole and Parulekar 1990), a similar habitat to Byers lakes where *Lumbricillus* is present.

The Antarctic chironomid *Belgica antarctica* was documented in three streams at one location of Byers Peninsula, on the south-facing slopes of Cerro Negro (Richard et al. 1994). Our data extends this record to other streams, and in wet mosses (*Sanionia uncinata*, equivalent to *Drepanocladus uncinatus*) associated with streams and coastal lagoons situated between longitudes 61°02′ and 60°58′W near to Rotch Dome. No individuals were found in ponds or streams at higher altitudes on the plateau.

Microinvertebrates associated with cyanobacterial mats in lakes and streams included several non-determined species of Nematoda, Tardigrada, Rotifera and Protozoa. Ciliate protozoa showed a high diversity in Byers Peninsula, with up to 120 different species, mostly associated to benthic environments, both in running and stagnant waters (Petz et al. 2005).

Microbial mats

Microbial mats are extremely abundant in Byers Peninsula, and favored by the presence of liquid water for weeks to months each year. They are composed of a cyanobacterial matrix with several diatom genera distributed through the mats (*Navicula, Nitzschia, Achnanthes* and *Pinnularia*), and resemble the mat communities found elsewhere in the region (Vinocur and Pizarro 2000). The main constituents in our mat samples were non-heterocystous filamentous cyanobacteria identified as species of Oscillatoriales corresponding to the genera *Phormidium, Oscillatoria, Lyngbya* and *Leptolyngbya*, with large differences in their relative abundance and mat structure between locations.

The cyanobacterial mats were typically between 3 and 6 mm thick, and many different communities could be distinguished based on their surface coloration. For example, in a short section of a temporary stream, five different communities were clearly identified, but dominated by orange and purple coloured communities. In slow flowing waters over gentle slopes or flat surfaces, the latter two communities formed large expanses up to several hundred m^2, in extent, and likely represent the largest non-marine biomass on the Byers Peninsula. The orange community typically appeared at the sites where liquid water remained for longer periods, such as small holes or ponds. This community was of leathery consistency and its surface was smooth. It was dominated by a species of *Phormidium* of 3–4 μm width (Table 3), but also contained many diatoms and heterotrophic organisms. In contrast, the purple community was more brittle and of nonuniform surface, following the microtopography of the gravel underneath. Its matrix was formed by narrow cyanobacterial trichomes (<1 μm) of the genus *Leptolyngbya*. This mat had a striking diversity of cyanobacteria, with at least nine additional taxa of filamentous taxa of variable diameter. Diatoms were especially scarce in this mat. The oligotrophic ponds and lakes of the Byers Peninsular often had thick microbial mats similar to those found in other maritime Antarctic lakes from King George Island (Vinocur and Unrein 2000) and Signy Island (Heywood 1978). Cyanobacterial microbial mats are though to be responsible for much of the primary production in extreme polar environments (Tang et al. 1997; Vincent 2000), and such communities are often characterized by increased nutrient supply relative to the overlying planktonic communities (Bonilla et al. 2005).

Benthic eukaryotic algae and mosses

Benthic diatoms occurred in many aquatic habitats in Byers Peninsula, either as epiphyton on aquatic mosses communities, or as epilithon, epipsammon and epipelon biofilms, both in lentic and lotic water-bodies, or in algal communities growing on the ice and snow. On the alluvial material located along the streams banks in Byers Peninsula, a diatom biofilm community developed during the summer period. The main species were *Hantzschia amphioxys*, *Nitzschia* sp., *Pinnularia* sp., *Achnanthes delicatula*, many of them showing mobility during the continuous alluvial redistribution and alternation of local air-exposition and flood phases.

Table 3 Community structure of the two most abundant microbial mat types (*CB* cyanobacteria)

Mat	Dominant cyanobacterium	Other cyanobacteria	Green algae	Diatoms	Animals	Others
Orange	*Phormidium* (3–4 μm)	Large Oscillatorians (12 μm) Some *Nostoc* colonies	Colonial	Very abundant	Very abundant	Fungi
Purple	*Leptolyngbya* (<1 μm)	*Phormidium* (8 μm) High CB diversity (eight different sizes)	Filamentous and unicellular	Scarce	Abundant	

Among the main diatom taxa found in benthic assemblages of most of lakes from Byers Peninsula were *Pinnularia microstauron*, *Sellaphora seminulum*, *Stauroneis anceps*, *Achnanthes* sp., *Fragilaria pinnata*, *Hippodonta capitata/hungarica*, *Nitzschia homburgiensis*, *N. gracilis*, and in lakes with higher conductivity, *Luticola* ssp. were more common. Diatoms from Byers Peninsula have been reported to be strongly correlated with salinity (Jones et al. 1993) and *N*/*P* ratios (Hansson and Håkansson 1992), and with silica availability in other parts of Antarctica (Roberts and McMinn 1996).

Diatom communities in the surface sediments of lakes on Byers Peninsula were relatively diverse, although we have found a major number of cosmopolitan taxa rather than typical Antarctic taxa as in previous reports from Byers Peninsula (Hansson and Håkansson 1992; Jones et al. 1993) or nearby maritime Antarctic islands (Schmidt et al. 1990; Van de Vijver and Beyens 1997); this could be partially due to current uncertainties in Antarctic diatom taxonomy (Jones 1996). Maidana et al. (2005) have also found a large number of diatom species common to Patagonia and South Shetland Islands and Antarctic Peninsula that might reflect dispersion from southern South America. However, in palaeolimnological studies carried out in some lakes in Byers Peninsula, this dominance of cosmopolitan diatom species in sediment cores has also been observed (Björck et al. 1991, 1993). Due to intense erosion processes during thaw and rainfall events in lake catchments, and because the lake sizes are relatively small, the benthic diatom assemblages present in lake bottoms are probably a mixed community with a significant presence of allochthonous diatom taxa from stream benthic communities. Fossil diatom studies in lake sediments in Byers Peninsula suggest this possibility (Björck et al. 1993), and our surface lake bottom sediment survey in Lake Limnopolar also showed that stream benthic species were conspicuously present.

Some of the lakes in the Byers Peninsula had benthic carpets of mosses growing at the bottom, under the shallow littoral zone contacting with the ice-cover in winter. Such communities are widely reported in oligotrophic Antarctic lakes, usually at depths over 5 m (Imura et al. 1999), although in Livingston Island lakes we have not found pillar-like colonies of mosses as found in lakes from continental Antarctica (Imura et al. 1999), and *D. longifolius* is the single aquatic moss species found so far in Byers lakes. Lakes with a well-developed, benthic moss carpet were Limnopolar, Midge Lake and Chester Cone. In other lakes such as Cerro Negro, Escondido and Aså, small moss patches of *Drepanocladus* were found at the bottom or close to the lake shore. All these lakes are oligotrophic, with low values of Chl-a in the water column and a high irradiance reaching the lake bottom during the short summer. These benthic mosses experience a 9–10 month period each year of severe shade conditions, with low ambient irradiances in combination with light-attenuating snow and ice cover. These conditions may be compensated for by shade acclimation and an ability to photosynthesise with low stable temperatures at low irradiance (Priddle 1980). However, net annual growth rates are likely to be extremely slow as found, for example, in analogous moss communities in High Arctic lakes (Sand-Jensen et al. 1999).

Conclusions

Byers Peninsula shows a range of limnological conditions, from plateau lakes with small watersheds and ultra-oligotrophic conditions, to the coastal water bodies close to the sea, with higher salt and nutrient concentrations. This ecological diversity of water bodies in terms of species composition and environmental conditions makes Byers Peninsula one of the richest limnological areas in the Antarctic region. In these lakes phytoplankton composition is dominated by chrysophytes and diatoms, although many of the latter are probably resuspended from the benthic communities. Several of the lakes have well developed monospecific stands of the benthic moss *D. longifolius*, which might dominate overall lake productivity because of its large standing stocks. The macrozooplankton community comprises the calanoid copepod *B. poppei* and the fairy shrimps *B. gainii*. The nekton-benthic cladoceran *M. ciliata* is recorded for the first time in Antarctica. In spite of the low nutrient status of most lakes, heterotrophic bacterioplankton were relatively abundant, while autotrophic bacterioplankton (picocyanobacteria) occurred in all the lakes but at low concentration. Benthic invertebrate diversity was relatively high in comparison with other documented Antarctic localities. The presence of aquatic Oligochaeta, two species of Antarctic chironomids, as well as several species of Nematoda, Tardigrada and Rotifera increases the importance of Byers Peninsula in terms of faunal diversity. Protist analyses showed the presence of nanoflagellates and ciliates (notably *Balanion planctonicum*) indicating a well developed microbial food web. Interdisciplinary research and monitoring activities should continue on the Byers Peninsula as a limnologically rich reference site for the study of environmental change at local as well as global scales.

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