Comparative study of the planktonic communities of three lakes of contrasting trophic status at Hope Bay (Antarctic Peninsula)

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Three water bodies of contrasting trophic status located at Hope Bay (Antarctic Peninsula) were studied during the summer of 1999, analysing all of their planktonic communities (zooplankton, phytoplankton and bacterioplankton) and their main limnological features. Important differences associated with their trophic conditions were found among lakes. At one extreme of the gradient, in the most oligotrophic lake (Lake Chico), the nektobenthic copepod Boeckella poppei and the rotifer Philodina gregaria were dominant in the open waters, and copepods presented a single reproductive event (univoltine life cycle); phytoplankton exhibited the lowest densities, dominated by nanoplanktonic Chrysophyceae and picocyanobacteria. In the meso-eutrophic Lake Boeckella, B. poppei, the dominant zooplankter, exhibited a multivoltine life cycle; phytoplankton were mainly represented by nanoplanktonic species of Volvocales, alternating with flagellate Chrysophyceae, and a great abundance of picocyanobacteria. In the hypertrophic Pingüi Pond, zooplankters were exclusively represented by bdelloid rotifers and ciliates; phytoplankton samples included some strictly planktonic species (Volvocales), a great proportion of picocyanobacteria and many typically benthic species (oscillatorians and diatoms) due to the shallowness of the water body. Bacterioplankton densities did not show important differences among lakes, but fluctuations, probably associated with a top-down control, were observed in the hypertrophic pond. This paper constitutes the first survey concerning all the planktonic compartments of water bodies of different trophic status at Hope Bay, describing the relative contributions of autotrophic and heterotrophic components to their food webs.

INTRODUCTION

A first characterization of the lakes and ponds at Hope Bay (Izaguirre *et al.*, 1998) revealed important differences in their trophic status, which are associated with natural eutrophication caused by seabird activities. In this typology, a description of the main features of the phytoplanktonic communities was provided. Based on the results of this survey, three lakes with very distinct trophic status were selected in order to conduct a comparative study on all of the planktonic components: zooplankton, phytoplankton and bacterioplankton.

The term zooplankton is applied herein in a very general sense, since some authors consider that nektobenthos describes more properly the pelagic community of Antarctic lakes (Heywood, 1970a, 1977; Weller, 1977; Paggi, 1986). This assemblage includes a few truly planktonic organisms, benthic rotifers and copepod stages that can shift their habitat, and benthic animals released from the bottom by wind-induced turbulence (Heywood, 1970a; Weller, 1977; Paggi, 1986). Lakes along the Antarctic coast and on sub-Antarctic islands are characterized by the low biodiversity of their zooplanktonic communities and by the absence of vertebrate predators (Tranvik and Hansson, 1997). A few species of herbivorous copepods and/or cladocerans dominate, and

constitute the highest trophic level in the food webs of many Antarctic lakes (Hansson *et al.*, 1996; Tranvik and Hansson, 1997). The centropagid copepod *Boeckella poppei*, formerly considered as a *Pseudoboeckella* (Bayly, 1992), is the only significant crustacean herbivore occurring in freshwater and brackish Antarctic water bodies (Brazier and Ellis-Evans, 1993; Hansson and Tranvik, 1996; Hansson *et al.*, 1996). However, other organisms such as rotifers and ciliates are also important zooplankters, whereas benthic Tardigrada and Nematoda frequently appear in the samples (Heywood, 1970a; Paggi, 1986; Hansson *et al.*, 1996).

Despite the abundant literature on zooplankton from maritime Antarctic lakes, the information on the northern end of the Antarctic Peninsula is limited to the records of *B. poppei* by Ekman (Ekman, 1905) and Corte (Corte, 1962) in lakes of Hope Bay. *Boeckella poppei* was collected for the first time in this area by the Swedish Antarctic Expedition during the summers of 1902 and 1903 in Boeckella Lake, which was named in reference to the only freshwater invertebrate known by then from the Antarctic continent (Ekman, 1905). The present study constitutes a first attempt at evaluating the composition and structure of zooplanktonic communities of the lakes at Hope Bay.

Information on the planktonic algal communities of the freshwater ecosystems located in the maritime Antarctica is restricted to some particular zones rich in lakes and/or where limnological studies were conducted. In particular, there is a substantial literature on the lakes at Signy Island (Light *et al.*, 1981; Hawes, 1990; Ellis-Evans, 1991; Laybourn-Parry *et al.*, 1996; Butler, 1999). More recently, several studies on the phytoplanktonic communities were carried out in lakes at Potter Peninsula, King George Island (Unrein and Vinocur, 1999; Vinocur and Unrein, 2000). For the Antarctic Peninsula, studies in freshwater lakes were mainly centred in two areas: Cierva Point and Hope Bay. In Cierva Point, the phytoplanktonic community of the main lake was studied over the last 7 years (Mataloni *et al.*, 1998, 2000).

The current studies on the phytoplanktonic communities of the lakes located at Hope Bay started ~10 years ago. A previous report by Corte describes some limnological features of the main lakes located in this region and provides general information on aquatic organisms (Corte, 1962). The summer variations of the phytoplanktonic community of Boeckella Lake, the largest water body at Hope Bay, were described for the first time by Izaguirre (Izaguirre *et al.*, 1993). Subsequent papers provided floristic information on the main lakes and streams, including phytoplanktonic and epilithic taxa (Vinocur and Izaguirre, 1994; Tell *et al.*, 1995; Vinocur and Pizarro, 1995; Izaguirre and Pizarro, 1998) and

ecological information about the phytoplanktonic community (Izaguirre *et al.*, 1996, 1998).

With respect to the autotrophic picoplankton, there has been an increasing interest in studying its dynamics and composition in the past two decades. In particular, for Antarctic lakes, Hawes, surveying water bodies of differing trophic status, has shown that this fraction is an important component of the phytoplanktonic community in terms of abundance and chlorophyll (Chl) *a* (Hawes, 1990). However, the literature concerning this size fraction in Antarctic lakes is relatively sparse (Ellis-Evans, 1991, 1996; Andreoli *et al.*, 1994; Laybourn-Parry *et al.*, 1997).

The importance of planktonic bacteria in aquatic food webs is clear (Coveney and Wetzel, 1995; del Giorgio and Gasol, 1995; Pace and Cole, 1996; Reche *et al.*, 1998; Simon *et al.*, 1998; Reitner *et al.*, 1999). In Antarctica, the dynamics of bacterioplankton was studied in lacustrine ecosystems representing a gradient of trophic conditions (Ellis-Evans, 1991; Takacs and Priscu, 1995, 1998; Laybourn-Parry *et al.*, 1996, 1997; Bell and Laybourn-Parry, 1999; Butler, 1999).

In this contribution, we present the results of the first integrated analysis of the planktonic components of three water bodies from Hope Bay (zooplankton, phytoplankton and bacterioplankton). The relationships between the communities and the trophic status of the lakes are discussed.

METHOD

Site description

The water bodies studied are located near Esperanza Argentine Antarctic Station (63°24′S–57°00′W), at Hope Bay, in the northern end of the Antarctic Peninsula (Figure 1).

Chico Lake

Chico Lake is located on the Mount Flora shelf, at an altitude of 100 m a.s.l. and 1100 m away from the sea. According to Drago (E. Drago, unpublished data), its area is ~2972 m^2 and its maximum depth 5.5 m. The surface of the lake is ice free during brief periods throughout the summer season. It is a typical oligotrophic small lake.

Boeckella Lake

On a size basis, this is the most important water body at Hope Bay, and provides drinking water to Esperanza Station. It lies in a fluvio-glacial depression dammed by moraine sediments, which, at the south-west margin, are covered by a thick layer of guano rich in calcium phosphates, derived from a nearby penguin rookery. Located
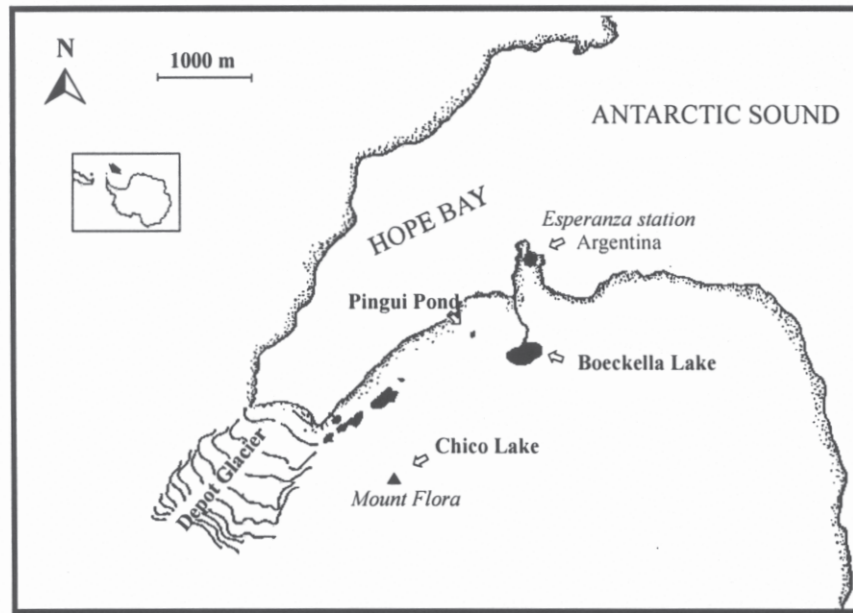
Fig. 1. Map showing the location of the water bodies surveyed.

at an altitude of 49 m a.s.l. and at a distance of 650 m from the sea, this lake has an area of 67 454 m² and a maximum depth of 4 m (Corte, 1962). Its ice-free period occurs during summer. It is considered as mesotrophic.

Pingüi Pond

Pingüi Pond is located within a large penguin rookery at an altitude of 20 m a.s.l., at ~450 m from the seashore. With an area of 1540 m² and a maximum depth of ~1 m, this shallow water body shows a typical hypertrophic status, with extremely high amounts of all nutrients associated with penguin guano. It is ice free most of the summer, but due to its shallowness, its surface can freeze during short periods during the season, when temperatures remain below zero for several days.

Sampling and analyses

The lakes were sampled weekly during the Antarctic summer, from 28 January through 24 March 1999. Samples and physical measurements were taken from a single station in each of the study lakes: from a pier in Boeckella Lake, from a coastal hanging rock in Chico Lake and from a rock near the central part of Pingüi Pond. Temperature, pH and conductivity were measured with a Hanna CT-1 portable meter (Hanna Instruments, USA). Dissolved oxygen concentrations were estimated using the manual Winkler method, and water transparency with a Secchi disk.

Samples for Chl *a* and nutrient analyses were taken in acid-washed PVC flasks, and immediately filtered through Whatman GF/F at the laboratory. Dissolved reactive

phosphorus (DRP), nitrates, ammonia, silicates, hardness and chemical oxygen demand (COD) (dissolved fraction) were determined *in situ* using a Hach DR/890 (Hach, USA) colorimeter and its corresponding reagent kits.

Filters for Chl *a* determinations were preserved frozen at –20°C for transport to Buenos Aires. Concentrations were determined by spectrophotometry before and after acidification; pigments were extracted with hot ethanol (60–70°C) and stored for 24 h at 4°C in darkness. Equations given by Marker *et al.* were used for calculations of Chl *a* concentrations (Marker *et al.*, 1980).

Bottom-to-surface vertical hauls were taken with a 55-µm-mesh plankton net for microzooplankton (rotifers and copepod nauplii) and protozooplankton (large ciliates), and with a 100-µm-mesh net for macrozooplankton (copepodites and adult copepods). Although nets are not ideal for ciliate collection, since samples were taken using the same technique in all three water bodies, we considered them comparable in order to estimate the relative abundance of large ciliates (>80 µm). At least three replicate hauls (up to 16) were taken in order to collect enough individuals to evaluate the density and structure of copepod populations. The effects of diurnal migrations were minimized by sampling at approximately the same time (at noon) at all sites and dates. Sampling was extremely difficult in Chico Lake, where copepods were mostly concentrated on the shelf and sides of the water body, and not in the open water. The samples were fixed immediately after collection in 5% formaldehyde.

Micro- and protozooplankton samples were analysed in

a 1 ml Sedgwick–Rafter counting cell under a binocular microscope, and subsamples of dense samples were taken with a Hensen–Stempel pipette. Macrozooplankton samples were examined and enumerated in a 5 ml Bogorov chamber under a stereomicroscope, and large samples were subsampled with a Russell device. Naupliar stages were not discriminated, whereas all copepodite stages were sorted before counting. Adult males and females were also discriminated. The number of aliquots to be counted (at least three) was calculated in order to keep the estimation error below 10%. Mean clutch size was estimated from the egg sacs of 18 ovigerous females per sample or from all of the ovigerous specimens present in the sample. Zooplankton abundance is expressed as individuals per litre of water theoretically filtered, assuming 100% filtering efficiency, since suspended material was scarce and towing distances short.

Samples for quantitative analyses of phytoplankton were preserved with 1% Lugol's iodine solution. Another set of samples was collected for heterotrophic and autotrophic picoplankton counts, which were preserved with 2% glutaraldehyde. The counts of micro- and nanoplanktonic fractions of phytoplankton were performed using an inverted microscope following Utermöhl's technique (Utermöhl, 1958). Replicate chambers were allowed to sediment during at least 24 h, and a maximum error of 20% was accepted in estimating the density of the most abundant species.

Using epifluorescence microscopy, autotrophic picoplankton (APP) cells were observed and counted from the fluorescence given off by photosynthetic pigments (Callieri and Pinolini, 1995). Samples were filtered through 0.2 μm black polycarbonate filters (Isopore GTPB 02500; Millipore), which were then mounted on a microscope slide with a drop of immersion oil for fluorescence (Immersol 518 F). Each filter was examined for pigment autofluorescence with a Zeiss Axioplan Microscope equipped with an HBO 50W lamp, a plan-Apochromat ×100 objective and a filter set for blue light excitation (BP 450–490 nm, FT 510 nm, LP 520 nm) and green light excitation (BP 546 nm, FT 580 nm, LP 590 nm) (Wynn-Williams, 1992; Rankin et al., 1997).

Heterotrophic picoplankton (HPP) were counted on the same filter type. The material was stained with DAPI (Porter and Feig, 1980), and bacterial numbers were obtained using an epifluorescence microscope under UV excitation (BP 365 nm, FT 395 nm, LP 397 nm). For both APP and HPP density estimates, two filters were prepared per sample. A minimum of 20 fields and 400 individuals were counted on each microscope slide, in order to keep the error level below 15%.

RESULTS

Physical and chemical variables

Ranges and mean values of the physical and chemical variables for each lake are presented in Table I. Chico Lake was the coldest water body, and its surface was ice free only during short intervals during the season. Boeckella Lake remained ice free until the end of the summer, when it became covered by a 7-cm-thick ice layer. Pingüi Pond showed pronounced temperature fluctuations (0–7.2°C) and short freezing events throughout the summer (Figure 2a).

Table I: Ranges of the physical and chemical variables for the three lakes

	Chico	Boeckella	Pingüi
Temperature (°C)	0–1.5 (0.42)	0–4 (2.36)	0–7.2 (3.2)
pH	6.62–7.26 (6.97)	6.5–6.79 (6.68)	7.25–7.76 (7.51)
Conductivity (μS cm^{-1})	34–62 (47)	25–67 (48)	1125–2000 (1520)
Dissolved oxygen (mg l^{-1})	10.78–13.81 (12.83)	11.95–13.9 (12.8)	10.77–supers. (16.47)
Secchi depth (m)	Up to the bottom (>1)	0.43–0.60 (0.46)	Up to the bottom (0.40)
DRP (μM l^{-1})	2.58–15.01 (6.40)	7.65–34.0 (21.21)	322.84–2444.85 (1387.21)
Nitrates (μM l^{-1})	12.85–58.54 (26.81)	25.7–222.03 (89.64)	588.99–4911.83 (2956.85)
Ammonium (μM l^{-1})	ND–24.27 (4.2)	25.7–164.2 (92.73)	196.33–11651 (7537.9)
SiO$_2$ (μM l^{-1})	4.66–21.47 (12.11)	9.65–17.97 (13.17)	173.07–985.19 (498.51)
Hardness (Mg) (mg l^{-1})	2.38–4.40 (3.34)	2.27–4.07 (3.17)	1.74–16.6 (6.23)
Hardness (Ca) (mg l^{-1})	0–5.36 (1.51)	0–1.71 (0.59)	0–1.25 (0.29)
COD (mg l^{-1})	0–6 (2.62)	0–10 (6.12)	65–307 (127.1)
Chl *a* (μg l^{-1})	ND–2.45 (1.17)	ND–8.71 (2.66)	4.35–58.79 (24.00)

Mean values are indicated in parentheses.
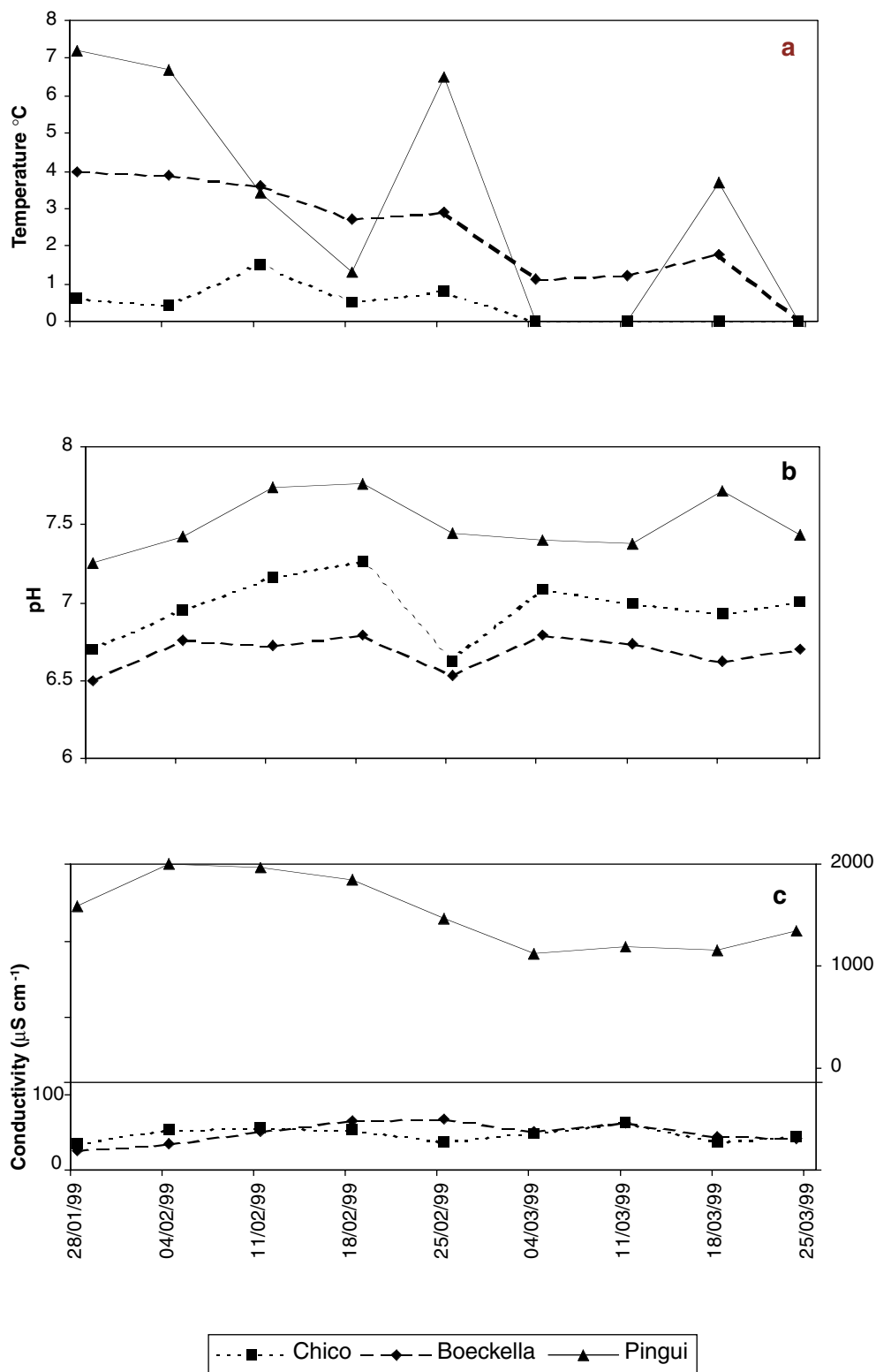
Fig. 2. Summer fluctuations in temperature (**a**), pH values (**b**) and conductivity (**c**) in the three water bodies studied.

The highest pH values were recorded in Pingüi Pond (always >7), while Boeckella and Chico lakes presented circumneutral or slightly acidic values (Figure 2b). In Boeckella and Chico lakes, conductivities were constantly low during the summer. On the contrary, the hypertrophic Pingüi Pond had extremely high conductivities that declined towards the end of the season (Figure 2c).

The values of the main nutrients analysed (Figure 3) were within the ranges reported previously for these lakes (Izaguirre *et al.*, 1998), and reflected the strong differences in trophic status among the water bodies.

The values of hardness (Ca and Mg) are reported in Table I. Hardness due to Ca was relatively low, showing an inverse relationship with nutrient content due to the retention of this cation in the sediments by phosphates. In this sense, geological surveys carried out in Hope Bay (Tatur, 1989) showed that the ornithogenic soils are rich in calcium phosphates.

Transparency reached its greatest values in Chico Lake, with Secchi disk depths down to the bottom. In Boeckella Lake, transparency varied between 0.43 and 0.60 m. A previous study (Izaguirre *et al.*, 1996), however, reports a broader range, since transparency is strongly associated with discharge events of meltwater streams that carry a great deal of sediments into the lake. In Pingüi Pond, Secchi disk values fluctuated from 0.27 to 0.43 m, but due to its shallowness, transparency reached the bottom, showing a strong attenuation towards the bed. As reported previously (Izaguirre *et al.*, 1998), dissolved oxygen concentrations were always around the saturation point.

Zooplankton

In agreement with previous studies on maritime Antarctic lakes, the zooplanktonic communities of all three water bodies are very simple and lack true predators, both vertebrate and invertebrate. The copepod *B. poppei* was the only crustacean found in the pelagic habitat of freshwater bodies at Hope Bay, also including surveys of the lakes Esperanza and Flora (M. C. Marinone, unpublished data). The diversity of rotifers in the water column was strikingly low in all three water bodies. The most frequently occurring rotifer taxa were the planktonic species *Notholca walterkostei* (José de Paggi, 1982; Paggi, 1986), the nektobenthic bdelloid *Philodina gregaria* and other unidentified bdelloid rotifers. Large ciliates (Peritrichia) were almost exclusively found in Pingüi Pond. As reported for other lakes of Western Antarctica (Heywood, 1970a; Paggi, 1986; Hansson *et al.*, 1996), low numbers of benthic Tardigrada and Nematoda were present in the plankton samples from all three water bodies, being most abundant in Pingüi Pond and least abundant in Boeckella Lake.

Although simple, the structure of the three zooplanktonic communities analysed differed markedly, reflecting the contrasting trophic status of these water bodies. The highest zooplankton abundances were observed in Pingüi Pond [303–2869 individuals (ind.) l^{-1}, including large ciliates], followed by the lakes Chico (0.5–74.3 ind. l^{-1}) and Boeckella (0.4–12.5 ind. l^{-1}). Similarly, rotifers (mainly represented by *P. gregaria*) were most abundant in Pingüi Pond (146–1458 ind. l^{-1}), reached intermediate values in Chico Lake (0.4–72.8 ind. l^{-1}) and showed their poorest representation in Boeckella Lake (0.14–1.56 ind. l^{-1}) (Figure 4). Copepod abundance showed the opposite pattern (Figure 5), with highest values in Boeckella Lake (0.13–12.2 ind. l^{-1}), lower figures in Chico Lake (0.03–4.3 ind. l^{-1}) and an absolute absence in Pingüi Pond. In the two lakes, rotifers were numerically dominant, whereas *B. poppei* was dominant in biomass owing to its larger size. Rotifers and ciliates alternatively shared their dominance in Pingüi Pond (Figure 6). Ciliate abundances in Pingüi Pond (157–1411 ind. l^{-1}) are within the range reported for other Antarctic lakes (Laybourn-Parry, 1997), whereas rotifer densities in Pingüi Pond and Chico Lake exceed published values for maritime Antarctic lakes (Paggi, 1986). In both lakes, the abundances of *B. poppei* are comparable with those reported for sub-Antarctic lakes and ponds (Paggi, 1986) and maritime Antarctic lakes (Hansson and Tranvik, 1996; Hansson *et al.*, 1996), but they lie in the lower limit of the abundance range of more productive Antarctic lakes (Heywood, 1970b; Hansson *et al.*, 1996).

Differences in the population structure of copepods clearly illustrate the contrasting trophic status of the two lakes (Figure 6). In Chico Lake, *B. poppei* was mostly represented by copepodites V (at the beginning of the study period) and adults (at the end of the summer). Almost no ovigerous females and very few nauplii and early copepodites were collected in Chico Lake, denoting a single annual recruitment associated with a mean clutch size of 15.7 eggs (range 6–24, based on three sampling dates with ovigerous females). In Boeckella Lake, *B. poppei* was mainly represented by adults, nauplii and early copepodites. Mating couples and a high proportion of ovigerous females (43.7% on average), with clutch sizes of 20.6 eggs on average (range 8–39), were present throughout the summer. A low proportion of females carrying resistant eggs (5%) was also detected on most sampling dates.

Phytoplankton (>2 μm)

Chlorophyll *a* concentrations (Figure 7a) also reflected the strong differences in trophic status among the lakes. The lowest figures were observed in Chico Lake, with typical oligotrophic values. The highest and more variable values were recorded in Pingüi Pond, reaching concentrations
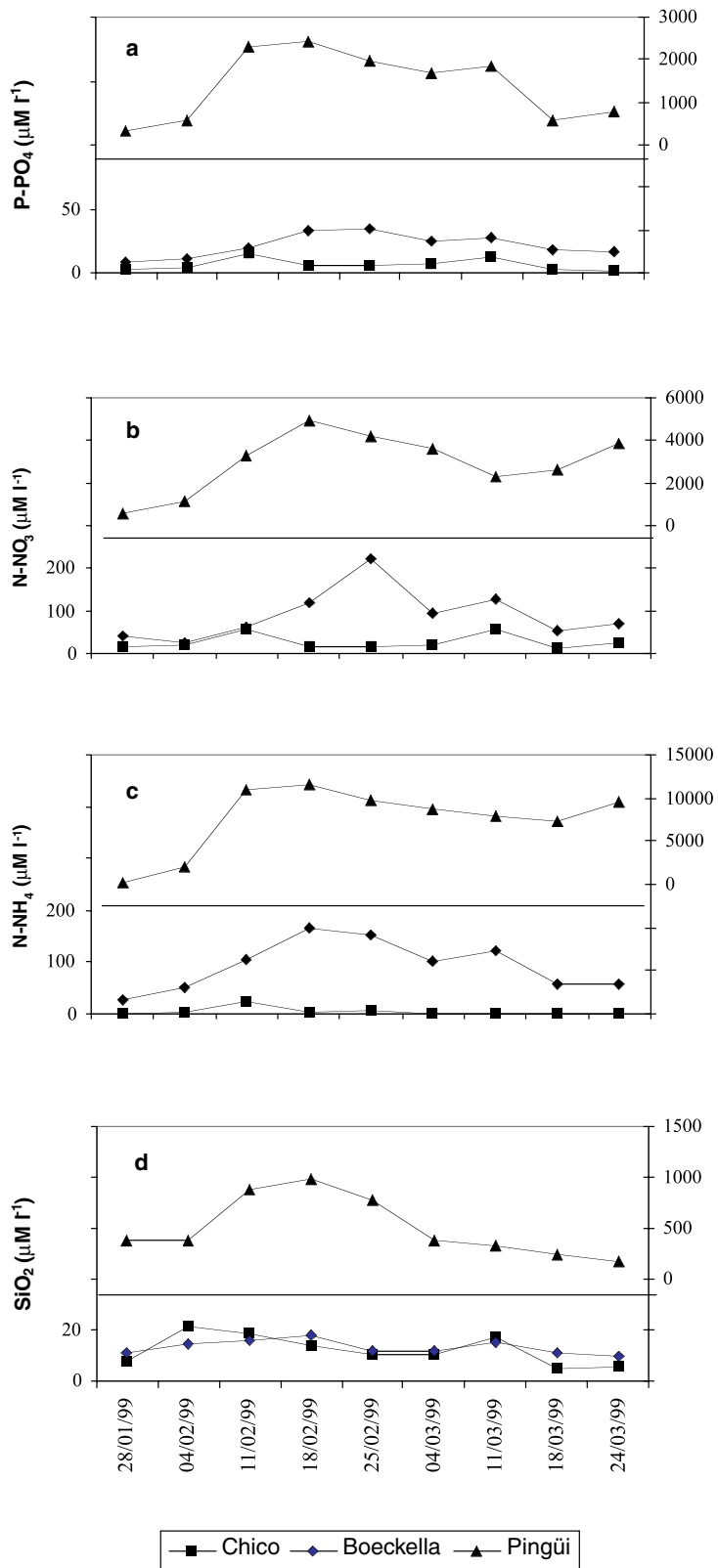
Fig. 3. Summer fluctuations in nutrient concentrations in the three water bodies studied. (**a**) Dissolved reactive phosphorus (DRP). (**b**) Nitrates (N-NO$_3$). (**c**) Ammonium (N-NH$_4$). (**d**) Silicates (SiO$_2$).
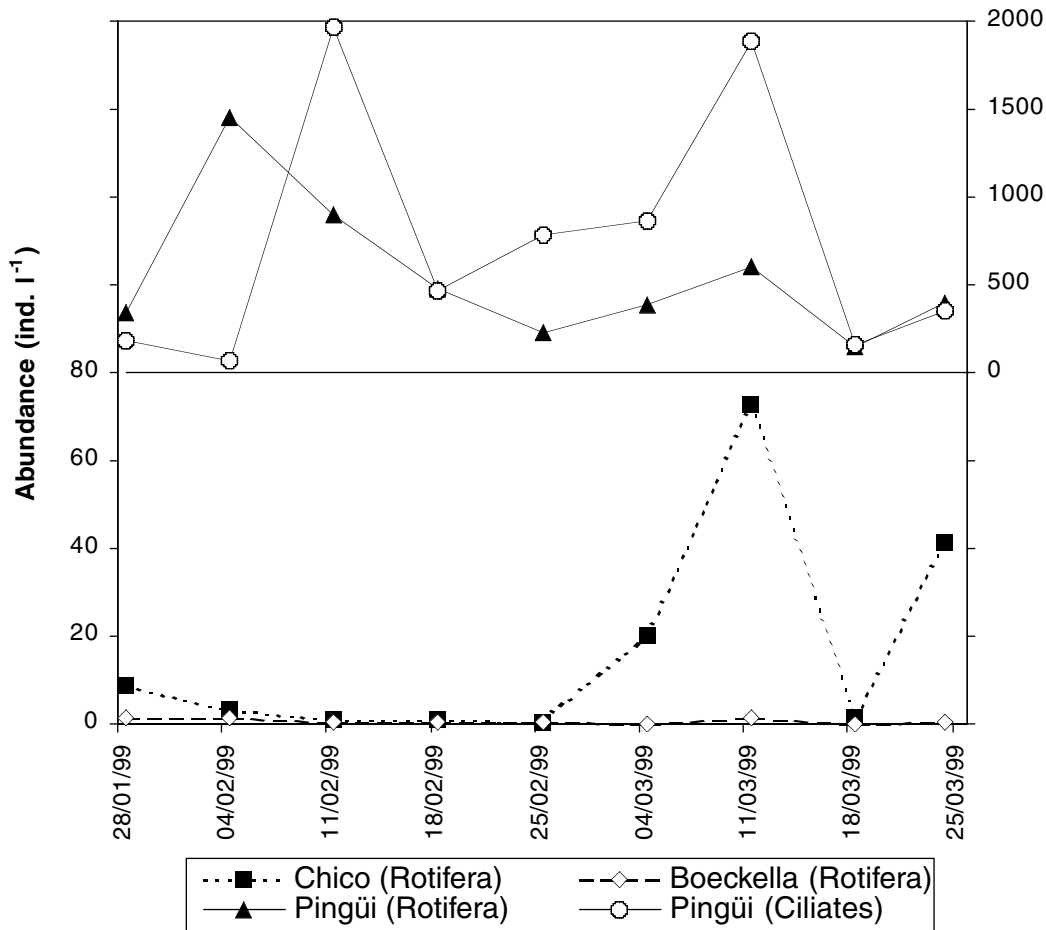
Fig. 4. Summer fluctuations in the abundances of rotifers and ciliates in the three water bodies studied.

characteristic of eutrophic and hypertrophic lakes. In agreement with previous observations (Izaguirre *et al.*, 1996), Chl *a* concentrations in Boeckella Lake exhibited fluctuations that can characterize this lake as meso-eutrophic. Although in general terms this variable showed values typical of oligotrophic systems, it reached higher concentrations when the environmental conditions favoured algal development. Thus, in this lake, Chl *a* was positively correlated with temperature ($r = 0.78$; $P < 0.05$).

Phytoplankton density (micro- and nanoplankton) showed rather constant and low values in Chico Lake. Pingüi Pond exhibited the widest fluctuations, and maximum concentrations were registered at the end of February (>10 000 ind. ml^{-1}). In Boeckella Lake, phytoplankton increased from the beginning to the end of the study period (Figure 7b).

Algal composition differed strongly in the three lakes (Figure 8; Table II). The oligotrophic Chico Lake showed

a clear dominance of nanoflagellate chrysophytes throughout the summer. In Boeckella Lake, the dominance changed throughout the season: chlorophytes, mainly represented by volvocaleans, were more abundant until mid-February, when they were replaced by chryso-phytes. The hypertrophic Pingüi Pond showed a more diverse phytoplankton, with dominance of chlorophytes (mainly volvocalean species), followed by benthic cyanobacteria and diatoms. Among the cyanobacteria, the most abundant groups in the three lakes were the picocyanobacterial *Synechococcus*-like cells, and oscillatori-ans. Other species frequently appearing in phytoplankton samples come from the snowfields and/or from terrestrial ecosystems, such as *Cylindrocystis crassa*, which was reported by Broady (Broady, 1979) as a terrestrial alga in Signy Island, and *Mesotaenium berggrenii* and *Raphidonema nivale*, two typical Antarctic cryobiontic taxa (Ling and Seppelt, 1990; Mataloni and Tesolín, 1997).
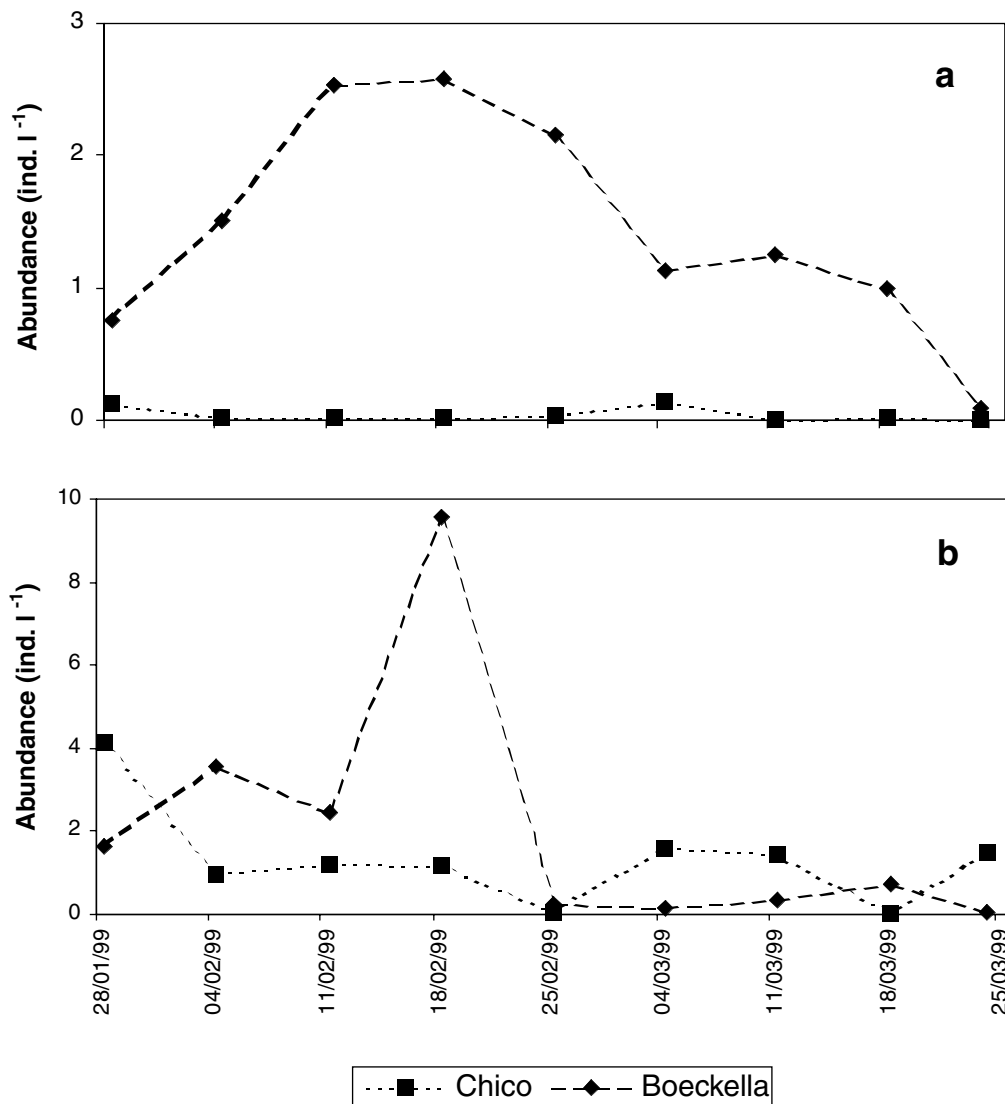
Fig. 5. Summer fluctuations in copepod abundances in the three water bodies studied. (**a**) Nauplii and copepodites I, II and III. (**b**) Copepodites IV, V and VI (adults).

Autotrophic picoplankton

In the three lakes, APP were mostly represented by pico-cyanobacteria (*Synechococcus* spp. and *Synechocystis* spp.), in agreement with information obtained for different Antarctic lakes (Vincent, 2000). Comparing the three water bodies, Boeckella Lake presented a higher abundance of APP, with densities ranging from 5×10^4 to 3.6×10^5 cells ml^{-1}. In Chico Lake, APP numbers were rather constant during the season, fluctuating between 3.7×10^4 and 8.8×10^4 cells ml^{-1}, whereas in Pingüi Pond, the figures varied from 5×10^4 to 2×10^5 cells ml^{-1} (Figure 9a). These values are within the range reported for lakes of

other latitudes (Stockner *et al.*, 2000), as well as for other Antarctic lakes (Hawes, 1990; Ellis-Evans, 1991).

Considering the contribution of APP to the total phytoplankton density, this fraction was dominant in terms of cell concentration in all three water bodies, in agreement with the observations by Hawes (Hawes, 1990) for lakes of different trophic status from Signy Island (Maritime Antarctica).

Bacterioplankton

Bacterioplankton density ranges were similar in the three studied lakes (Chico Lake, 5.96×10^4–1.56×10^5 ind. ml^{-1}; Boeckella Lake, 8.94×10^4–2.25×10^5 ind. ml^{-1};

Table II: Phytoplankton species collected in the studied lakes during summer 1999

	Chico	Boeckella	Pingüi
Bacillariophyceae			
Achnanthes laevis var. *ninckei* (Guerm.et Mang.) L.-Bert.		x	x
Achnanthes subatomoides (Hust.) L.-Bert. et Archibald		x	
Achnanthes spp.		x	
Gomphonema sp.		x	
Luticola muticopsis (V. Heurck) D. G. Mann		x	x
Nitzschia gracilis Hantz.	x	x	
Nitzschia homburgiensis L.-Bert.	x	x	
Nitzschia paleacea Grun.	x	x	
Nitzschia sp. 1	x	x	
Nitzschia sp. 2	x	x	
Pinnularia microstauron (Ehr.) Cl.	x	x	x
Chlorophyta			
Carteria sp.	x		
Chlamydomonas spp.	x	x	x
Chlamydomonas cf. *braunii* Goroschankin	x	x	x
Chlamydomonas subcaudata Wille			x
Chlorogonium sp.		x	
Cylindrocystis crassa De Bary	x	x	
cf. *Hyalogonium* sp.	x		
Spores of *Desmotetra* sp.	x	x	
Monoraphidium griffithii (Berk.) Kom.-Legn.			x
Monoraphidium minutum (Näg.) Kom.-Legn.			x
Prasiola callophylla (Carm.) Menegh.	x	x	
Prasiola crispa (Lightf.) Menegh.			x
Raphidonema nivale Lagerh.	x	x	x
Ulothrix sp.	x	x	
Zygotes of Chlamydomonadales			x
Cyanobacteria			
Aphanocapsa delicatissima W. et G. S. West			x
Aphanocapsa elachista W. et G. S. West		x	x
Aphanothece nidulans Richter			x
Chlorogloea purpurea Geitler			x
Chroococcus minimus (Keissler) Lemm.			x
Chroococcus minutus (Kütz.) Näg.	x	x	x
Eucapsis minuta Fritsch.		x	x
cf. *Gloeocapsa dermochroa* Näg.			x
Gloeocapsa ralfsiana (Harv.) Kütz.	x	x	x
Gloeocapsa sp			x
Isocystis pallida Woronichin	x	x	
Leptolyngbya antarctica (W. et. G. S. West) Anag. et Kom.		x	x
Leptolyngbya cf. *tenue* (Gomont) Anag. et Kom.		x	x
Leptolyngbya fragilis (Gomont) Anag. et Kom.	x	x	x
Leptolyngbya frigida (Fritsch) Anag. et Kom.	x	x	x
Merismopedia tenuissima Lemm.			x
Myxosarcina concinna Printz		x	x
Phormidium autumnale (Ag.) Gomont	x	x	x
Phormidium spp.			x

Table II: Continued

|	Chico	Boeckella	Pingüi
Pseudoanabena catenata Lautern.		x	x
Synechococcus elongatus Näg.		x	x
Synechococcus spp.	x	x	x
Chrysophyceae			
Chromulina sp. 1	x	x	
Chromulina sp. 2		x	
cf. *Chrysidalis* sp	x	x	
Ochromonas sp.		x	
Chrysophyceae (n.i)		x	x
Cysts of Chrysophyceae	x	x	x
Tribophyceae			
Tribonema australis Vinocur et Pizarro		x	
Tribonema monochloron Pascher et Geitler	x	x	
Tribonema utriculosum (Kütz.) Hazen		x	

n.i., not identified.
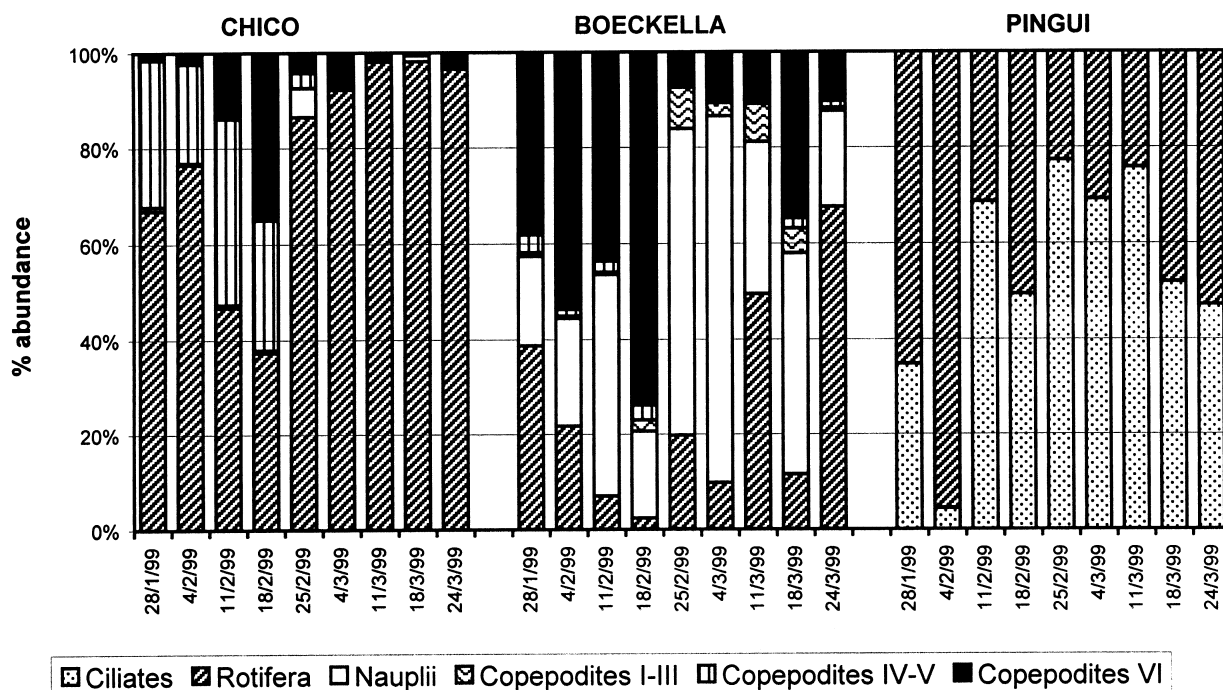
Fig. 6. Summer fluctuations in the percentage abundance of the different zooplanktonic groups in the three water bodies studied.

Pingüi Pond, 7.69×10^4–3.59×10^5 ind. ml^{-1}) and remained nearly constant throughout the study period except for the hypertrophic pond (Figure 9b).

DISCUSSION

The contrasting trophic status of the water bodies studied is clearly reflected in their physical and chemical features,

as well as in the composition and abundance of their planktonic communities (Table III). As in a previous typology of Hope Bay lakes (Izaguirre *et al.*, 1998), the influence of seabirds as a natural agent of eutrophication is evident.

Nutrient concentrations particularly show these differences in trophic status. On one side of the gradient, Chico Lake exhibited mean values comparable with those
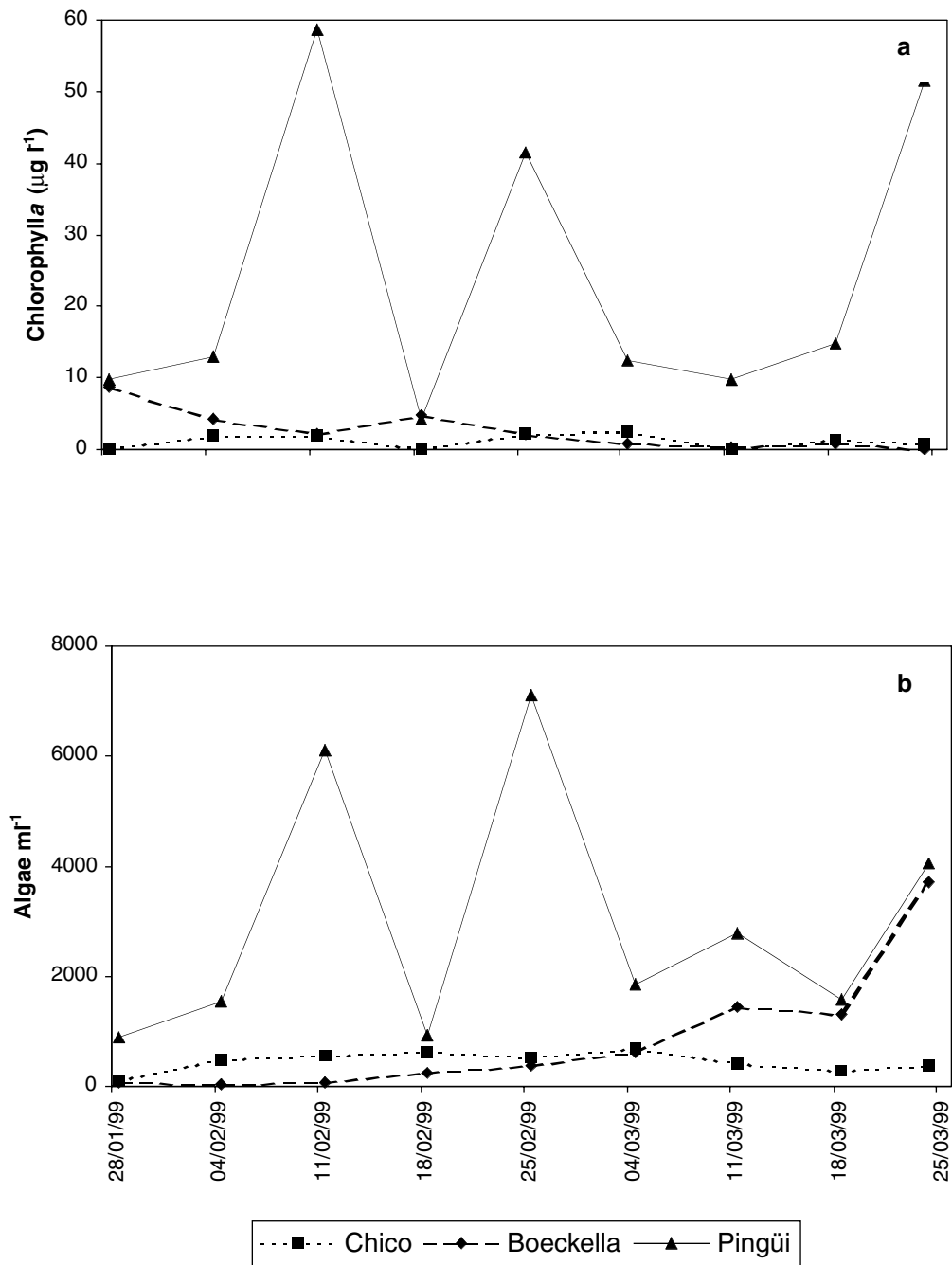
Fig. 7. Summer fluctuations in Chl *a* concentrations (**a**) and in phytoplankton densities (nano- and microphytoplankton) (**b**) in the three water bodies studied.

observed in a small oligotrophic pond of Signy Island with no influence from sea animals (Hawes, 1990). Boeckella Lake presented intermediate mean values, similar to those reported for lakes exposed to the effect of a nearby penguin rookery in King George Island (Vinocur and Unrein, 2000). On the opposite extreme of the gradient, Pingüi Pond showed figures even higher than those mentioned for other hypertrophic maritime Antarctic systems (Butler, 1999; Mataloni *et al.*, 2000; Vinocur and Unrein, 2000).
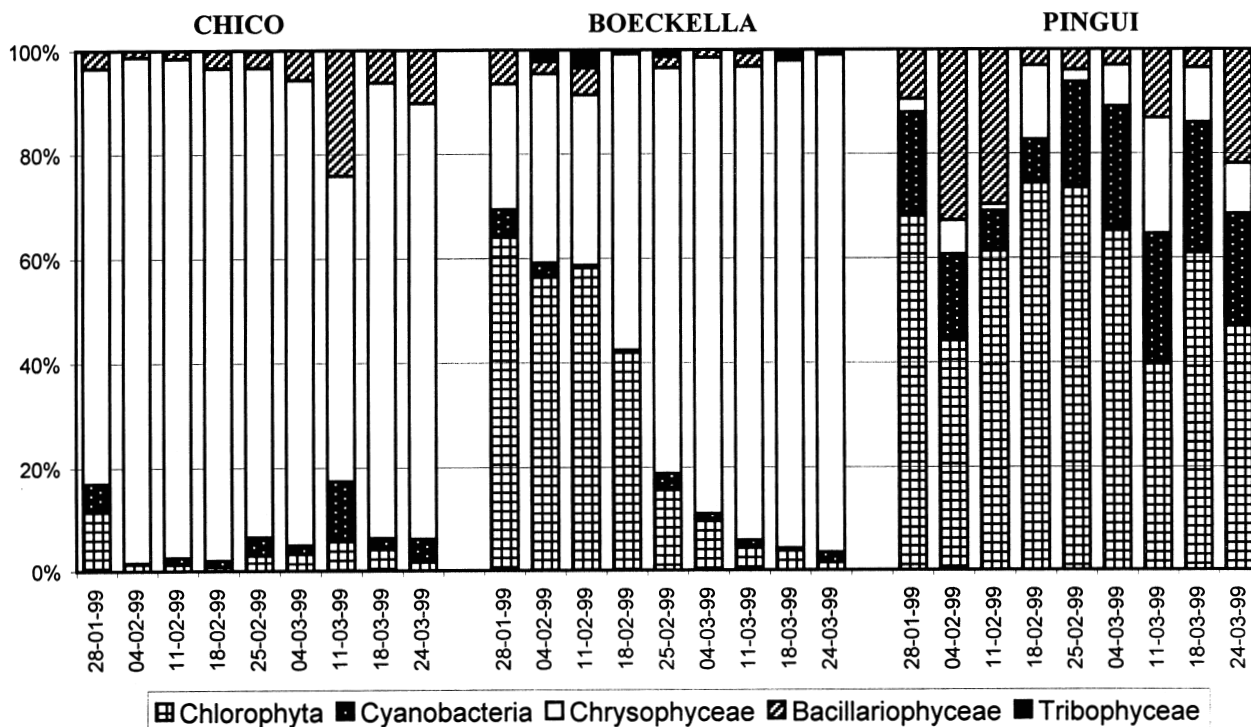
Fig. 8. Summer fluctuations in the percentage abundance of the different algal groups in the three water bodies studied.

As a whole, the concentrations of nutrients in these lakes were within the ranges reported previously (Izaguirre *et al.*, 1996, 1998; Allende and Izaguirre, 2003). Nevertheless, during the summer studied, some figures exceeded the upper limit of the range, as a consequence of the greater thawing of the snowfields in the catchment of the lakes. Since the study was carried out during the peak of penguin abundance and activity, melting waters presumably transported high amounts of nutrients.

The results of this research also evidence important differences among the planktonic communities of these lakes, which are associated with their trophic status, morphometric features and location (mainly altitude). The oligotrophic Chico Lake is characterized by its low abundance of zooplankton and all phytoplankton fractions (Figures 4, 5, 7a and 9a). Among zooplankters, rotifers were numerically dominant, whereas copepods dominated in biomass. The population structure of *B. poppei* revealed a single annual recruitment, and the small clutch size of females (Heywood, 1970a; Paggi, 1986) denotes a low fecundity, probably originating in food limitations. Phytoplankton are dominated by small algae (nanoflagellated, chrysophytes and picocyanobacteria). These species are able to develop brief episodes of rapid growth, followed by sharp declines. Following Reynolds'

categories, according to their size, surface-to-volume ratio and growth rate, these algae are typical C-strategists (Reynolds, 1988). Moreover, the high transparency of this lake also accounts for a great development of benthic algal mats dominated by cyanobacteria, which usually appear as tychoplanktonic components in the phytoplankton samples.

Reflecting its mesotrophic condition, Boeckella Lake presents higher abundances of all biological compartments except for rotifers and ciliates, which were practically lacking in the open waters. The summer population structure of *B. poppei*, the dominant zooplankter, revealed the existence of a multivoltine life cycle, as observed in phytoplankton-rich Antarctic lakes (Heywood, 1970a; Clarke *et al.*, 1989; Brazier and Ellis-Evans, 1993). However, the relatively small clutch size found in this lake, as compared with reports from eutrophic Antarctic lakes (19–145 eggs) (Heywood, 1970a; Paggi, 1986), would indicate that food availability is not as high. Phytoplankton show a great abundance of picocyanobacteria together with algae of other size fractions (mainly volvocaleans and a few chrysophytes). Chrysophyceae dominate the phytoplanktonic community when the lake surface is frozen, generally at the beginning and/or at the end of the summer season (Izaguirre *et al.*, 1998). As
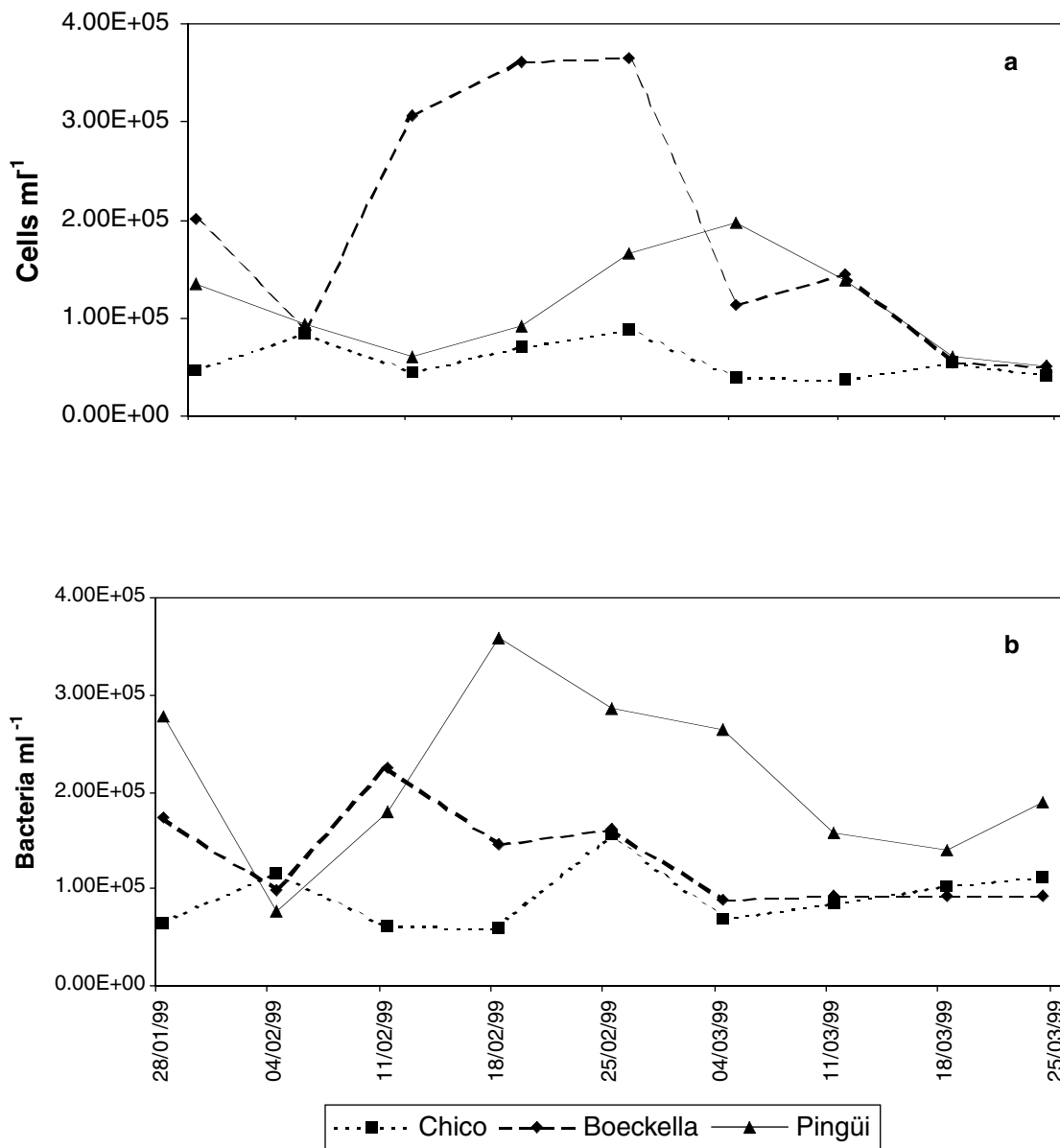
1091

Fig. 9. Summer fluctuations in picophytoplankton densities (**a**) and in bacterioplankton densities (**b**) in the three water bodies studied.

reported previously for a maritime Antarctic lake (Sánchez Caro and Gantes, 2001), the lowest copepod abundances recorded in the two lakes were related to downstream washout produced by meltwater pulses. Conversely, maximum abundances of bdelloid rotifers occurred after an episode of intense thawing.

The abundances of all organisms, including ciliates, were remarkably higher in the hypereutrophic Pingüi Pond as compared with both lakes, except for pico-cyanobacteria and for the absence of copepods. The rotifer *P. gregaria* and large ciliates were the main grazers.

Phytoplankton assemblages included volvocaleans, cyanobacteria and diatoms, many of which were associated with the benthic algal mats owing to the shallowness of the water body.

The zooplankton of lakes Boeckella and Chico conform to the community pattern observed in other Antarctic lakes, where planktonic cladocerans are lacking and *B. poppei* represents the only significant crustacean herbivore (Brazier and Ellis-Evans, 1993). In maritime Antarctic lakes, crustaceans and rotifers impose a 'top-down' control during occasional peaks of abundance,

Table III: Mean abundances of the planktonic communities of the studied lakes at Hope Bay throughout the 1999 Antarctic season (28 January–24 March)

	Chico	Boeckella	Pingüi
Bacterioplankton (bact. ml^{-1})	91 878	129 972	214 316
Picophytoplankton (cells ml^{-1}) mainly cyanobacteria	56 330	187 061	110 584
Phytoplankton (nano- and microplankton) (ind. ml^{-1})	449	874	3386
Dominant groups of phytoplankton	nanoflagellated Chrysophyceae (*Ochromonas* sp., *Chromulina* spp.)	Volvocales (*Chlamydomonas* spp.) nanoflagellated Chrysophyceae (*Ochromonas* spp.)	Volvocales (*Chlamydomonas* spp.), cyanobacteria and Bacillariophyceae from the algal mats (*Leptolyngbya* spp., *Luticola muticopsis*)
Large ciliates (ind. l^{-1})	–	–	747.9 (Peritrichia)
Rotifera (ind. l^{-1})	16.7 (*P. gregaria*)	0.7 (*P. gregaria* and *N. walterkostei*)	548.8 (*P. gregaria*)
Copepoda (ind. l^{-1})	1.4 (*B. poppei*)	3.5 (*B. poppei*)	–

while continental lakes lacking large metazoan grazers are entirely driven by 'bottom-up' forces (Laybourn-Parry *et al.*, 1996, 1997).

From its gut content analyses, *B. poppei* might be considered as omnivorous with a herbivorous tendency (Heywood, 1970b; Weller, 1977). While nauplii and early copepodites feed on phytoplankton and small organic particles suspended in the water, copepodites III and IV and adults can feed on organic matter and algal filaments stirred up from the sediment (Heywood, 1970b; Weller, 1977). Mesocosm experiments carried out in Boeckella Lake and gut content analyses confirm this feeding pattern (Almada, 2002). It has been reported that *B. poppei* is specialized on large food particles and does not graze on heterotrophic nanoflagellates, even at high densities (Tranvik and Hansson, 1997), and despite the low Antarctic temperatures, its clearance rate on algae is of the same order of magnitude as *Daphnia*, and higher than that of small calanoids from temperate regions (Hansson and Tranvik, 1996).

In fact, the predatory morphology of the mouth parts of the later stages of *B. poppei* (Pezzani-Hernández, 1973) and their large size [up to 3445 µm (Heywood, 1970a)] indicate that they should be able to seize small animals. Large Australian *Boeckella* not only consume algae, but also feed extensively on animals, a conclusion in line with the modern view that calanoids are fundamentally omnivorous, with varying tendencies to herbivory or carnivory

(Green and Shiel, 1999). Preliminary laboratory experiments carried out at Esperanza Station revealed that, deprived from other food sources, *B. poppei* males preyed upon the rotifer *P. gregaria*, and their own nauplii, but not on copepodites II, which seem to be already too large to be handled (M. C. Marinone, unpublished results). In copepod-dominated sub-Antarctic lakes, rotifers and ciliates are scarce in the open water, and mainly restricted to the sediment surface or to vegetation (Hansson *et al.*, 1996). Such a distribution pattern, the same as observed in Hope Bay lakes, might be explained by the predatory activity of *B. poppei*. Therefore, either direct or indirect evidence indicates that the later stages of *B. poppei* might be facultative predators on small prey, and that calanoids play a crucial role in regulating the microbial food web of Antarctic lakes (Tranvik and Hansson, 1997).

On the other hand, the seasonal variation of the lipid content shows that *B. poppei* is not directly dependent upon phytoplankton; rather, it is the availability of benthic material, particularly organic-rich detritus, which is important (Clarke *et al.*, 1989). This niche partitioning among stages optimizes the utilization of scarce food resources, also minimizing the intraspecific competition. The success of *B. poppei* in Antarctica is also explained by its great potential for survival in adverse environments (Pezzani-Hernández, 1973; Paggi, 1986), owing to its capability to produce resting eggs and withstand rapidly fluctuating temperatures, a wide range of salinities and

low oxygen levels (Heywood, 1970a,b; Weller, 1977).

Despite particular differences among the studied lakes, which are mainly associated with the trophic status, certain algal strategies are generally present in most Antarctic lacustrine ecosystems. The flagellated forms (chrysophytes, volvocaleans) are well adapted to stratified lakes, since their motility allows them to regulate their position in the water column, so as to obtain an adequate light intensity. As reported previously (Izaguirre *et al.*, 1993; Pose and Izaguirre, 1997), we observed that the proportion of flagellates increases as the surface of the lake freezes. On the other hand, its shade acclimation is another advantage below the ice layer (Priddle *et al.*, 1986; Burch, 1988). Moreover, chrysophytes have been mentioned as facultative heterotrophic algae, which can survive in the dark (Tuchman, 1996). This group has the opportunistic faculty of switching between autotrophy, heterotrophy and phagotrophy, which is a benefit in environments subject to periodic freezing (Sandgren, 1988).

The dominance of *Synechococcus*-like cells and oscillatorians among the cyanobacteria in these lakes is in agreement with observations given by Vincent for different polar lakes (Vincent, 2000). As was pointed out by this author, small coccoid or ovoid cells, as well as the thin trichomes (1 μm in diameter), have a similar light-absorbing efficiency.

The higher densities of APP registered during some dates during the summer in Boeckella Lake are probably associated with the lack of important densities of protozoan grazers. Protozoa (nanoflagellates and ciliates) are recognized as the most important picocyanobacteria consumers in lakes (Stockner *et al.*, 2000). The decline of APP observed towards the end of the season in the same lake coincided with an increase in flagellated chrysophytes (*Ochromonas* sp.), which seems to indicate a negative interaction between them. Different authors (Stockner, 1988; Jones, 2000) provided relevant information on this subject, reporting that mixotrophic freshwater flagellates, such as *Ochromonas* sp., are capable of supplementing their photoautotrophic nutrition with direct ingestion of bacteria and algal picoplankton. Nevertheless, more evidence is necessary to confirm this hypothesis for this lake. On the other hand, although Pingüi Pond has extremely high amounts of nutrients, APP densities are not as important as those reported for other hypertrophic lakes of lower latitudes (Sommaruga and Robarts, 1997).

Although the contribution of APP to the total phytoplankton density was important in terms of cell concentration in all three water bodies, it was reported that the relative importance of this fraction is generally more relevant in the most oligotrophic lakes (Sommaruga and Robarts, 1997; Vörös *et al.*, 1998; Agawin *et al.*, 2000).

Picophytoplankton can outcompete the larger phytoplanktonic algae when nutrients are scarce in the ultra-oligotrophic extreme of the gradient, since their high surface-to-volume ratio provides them with a competitive advantage (Søndergaard, 1990; Callieri and Stockner, 2000; Vincent, 2000). Nevertheless, different authors also observed a great abundance of this fraction in enriched Antarctic lakes (Ellis-Evans, 1991; Andreoli *et al.*, 1996). In the latter case, the success of the phototrophic picoplankton fraction would be the result of the selection for small organisms that have a superior light-capturing ability (Agawin *et al.*, 2000), and are less prone to grazing than larger ones (Sommaruga and Robarts, 1997; Vincent, 2000). In agreement with Callieri and Stockner, the relationship between the trophic status of a lake and the presence and importance of picoplankton-sized phototrophs would not be linear (Callieri and Stockner, 1997). Picophytoplankton would be of great importance in terms of biomass all along the trophic spectrum of Antarctic lakes (Ellis-Evans, 1996).

According to Laybourn-Parry, if the bacterioplankton abundances of lakes of different latitudes are compared, the Antarctic ones are generally at the lower limit of the range of values registered in lakes with similar trophic status (Laybourn-Parry, 1997). The densities observed in the three water bodies fall within the ranges reported for maritime Antarctic lakes (Ellis-Evans, 1991; Laybourn-Parry *et al.*, 1996; Butler, 1999) and for those from Continental Antarctica (Laybourn-Parry *et al.*, 1997; Ellis-Evans *et al.*, 1998; Takacs and Priscu, 1998; Bell and Laybourn-Parry, 1999). Bacterioplankton densities in the nutrient-enriched Pingüi Pond were lower than expected, taking into account its extremely high eutrophic condition, and the ranges provided by Sorokin (Sorokin, 1999). As reported by Reche *et al.* under nutrient-replete conditions, a 'top-down' control could be exerted over the bacterioplankton by the zooplankton (Reche *et al.*, 1998). Bacterioplankton can be an important food source for rotifers (Ooms-Wilms, 1997) and ciliates (Laybourn-Parry *et al.*, 1996). In this sense, it must be pointed out that high abundances of the rotifers and ciliates were observed in Pingüi Pond. These factors might regulate the bacterial growth in this lake, but this issue deserves further study.

This work constitutes the first attempt to compare all the planktonic compartments of lakes of different trophic status at Hope Bay. The results obtained describe the relative contributions of autotrophic and heterotrophic components to the food webs. In this sense, this is the starting point for future experimental studies in order to test hypotheses concerning the trophic interactions that take place at each particular trophic condition in Antarctica.

ACKNOWLEDGEMENTS

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