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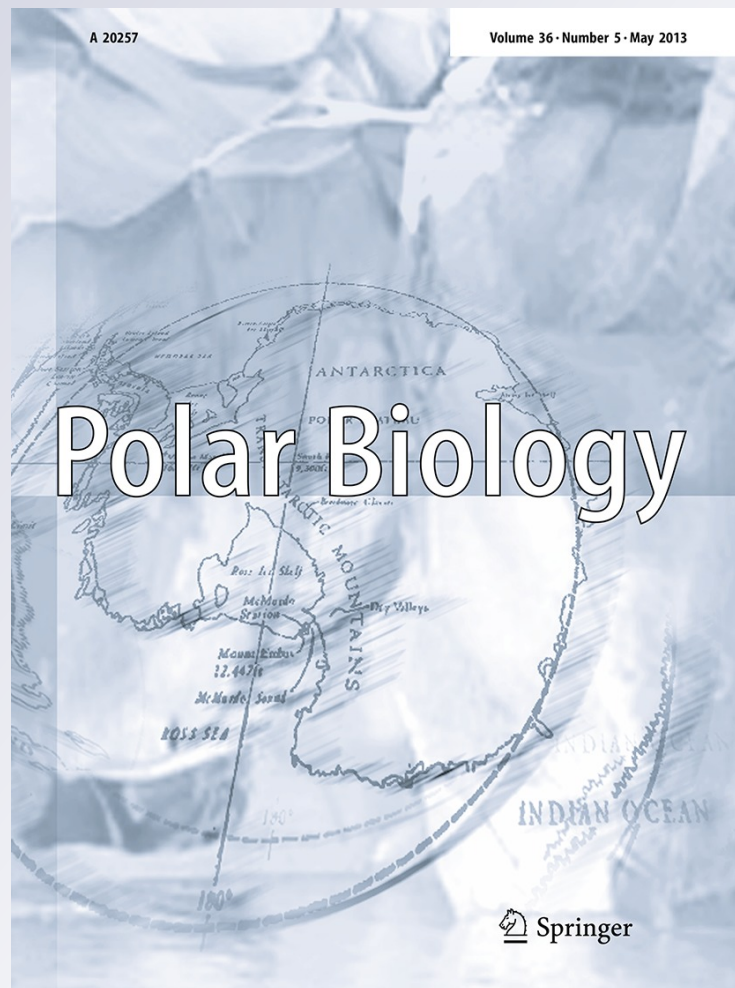
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# Short-term analysis of the phytoplankton structure and dynamics in two ponds with distinct trophic states from Cierva Point (maritime Antarctica)

Luz Allende · Gabriela Mataloni

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**Abstract** Phytoplankton communities dominating Musgos and Papúa ponds with differing trophic states were sampled over 3 days enabling the detection of the physiological and population responses of microalgae to short-scale changes in biotic and abiotic factors, rather than frequently analyzed changes in community composition responses to long-scale environmental changes. We hypothesized that both environments undergoing diel changes would be dominated by phytoplankton with generalist strategies, while community structure would be mostly dictated by the trophic state of each water body. The phytoplankton biovolumes of both ponds were strongly dominated by euplanktonic nanoflagellated Chlorophyta, while phycocyanin-rich picocyanobacteria dominated the picophytoplankton. Parallel diel cycles of air and water temperatures were more pronounced on a sunny, warm day which prompted algal photosynthesis,

revealed by strong increases in dissolved oxygen and pH. Nutrient and phytoplanktonic chlorophyll *a* confirmed the hypertrophic condition of Papúa pond. This accounted for the distinct community composition encountered in each pond, which remained stable throughout the study, as revealed by the SIMI index. The inverse relationship between the chl *a*/abundance ratio and the abundances of dominant species together with varying net growth rates ( $k'$ ) showed algal reproduction, yet densities remained rather stable in both cases. In Musgos pond, fluctuations in  $k'$  for small and median ciliates shadowed those of pico- and nanophytoplankton, respectively, strongly suggesting that they can control algal growth in these 2-level trophic chains.

**Keywords** Maritime Antarctica · Ponds · Phytoplankton structure · Short-term study

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## Introduction

Phytoplankton ecology is affected by the interaction between organisms and the natural, fluctuating environment. Environmental fluctuations occur over a range of superposed time scales, and phytoplankton responses accordingly span from physiological mechanisms to inter-annual variability. Harris (1986) defined two main time scales eliciting different response mechanisms: when the environmental conditions fluctuate over shorter times than phytoplankton growth rates (hours), they exert physiological and structural responses, such as chlorophyll *a* synthesis, while those in the scale of 50–200 h interact with population growth parameters. As a result of the latter over a longer period (days–weeks), differential population growth among phytoplankton species will result in the changes in community composition and

dominance commonly observed throughout seasonal samplings.

In Antarctica, some of the most variable terrestrial environments are freshwater ponds, defined by Ellis-Evans (1996) as water bodies undergoing complete winter freezing, with a maximum depth of about 0.6 m. Organisms inhabiting these systems must tolerate freezing and/or high conductivity resulting from salt exclusion during freezing for at least 10 months per year, as well as exposure to high UV-PAR irradiation levels and possible desiccation during the brief summer period. According to Vincent (2000), such extremely variable systems would select generalist organisms—likely cosmopolitan species—in contrast to the cold-adapted species thriving in more constant environments such as snow.

The best studied Antarctic ponds are mostly the coastal meltwater ponds located on the McMurdo Ice Shelf (Vincent et al. 1993; Hawes et al. 1997; Healy et al. 2006; Wait et al. 2006), many of which have highly saline basal brines which remain liquid at below-zero temperatures. Found virtually throughout Antarctica, most ponds are dominated by microbial mats, and therefore, fine-scale ecological studies of these environments have focused on these communities (Vincent et al. 1993; Hawes et al. 1999). On the other hand, Davey (1993) observed that, in spite of being very common transient environments in the deglaciated areas of maritime Antarctica, ponds had received far less attention from researchers than lakes. As stated by Goodman (1969), ponds are extremely dynamic environments, in which hydric balance is mainly controlled by weather. Also Howard-Williams and Hawes (2007) recognized that ponds are highly variable over a number of time scales. Nevertheless, most phytoplankton studies in these environments were undertaken at long time scales, with sampling events being performed several days to even months apart. As an exception, in the weekly study of Bird pond, Spurr (1975) included a single series of 5 samplings over 24 h, which unfortunately lacked replication. In this research, and in line with investigations dealing with the influence of spatial environmental heterogeneity on the phytoplankton, which included ponds (Mataloni and Pose 2001; Pizarro et al. 2004), or focused solely on these environments (Tesolín et al. 1997), our objective was to study the phytoplankton communities dominating two distinct ponds over a short time scale but with a sufficient number of sampling occasions that would enable detection of the growth-level responses of the microalgae to short-scale changes in biotic and abiotic factors, rather than those affecting community composition (Harris 1986).

The location of Cierva Point (64°09'S, 60°57'W) on Danco Coast, on the leeward side of the Antarctic Peninsula, together with its high environmental heterogeneity, allows for an outstanding biological diversity that justified

its designation as the Antarctic Specially Protected Area (ASP) No. 134 by the Scientific Committee for Antarctic Research (SCAR). For the past 20 years, research on the microalgal communities from this area has been conducted in lakes (Mataloni et al. 1998, 2000a; Izaguirre et al. 2001), streams (Izaguirre and Pizarro 2000; Mataloni et al. 2005) snow (Mataloni and Tesolín 1997) and soils (Mataloni et al. 2000b; Mataloni and Tell 2002; Mataloni et al. 2010; González Garraza et al. 2011). In particular, Tesolín et al. (1997) surveyed the phytoplankton of 16 ponds from different origins and located on various substrates, dominated by benthic mats, epilithic communities or phytoplankton itself. These communities displayed a wide range of taxonomic compositions and abundances owing to the strong influence of their different surrounding environments and trophic states.

Our research compares the phytoplankton communities of two ponds located in nearby zones from Cierva Point: One of them (Papúa pond) is located within a *Pygoscelis papua* rookery, and the other (Musgos pond) is situated on a rocky spot surrounded by an extensive vegetation mat dominated by *Polytrichum* spp. mosses. Although both ponds are submitted to dramatic seasonal changes in environmental conditions, the time scale selected for this research focuses on daily variations. In this sense, we expect Musgos pond to undergo marked daily cycles in light and temperature, while in hypertrophic, turbid Papúa pond the continuous mixing would submit phytoplankton to constantly and dramatically changing light conditions as they move up and down the water column. According to Harris (1986) this high-frequency perturbation would render this phytoplanktonic community able to integrate the PAR signal over short time periods, thus masking the effect of the diel cycle of PAR. Also, as the very high nutrient concentration is permanently in excess regarding algal requirements, the nutrient load would be perceived by phytoplankton as constant. On this basis, we hypothesize that

1. Both ponds will show contrasting abiotic features on account of their different surroundings, which in turn will render the structure of their phytoplanktonic communities different. Therefore, phytoplankton chlorophyll *a*, biovolume and floristic composition would be mostly dictated by the trophic state of each water body.
2. Despite the trophic differences, the small size of the ponds renders their abiotic features highly sensitive to environmental diel cycles. As a consequence, both these changing environments would be dominated by phytoplankton species with generalist strategies sensu Vincent (2000). Nevertheless, Papúa pond would be a more stable environment for algae in terms of light and nutrient availability.

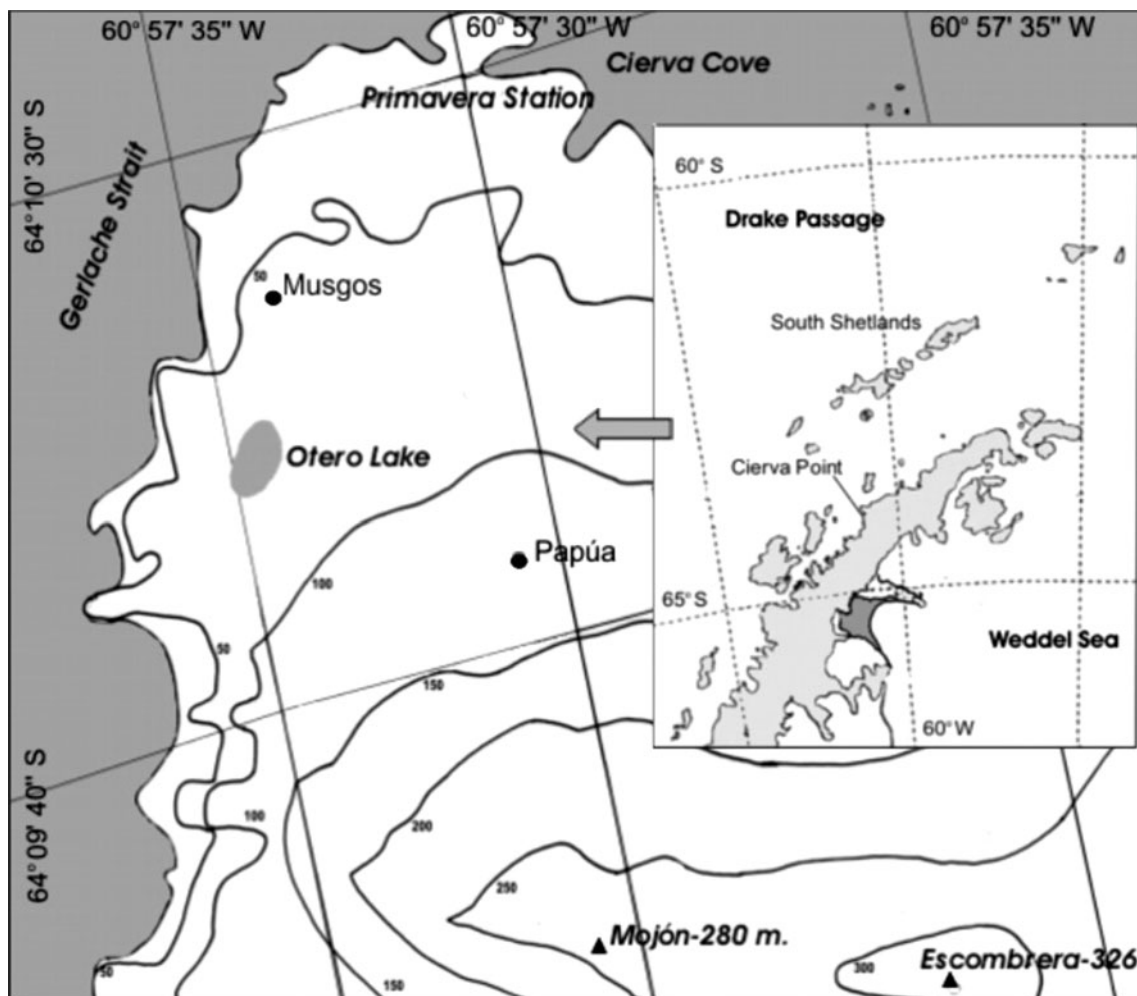
3. Events spanning different time scales are dealt with by organisms in different ways. Variations in environmental parameters occurring over longer time periods than phytoplankton growth rates ( $>200$  h) would be reflected by changes in community structure (taxonomic composition and diversity). Yet variations in the same scales as phytoplankton growth (hours–days) would elicit responses to these at population levels, reflected by changes in the Chl *a*/abundance ratio and in the abundances of the dominant species.

## Materials and methods

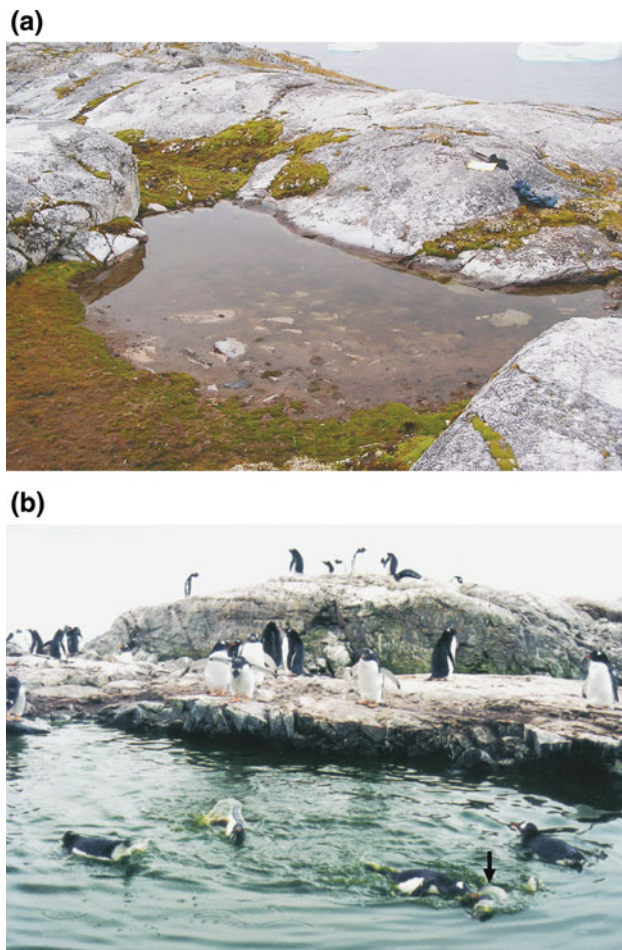
The two ponds studied (Papúa and Musgos) are located in the ASPA No. 134, Cierva Point, Antarctic Peninsula (Fig. 1). Though just 350 m apart, the extreme environmental diversity of this peninsula renders their surroundings completely different. While Musgos pond stands in an area mostly covered by *Polytrichum* spp. hummocks only

inhabited by a few skuas (*Catharacta macormickii*), Papúa pond is located in a depression amidst a very active Gentoo penguin (*Pygoscelis papua*) rookery and is intensely used by these birds as a swimming pool during the crèche period. Although it is impossible to use a Secchi disk without disturbing the loose sediment of the bottom in both shallow ponds, their color and clarity contrast markedly, even to the naked eye. While the bottom of Musgos pond is clearly visible, Papúa pond is much more turbid and green discolored (Fig. 2).

During Antarctic summer 2003, the geographic position of each pond was established with a Garmin-Etrex GPS, and morphometric measures taken in the field. Both sites were sampled on 8 occasions along a 55-h period between 27/2/2003, 13 h and 1/3/2003, 20 h. Samplings were carried out daily at 07, 13 and 20 h. Each time, both air and water temperature, pH and conductivity were measured with Al-tronix electronic meters (SAEN SRL, Argentina). Samples for dissolved oxygen were taken in wide mouthed ground glass stoppered bottles and measured on the same day at the



**Fig. 1** Map of the Antarctic Peninsula showing Cierva Point and the location of the studied ponds



**Fig. 2** Images from **a** Musgos pond, and **b** Papúa pond. The *arrow* shows phytoplankton-discolored water around penguins in the latter

Primavera Station laboratory according to Winkler (APHA 1975). Contents of dissolved nutrients ( $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$  and  $\text{PO}_4\text{-P}$ ) were sampled in acid-washed PVC containers, known appropriate volumes filtered onto  $0.7\ \mu\text{m}$  pore diameter Whatman GF/F prefilters, and nutrients measured using a Hach DR/890 colorimeter with the appropriate Hach reactivés for each analysis (Hach Company, USA). Detection limits of the analyses were  $0.02\ \text{mg L}^{-1}$  for  $\text{NH}_4\text{-N}$ ,  $0.01\ \text{mg L}^{-1}$  for  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$  and  $0.05\ \text{mg L}^{-1}$  for  $\text{PO}_4\text{-P}$ . Concentrations of phytoplanktonic chlorophyll *a* were measured spectrophotometrically through extraction of the filters in hot ethanol using the equations given in Marker et al. (1980). Absorbances at 665 and 750 nm were measured before and after acidification with  $0.1\ \text{N HCl}$  in order to correct for phaeopigments.

The nano- and micro-sized fractions of the phytoplankton ( $2\text{--}20$  and  $20\text{--}200\ \mu\text{m}$ , respectively) (Callieri and Stockner 2002) were qualitatively sampled by scooping a bucket through the surface of Musgos pond and then concentrating the known volume of the natural community by passing it

through a  $15\ \mu\text{m}$  pore net. At Papúa pond, the phytoplankton concentration was high enough to collect the sample with a 50 mL flask. These samples were observed *in vivo* at the Station laboratory with an Olympus BX-31 transmitted light microscope fitted with a *camera lucida*. Permanent slides were prepared for the taxonomic study of diatoms following the method of Van der Werff (1955). References used for algal identification included the authoritative works of Broady (1979) and Ettl and Gärtner (1995) for Chlorophyta and Tribophyceae, Komárek and Anagnostidis (1999, 2005) and Komárek (2003) for Cyanobacteria; Krammer and Lange-Bertalot (1986, 1991) and Van de Vijver et al. (2002) for diatoms, among a large number of papers dealing specifically with Antarctic microalgal flora. The species richness of each pond was estimated once a day by scanning as many slides as necessary until the number of new taxa on two consecutive slides was up to 2. This method, widely used in phycology, allows for the construction of an individual-based accumulation curve (Gotelli and Colwell 2001). The respective taxonomic lists resulting from each day were almost identical and therefore pooled in a single list for each pond.

In each sampling event, two sets of two replicates were taken for the quantification of the picosized ( $0.2\text{--}2\ \mu\text{m}$ ) (Callieri and Stockner 2002) and the nano- and micro-sized fraction of the phytoplankton, respectively, by scooping acid-washed 150 PVC bottles in the subsurface of both ponds. Water samples for quantitative analysis of prokaryotic (picocyanobacteria: PCy) and eukaryotic picophytoplankton (picoeukaryotic: Peuk) were fixed with 10 % ice-cold-glutaraldehyde (1 % final concentration). The samples were processed for epifluorescence following standard procedures (Kemp et al. 1993). Between 2 and 5 mL of the fixed sample was filtered through a  $0.2\ \mu\text{m}$  pore size black polycarbonate membranes (MSI), which were then mounted on a microscope slide with a drop of immersion oil for fluorescence (Immersion 518 F). The membranes were examined for pigment autofluorescence with a Zeiss<sup>TM</sup> Axioplan Microscope equipped with an HBO 50 W lamp; a filter set for blue light excitation (BP 450–490 nm, FT 510 nm, LP 520 nm) was used to count Peuk algae, and green light excitation (BP 546 nm, FT 580 nm, LP 590 nm) for Pcy (Wynn-Williams 1992). At least 400 individuals and 20 fields of view were observed on each filter in order to account for an error less than 15 %. Samples of the larger phytoplankton fraction were preserved in 1 % acidified Lugol's solution and stored in dark, cool conditions. Back in Buenos Aires, algal counts were performed in two replicate chambers with a Zeiss inverted microscope at  $400\times$  magnification following Utermöhl (1958). A sufficient number of fields was counted in each replicate to attain an error less than 20 % according to Venrick (1978). Individual biovolumes of the studied

planktonic organisms were calculated using appropriate geometric formulae according to their shapes (Hillebrand et al. 1999; Sun and Liu 2003) and the mean dimensions of the organisms in the samples. For mucillaginous colonial organisms, calculations were made for the whole colony including mucilage. Cell dimensions of the picophytoplankton were estimated based on data obtained from nearby maritime Antarctica freshwater systems (Unrein, unpublished data), and a mean biovolume was estimated for this fraction.

Examination of qualitative samples revealed that, as previously observed in other water bodies from Cierva Point (Mataloni et al. 2000a), ciliates largely dominated the heterotrophic plankton community. These were assigned into three distinguishable size categories: small (medium cell volume up to  $2 \times 10^3 \mu\text{m}^3$ ), medium (medium cell volume  $3.5 \times 10^3 \mu\text{m}^3$ ) and large (medium cell volume  $50 \times 10^3 \mu\text{m}^3$ ) following these authors, and counts of these organisms were performed on two replicates sets of quantitative samples also following Utermöhl (1958).

Between-pond and within-pond relationships among environmental variables were tested by means of multiple nonparametric correlations using the Spearman correlation coefficient (SPSS), which were performed on the whole data pool and also separately for each pond. Additionally, the daily coefficient of variation (CV) of physical variables (air and water temperatures, pH, conductivity and dissolved oxygen) over 24-h periods (27/2 20 h to 28/2 20 h, and 28/2 20 h to 1/3 20 h) was obtained.

We calculated the Stander's similarity index SIMI (Elber and Shanz 1989), in order to obtain a paired comparison of the phytoplankton community structure of both ponds at the beginning of the sampling period (27/213 h). This index ranges between 0 and 1, the latter value representing identical communities. As SIMI index can also compare communities which are part of a temporal succession, the similarity in the phytoplankton structure within each pond was tracked over the successive samplings using the same index, (27/213 h, 20 h; 28/2; 7 h, 13 h, 20 h; 1/3 7 h, 13 h, 20 h).

Daily net growth rates ( $k'$ ) for the different phytoplankton size fractions,  $>2 \mu\text{m}$ -dominant phytoplankton species, total ciliates and different ciliate size fractions were calculated based on cell counts for two 24-h periods (27/2 20 h to 28/2 20 h and 28/2 20 h to 1/3 20 h):

$$k' = \ln(N_f/N_i)/T_f - T_i$$

where  $N_i$  is the abundance of organisms at the initial time (20 h) of each of the two studied periods, and  $N_f$  is the abundance of organisms at the end of it (20 h next day) ( $T_f$ ). In order to analyze the impact of the selected time scale on the resulting daily  $k'$  value, this parameter was also calculated considering  $N_i$  as the abundance of organisms at

27/2 20 h,  $N_f$  as the abundance of organisms at the end of this 48-h period 1/3 20 h, and  $T_f - T_i$  as the 2-day gap between the initial and final samplings. In all cases, units of  $k'$  are  $\text{ind. days}^{-1}$ .

## Results

### Abiotic parameters

The 27 February and 1 March were “dull” days, while the 28 March was sunny. Air and water temperatures followed diel cycles, with air temperature showing a higher peak at noon on the sunny day (28/2), suggesting a strong dependence on solar radiation. Following sundown, water temperatures continued to be high at 20 h samplings (). Although both ponds are small and shallow, Musgos is smaller than Papúa (Table 1), which rendered it more sensitive to temperature changes. In spite of having a similar water temperature range, its surface was frozen on the three sampling occasions in which air temperature was  $0^\circ\text{C}$  or less. All environmental parameters listed in Table 2 showed similar coefficients of variation in both ponds in spite of very distinct absolute values. In both cases, all parameters varied more over day 1 (27/2 20 h to 28/2 20 h) than over day 2 (28/2 20 h to 1/3 20 h).

$\text{PO}_4\text{-P}$  concentrations were about 20-fold higher in Papúa pond than in Musgos pond (18.8–20.1 and  $0.90\text{--}1.11 \text{ mg L}^{-1}$ , respectively).  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$  concentrations in the former (11.7–14.1  $\text{mg L}^{-1}$ ) exceeded those of Musgos pond by 3 orders of magnitude ( $<0.01\text{--}0.06 \text{ mg L}^{-1}$ ), and  $\text{NH}_4\text{-N}$  constantly exceeded  $50 \text{ mg L}^{-1}$ , while in Musgos pond it varied between 0.05 and  $0.12 \text{ mg L}^{-1}$ . This was undoubtedly due to the heavy guano load supported by Papúa pond, while Musgos pond owed its high  $\text{PO}_4\text{-P}$  concentration to the washing out of the mosses around it. The nutrient enrichment in Papúa pond was accompanied by very high phytoplankton chlorophyll *a* concentrations (883–1,476  $\mu\text{g L}^{-1}$ ) and a constant oversaturation of dissolved oxygen (DO), which peaked to almost  $25 \text{ mg L}^{-1}$  (189 % saturation) in warm,

**Table 1** Location and maximum dimensions of Musgos and Papúa ponds

Pond	Musgos	Papúa
Location	64°09'26.6"S 60°57'25.5"W	64°09'36.8"S 60°57'16"W
Altitude (masl)	71	134
Maximum length (m)	5.37	13.7
Maximum width (m)	3	6.2
Maximum depth (cm)	15	48

**Table 2** Physical and chemical parameters measured in the studied ponds

Sample	Air temperature (°C)	Water temperature (°C)	pH	Conductivity (µS cm <sup>-1</sup> )	Dissolved oxygen (mg L <sup>-1</sup> )	Oxygen saturation (%)	PO <sub>4</sub> -P (mg L <sup>-1</sup> )	NO <sub>3</sub> -N (mg L <sup>-1</sup> )	NH <sub>4</sub> -N (mg L <sup>-1</sup> )	DIN (mg L <sup>-1</sup> )	Chlorophyll <i>a</i> (µg L <sup>-1</sup> )
<b>Musgos pond</b>											
27/2 13 h	-0.5	3.1	6.4	53	11.88	88	1.01	0.00	0.06	0.06	31.93
27/2 20 h	0.7	0.7	5.51	60	12.04	84	0.90	0.06	0.12	0.18	25.26
28/2 07 h	-0.5	1.2	5.80	66	11.75	82	0.98	0.03	0.08	0.11	48.18
28/2 13 h	4.6	7.3	6.43	60	14.72	123	0.97	0.09	0.10	0.19	25.76
28/2 20 h	1.8	7.1	5.88	62	11.75	97	1.02	0.00	0.06	0.06	No data
1/3 07 h	0.0	1.8	5.67	60	9.68	71	1.01	0.00	0.05	0.05	14.52
1/3 13 h	3.9	4.4	6.14	62	11.59	87	1.11	0.06	0.08	0.14	11.98
1/3 20 h	0.4	4.4	6.12	61	12.18	95	0.99	0.03	0.05	0.08	22.68
CV day 1	1.321	0.887	0.065	0.046	0.115	0.196	0.052	0.861	0.287	0.455	-
CV day 2	1.155	0.489	0.037	0.016	0.098	0.135	0.051	1.277	0.236	0.489	-
<b>Papúa pond</b>											
27/2 13 h	0.6	1.3	9.32	1,089	22.45	162	19.5	11.9	>50	61.9	883
27/2 20 h	0.0	1.0	7.69	1,199	22.60	162	19.3	12.5	>50	62.5	901
28/2 07 h	0.0	0.2	8.02	1,264	18.73	131	19.2	11.9	>50	61.9	1,015
28/2 13 h	7.2	3.8	9.62	1,212	24.53	189	20	14.1	>50	64.1	1,359
28/2 20 h	1.5	5.0	7.85	1,161	23.75	189	18.8	14.0	>50	64	941
1/3 07 h	0.5	2.0	7.26	1,178	23.00	169	20	11.7	>50	61.7	1,132
1/3 13 h	2.7	3.2	8.25	1,185	23.08	175	20.1	11.6	>50	61.6	1,476
1/3 20 h	0.0	3.5	8.84	1,202	20.57	157	19	12.1	>50	62.1	1,037
CV day 1	1.574	0.909	0.108	0.035	0.115	0.165	0.026	0.084	-	-	0.198
CV day 2	1.015	0.360	0.083	0.014	0.062	0.077	0.034	0.091	-	-	0.203

DIN Dissolved inorganic nitrogen, CV coefficient of variation. Day 1 27/2 20 h–28/2 20 h. Day 2 28/2 20 h–1/3 20 h. CV values not calculated for samples involving indetermined values (“no data” or “>50”)



sunny weather (28/2 13 h). DO was significantly correlated with water temperature ( $r = 0.714$ ,  $p < 0.05$ ) in this pond.

Multiple nonparametric correlations among abiotic parameters involving the two ponds revealed a set of strong correlations between conductivity, pH,  $\text{PO}_4\text{-P}$ ,  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ , dissolved oxygen (DO) and chlorophyll *a* (Spearman  $r = 0.640\text{--}0.862$ ,  $p < 0.01$ ). Also, there was a weaker correlation between air and water temperature (Spearman  $r = 0.593$ ,  $p < 0.05$ ). Clear environmental differences among both ponds accounted for these correlations, since very few of them held for each pond separately. Musgos pond showed a eutrophic character, with chlorophyll *a* ranging between 11.98 and 48.18  $\mu\text{g L}^{-1}$ . Dissolved oxygen varied between 9.68 and 14.72  $\text{mg L}^{-1}$ , representing 71 and 123 % saturation, respectively. pH was positively correlated with water temperature (Spearman  $r = 0.755$ ,  $p < 0.05$ ).

### Phytoplankton

Autotrophic picoplankton were mainly composed of phycocyanin-rich picocyanobacteria (PCy). Its absolute abundance in Musgos pond ( $3.12\text{--}9.77 \times 10^5$  ind.  $\text{mL}^{-1}$ ) was not only higher than in Papúa pond ( $1.85\text{--}2.52 \times 10^5$  ind.  $\text{mL}^{-1}$ ), but also accounted for most of the total phytoplankton density. Yet, in both ponds, the nano- and micro-sized fraction made up for most of the phytoplankton biovolume (Fig. 3).

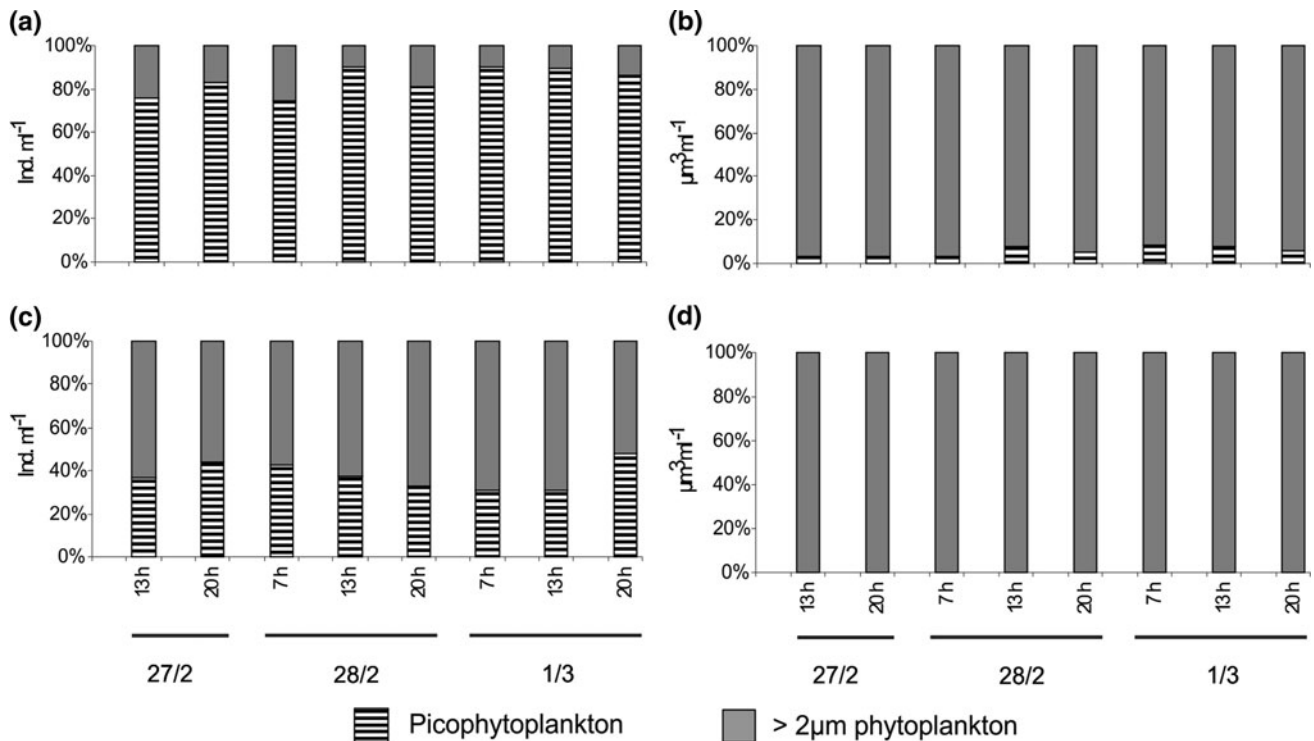
The taxonomic survey of the nano- and micro-sized phytoplankton revealed that both ponds were rich in species (Table 3), mainly Cyanobacteria, Chlorophyta and diatoms. Most Cyanobacteria from Musgos pond were planktonic Chroococcales and thin Oscillatoriales filaments, while thicker Oscillatoriales were more frequent in Papúa pond. The vast majority of Chlorophyta in both sites belonged to the order Volvocales. Although around 50 % of the species recorded in each pond were tycho planktonic, Musgos pond was strongly dominated by *Monomastix minuta* and *Gonium sociale*, which represented 86–93 and 1–3 %, respectively, of the nano + micro-sized algal density. The marked difference in the cell volume of these species accounted for subtle changes in their total abundances resulting in shifts in their dominance in terms of biovolume (Fig. 4). In Papúa pond, *Chlamydomonas obesa* made up for 82–92 % of the algal density and 86–97 % of the biovolume over the study period.

Even though the majority of the algae encountered in both ponds were strictly planktonic, the structure of these communities revealed by quantitative samples differed greatly between the two ponds as shown by the SIMI index (0.00035). The tracking of the community structures over successive samplings within each pond showed that they remained stable, with a high degree of similarity in both cases (all SIMI values  $\geq 0.99674$ ).

The relationship between chlorophyll *a* and density (or mean individual chlorophyll *a*) was one order of magnitude higher in Papúa pond ( $2.5\text{--}4.2 \times 10^{-3}$   $\mu\text{g ind.}^{-1}$ ) than in Musgos pond ( $1.0\text{--}3.9 \times 10^{-4}$   $\mu\text{g ind.}^{-1}$ ), on account of the larger cell volume of *Chlamydomonas obesa* compared to *Monomastix minuta*, which dominated the  $>2$   $\mu\text{m}$  phytoplankton abundance in the latter pond. Mean individual chlorophyll *a* showed an inverse relationship to abundance in both ponds ( $R^2 = -0.44$  for Papúa pond and  $R^2 = -0.51$  for Musgos pond) (Fig. 5), with rises in algal density (largely consisting of *C. obesa* and *M. minuta*, respectively) corresponding to declines in the amount of chlorophyll *a* per cell. This indicated the presence of more cells with smaller volumes, strongly suggesting the occurrence of cell division in both populations.

Daily net growth rates of the different plankton components differed according to the time scale considered (Table 4). As for the different phytoplankton size fractions and dominant algal species, we detected changes in the daily (24 h) scale that are overlooked when considering larger scales (whole period, 48 h) as the trends neutralize. This was especially evident in Musgos pond. In this case, day 1 presented high  $k'$  values almost reaching 1 ind.  $\text{day}^{-1}$  for the two phytoplankton size fractions, mainly represented by *Monomastix minuta*, while the net result for the 48-h period was positive but low for all phytoplankton studied components. In Papúa pond, the larger size fraction almost exclusively composed of *Chlamydomonas obesa* evidenced a slight decrease, while the picophytoplankton remained stable over the 48-h period. The population in Papúa pond at the end of February was in decline (negative values for  $k'$ ), but that of Musgos pond was still showing a net positive growth at the end of summer.

The ciliate community mainly comprised three morphotypes with distinct mean lengths (15, 24 and 54  $\mu\text{m}$ ), referred hereafter to as “small,” “medium” and “large,” respectively. In Musgos pond, small ciliates largely dominated the community over the study period in terms of abundance. Peaks of this size fraction occurring at noon were more distinct when considering their biovolume (Table 5; Fig. 6). In Papúa pond, the community was dominated by medium-sized ciliates, which accounted for more than 50 % of their abundance. Yet, the few large ciliates present made up for most of the ciliate biovolume from the second sampling onwards. As regards the growth rates (Table 4), total ciliates increased their  $k'$  values in Musgos pond, where changes in the abundances of median ciliates reflected those of *M. minuta*. Similarly, small ones increased over both day 1 and day 2, as well as picophytoplankton. Contrarily, in Papúa pond, total ciliates and each size fraction showed negative net growth rates, particularly small ciliates.



**Fig. 3** Relative proportion of the different phytoplankton size fractions to total phytoplankton abundance and biovolume throughout the study period (27/2/2003 to 1/3/2003). **a** Musgos pond abundance;

**b** Musgos pond biovolume; **c** Papúa pond abundance; **d** Papúa pond biovolume. Data were obtained from two replicates at each sampling event

## Discussion

### Abiotic parameters

As expected, characterization through chemical abiotic features revealed two remarkably different water bodies. While Musgos pond showed a eutrophic character, nutrient and chlorophyll *a* concentrations in hypertrophic Papúa pond were among the highest recorded in Antarctica (Hawes 1990; Izaguirre et al. 2003; Allende 2004), only surpassed by one chlorophyll *a* value observed by Spurr (1975), and later in the same season reached unparalleled values ( $5,785 \mu\text{g L}^{-1}$ , Mataloni pers. obs.). According to Lizotte (2008), the highest chlorophyll *a* concentration recorded so far in an Antarctic lake was measured in Otero Lake, also located in Cierva Point, which is submitted to the same mild climatic conditions and also fed by the drainage of the Gentoo rookery which encompasses Papúa pond. The location of this pond allows for large quantities of guano being washed to it and for penguins constantly using it during the crèche period. Molting is then the secondary source of ornithogenic organic matter in Papúa pond. Nutrient enrichment permitted a very active photoautotrophic community, as revealed by the constant oversaturation of dissolved oxygen (DO), already recorded in other hypertrophic Antarctic water bodies (Izaguirre et al.

2003). At Musgos pond, dissolved inorganic nitrogen (DIN) was calculated as the sum of  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$  and  $\text{NH}_4\text{-N}$ . In contrast to Papúa pond, DIN was less abundant than DRP and also more variable.

In spite of marked differences in trophic state, both ponds undergo parallel diel changes in their abiotic features (Table 2). These were stronger over sunny, warm day 1 (27/2 20 h to 28/2 20 h). Such conditions prompted algal photosynthesis, revealed by strong increases in dissolved oxygen saturation and pH at noon (13 h). In Papúa pond, this fact even caused a direct correlation among temperature and dissolved oxygen, which also reached unprecedented oversaturation values. In his study of a small pond from Signy Is., Davey (1993) found that the productivity of the inhabiting benthic mat was not limited by nutrient availability, but he could not separate the effects of irradiance and water temperature as productivity regulators. In this work, trophic state of the ponds and diel variations in photosynthesis following temperature and light changes also seem to underscore the importance of these two factors.

### Phytoplankton

In spite of their shallowness, both ponds were dominated by ephytoplanktonic communities, as also described for

**Table 3** Floristic composition of the phytoplankton in Musgos and Papúa ponds

Floristic list	Habitat	Musgos	Papúa
<b>Cyanobacteria</b>			
<i>Aphanocapsa elachista</i> W. et G.S. West	PLA	X	X
<i>Aphanocapsa</i> cf. <i>incerta</i> (Lemmermann) Cronberg et Komárek	PLA	X	X
<i>Aphanothece minutissima</i> (W. West) Komárková-Legnerová et Cronberg	PLA	X	
<i>Chamaesiphon subglobosus</i> (Rostafinski) Lemmermann	EPIL	X	X
<i>Cyanosarcina</i> sp.	BEN	X	
<i>Geitlerinema deflexum</i> (W. et G.S. West) Anagnostidis	PLA	X	
<i>Gloeocapsopsis aurea</i> Mataloni et Komárek	EPIL	X	
<i>Gloeocapsopsis</i> sp.	EPIL	X	
<i>Komvophoron</i> sp.	PLA	X	X
<i>Johannesbaptistia</i> sp.	PLA		X
<i>Leptolyngbya antarctica</i> (West & West) Anagnostidis et Komárek	MAT		X
<i>Leptolyngbya erebi</i> (W. & G.S. West) Anagnostidis et Komárek	PLA	X	
<i>Leptolyngbya fragilis</i> (Menegh.) Anagnostidis et Komárek	MAT	X	
<i>Leptolyngbya</i> cf. <i>vincentii</i> Komárek	MAT	X	
<i>Leptolyngbya</i> sp.	MAT	X	X
<i>Merismopedia tenuissima</i> Lemmermann	PLA	X	X
<i>Merismopedia</i> sp.	PLA		X
<i>Oscillatoria subproboscidea</i> W. et G.S. West	MAT		X
<i>Phormidesmis priestleyi</i> (Fritsch) Komárek et al.	EPIL		X
<i>Phormidium autumnale</i> (Agardh) Gomont	MAT		X
<i>Phormidium</i> cf. <i>koetzlitzii</i> (Fritsch) Anagnostidis et Komárek	MAT		X
<i>Pseudanabaena frigida</i> (Fritsch) Anagnostidis	PLA	X	
<i>Romeria nivicola</i> (Kol) Komárek O. et Komárek J.	CRYO		X
<i>Romeria</i> sp. 1	PLA	X	X
<i>Romeria</i> sp. 2	PLA		X
<i>Synechocystis</i> sp.	PLA		X
<i>Wolskyella filamentosa</i> Claus	PLA	X	
sarcinoid chroococcalean 1	BEN	X	
sarcinoid chroococcalean 2	BEN		X
<b>Chlorophyta</b>			
<i>Brachiomonas submarina</i> Bohlin	PLA	X	
<i>Chlamydomonas heterogama</i> Gerloff	PLA	X	X
<i>Chlamydomonas intermedia</i> Chodat	PLA	X	
<i>Chlamydomonas moewusii</i> Gerloff	PLA	X	
<i>Chlamydomonas nivalis</i> (Bauer) Wille	CRYO		X
<i>Chlamydomonas obesa</i> Ettl	PLA		D
<i>Chlamydomonas subcaudata</i> Wille	PLA		X
<i>Chlamydomonas tetravacuolata</i> Ettl	PLA	X	
<i>Chlamydomonas</i> sp. 1	PLA	X	
<i>Chlamydomonas</i> sp. 2	PLA	X	X
<i>Chlorella</i> sp.	PLA	X	
<i>Chlorococcum</i> sp.	EDA	X	X
<i>Chloromonas rosae</i> (Ettl H. et O.) Ettl	PLA	X	
<i>Cosmarium</i> sp.	PLA		X
<i>Gonium sociale</i> (Dujardin) Warming	PLA	SD	
<i>Monomastix minuta</i> Skuja	PLA	D	
<i>Monoraphidium contortum</i> (Thuret) Komárková-Legnerová	PLA	X	X

**Table 3** continued

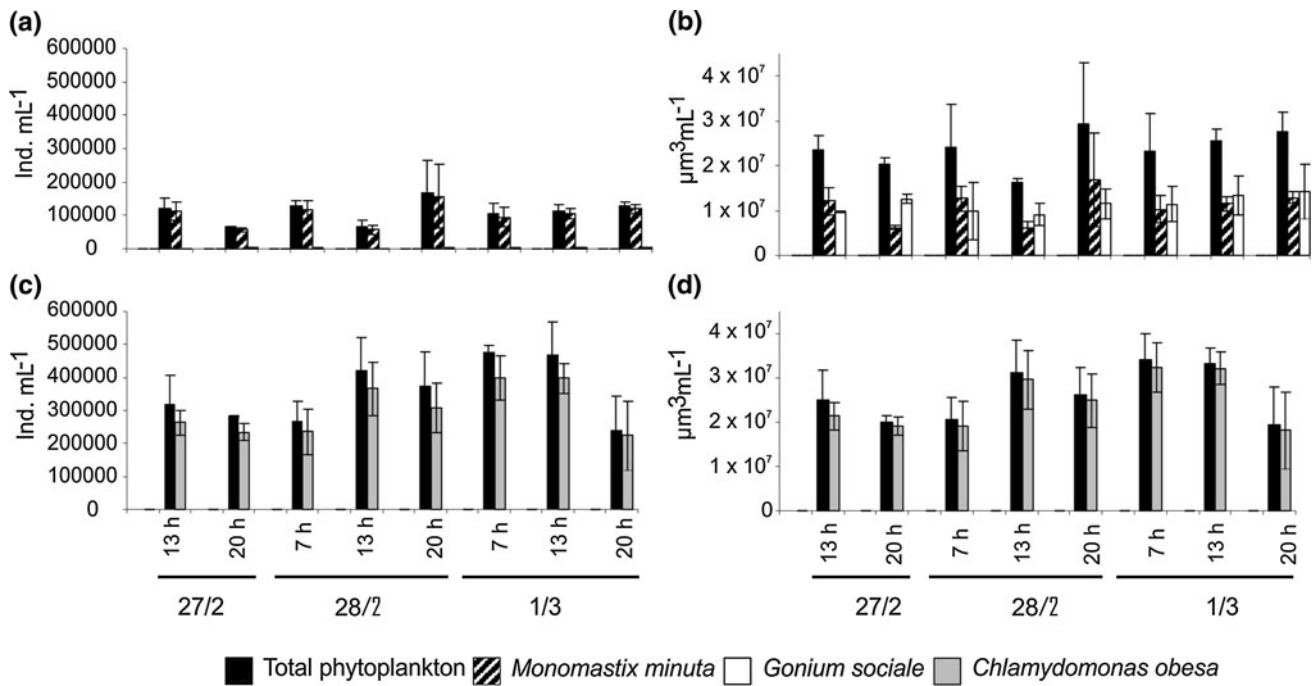
Floristic list	Habitat	Musgos	Papúa
<i>Monoraphidium minutum</i> (Nägeli) Komárková-Legnerová	PLA	X	
cf. <i>Prasiococcus calcarius</i> (Boye Petersen) Vischer	EPIL		X
<i>Pseudosphaerocystis</i> sp.	PLA	X	
<i>Raphidonema nivale</i> Lagerheim	CRYO		X
<i>Tetraedron minimum</i> (A. Braun) Hansgirg	PLA	X	
<b>Bacillariophyceae</b>			
<i>Achnanthes coarctata</i> var. <i>rhomboidea</i> Tarnavski et Jitariu	TYC	X	X
<i>Achnanthes germainii</i> Manguin	TYC	X	X
<i>Achnanthes kryophila</i> Petersen	TYC	X	X
<i>Achnanthes</i> sp.	TYC	X	
<i>Caloneis molaris</i> (Grunow) Krammer	TYC		X
<i>Fragilaria capucina</i> var. <i>rumpens</i> (Kützing) Lange-Bertalot	TYC	X	
<i>Gomphonema parvulum</i> Kützing	TYC		X
<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow	TYC	X	
<i>Luticola muticopsis</i> (V. Heurck) D.G. Mann	TYC	X	X
<i>Navicula gallica</i> (W. Smith) Van Heurck	TYC	X	X
<i>Navicula tabellariaeformis</i> Krasske	TYC	X	X
<i>Nitzschia homburgiensis</i> Lange-Bertalot	TYC	X	X
<i>Orthoseira rooseana</i> (Rabenhorst) O'Meara	TYC	X	X
<i>Pinnularia borealis</i> Ehrenberg	TYC	X	X
<i>Pinnularia microstauron</i> (Ehrenberg) Cleve	TYC	X	X
<i>Pinnularia stomatophora</i> (Grunow) Cleve	TYC	X	X
<b>Chrysophyceae</b>			
<i>Ochromonas</i> sp.	PLA	X	
Small flagellated Chrysophyceae	PLA	X	X
Flagellated Chrysophyceae sp.1	PLA		X
Flagellated Chrysophyceae sp. 2	PLA	X	
Chrysophycean cysts	BEN	X	X
<b>Tribophyceae</b>			
<i>Heterococcus</i> sp.	EPIL	X	
Total species number		53	45

D dominant, SD subdominant (see text for relative frequencies). *Species main habitats* PLA planktonic, BEN benthic, EPIL epilithic, CRYO cryoseston, EDA edaphic, TYC tychoplanktonic

hypertrophic Pingüi pond in Hope Bay, Antarctic Peninsula (Allende 2004). This pond was dominated by the picosized fraction in terms of density, while the nanosized fraction represented most of the biovolume. The same occurs in Musgos pond, while Papúa pond, which has even higher nutrient and chlorophyll *a* concentrations, is dominated by flagellated nanophytoplankton both in terms of density and biovolume. This fact adds confirmation to the idea that the contribution of the picosized fraction to total biomass decreases with increasing trophic state, as recognized worldwide (Sommaruga and Robarts 1997; Vörös et al. 1998; Agawin et al. 2000). In particular, the picophytoplankton from Musgos and Papúa ponds were dominated by phycocyanin-rich picocyanobacteria, reinforcing the accepted opinion that these organisms are relatively more

abundant in the eutrophic end of the trophic spectrum (Stockner et al. 2000; Callieri 2008 and cites therein; Silvano et al. 2011). Phycocyanin-rich picocyanobacteria are better adapted to harvest the red wavelengths characteristic of eutrophic and discolored waters, as compared to phycoerythrin-rich picocyanobacteria, which would be more efficient under the blue and green light conditions prevailing in oligotrophic ecosystems (Sommaruga and Robarts 1997).

Taxonomic composition of the nano- and micro-sized phytoplankton included a large number of tychoplanktonic species, most of them heavy benthic diatoms which did not account significantly in either abundance or biovolume. Some are very common species (e.g., *Hantzschia amphioxys*, *Luticola muticopsis*, *Pinnularia microstauron*,



**Fig. 4** Density and biovolume of >2 µm phytoplankton and dominant species throughout the study period (27/2/2003 to 1/3/2003). **a** Musgos pond abundance; **b** Musgos pond biovolume; **c** Papúa pond

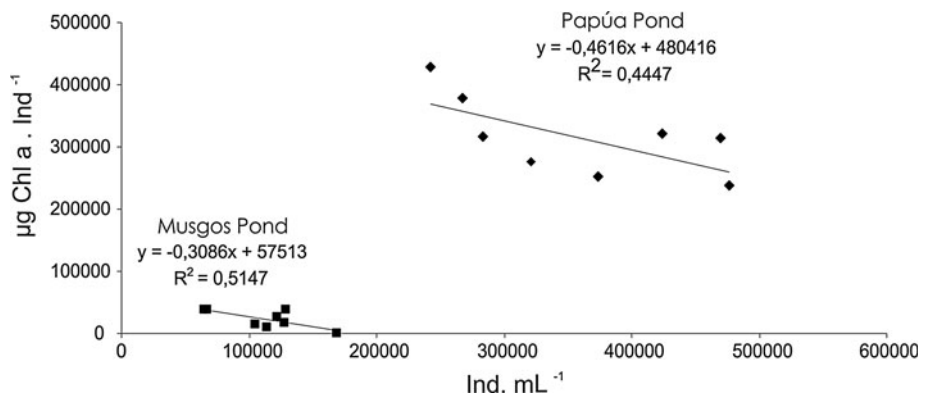
abundance; **d** Papúa pond biovolume. Data were obtained from two replicates at each sampling event. Bars show ± one standard deviation

*Pinnularia borealis*) and have already been encountered in a large variety of environments in Cierva Point (Mataloni and Tesolín 1997; Tesolín et al. 1997; Mataloni et al. 1998, 2005; González Garraza et al. 2011). A few epilithic Cyanobacteria such as *Chamaesiphon subglobosus* and *Gloeocapsopsis aurea* were already recorded from Cierva (Mataloni and Komárek 2004; Mataloni et al. 2005), as well as a number of mat-forming Oscillatoriales which dominate ornithogenic soils around the same rookery Papúa pond is located in (e.g., *Phormidium autumnale*, *Phormidesmis priestleyi*, *Oscillatoria subproboscidea*) (Mataloni and Tell 2002; Mataloni et al. 2010). Papúa pond, which is located at a higher altitude, and fed by snow thawing, also hosted a few individuals of the cryobionts *Raphidonema nivale* and *Romeria nivicola*, the former of

which was previously recorded by Mataloni and Tesolín (1997) in snow and ice from Cierva Point. Except for these two cold-adapted species, our results show an active propagule exchange of more generalist taxa between different environments (ponds, soils, snowfields, streambeds) as suggested by Tesolín et al. (1997). This was favored in this case by the small size of ponds, the high bird activity in Papúa pond and the ephemeral character of Musgos pond, which was observed to dry out in other summers (Mataloni pers. obs.).

As predicted by our hypothesis, the phytoplankton communities from both ponds showed distinct structures linked to trophic states. In their characterization of 16 microlimnotopes from this area through a single sampling, Tesolín et al. (1997) recorded the second highest

**Fig. 5** Relationship between chlorophyll *a*/phytoplankton abundance versus phytoplankton abundance in Papúa and Musgos ponds throughout the study period (27/2/2003 to 1/3/2003). Data were obtained from two replicates at each sampling event



phytoplankton density at Musgos pond (No. 5 according to these authors), which was at the time dominated by small flagellated chrysophyceans. Although these authors did not sample Papúa pond, it is worth noticing that two small ponds within the same rookery (No. 12 and 13) showed the highest concentrations of dissolved nutrients in general and of ornithogenic NH<sub>4</sub>-N in particular, as well as the highest pH values and chlorophyll *a* concentrations, similarly to Papúa pond. One of them was dominated by flagellated Volvocales and the other one by benthic filamentous Oscillatoriales.

In spite of the high species richness, almost 100 % of the algal abundance and more than 90 % of the biovolume was represented by euplanktonic flagellated microalgae (mainly Chlorophyta) in both environments. This coincides with the observed success of flagellated Chlorophyta in eutrophic to hypertrophic water bodies around Antarctica (Bell and Laybourn-Parry 1999; Vinocur and Unrein 2000; Mataloni and Pose 2001; Allende and Pizarro 2006). In particular, Otero Lake, the largest water body in Cierva Point, is to date the most hypertrophic Antarctic Lake (Lizotte 2008) dominated by a *Chlamydomonas* species. Flagellated Chlorophyta belong to the Group V in the morphologically based functional groups (MBFG) classification of the phytoplankton given by Kruk et al. (2010). Kruk and Segura (2012) proposed a habitat template relating the dominance of different MBFG to sets of environmental conditions. In their scheme, Group V flagellates would dominate turbid, meso- to eutrophic

**Table 5** Minimum–maximum abundances of total ciliates and each of the three size fractions over the study period

Ciliates (ind. mL <sup>-1</sup> )	Musgos	Papúa
Small (15 μm)	44–313	0–414
Medium (24 μm)	0–39	210–1,698
Large (54 μm)	0–5	0–263
Total ciliates	48–342	336–2,083

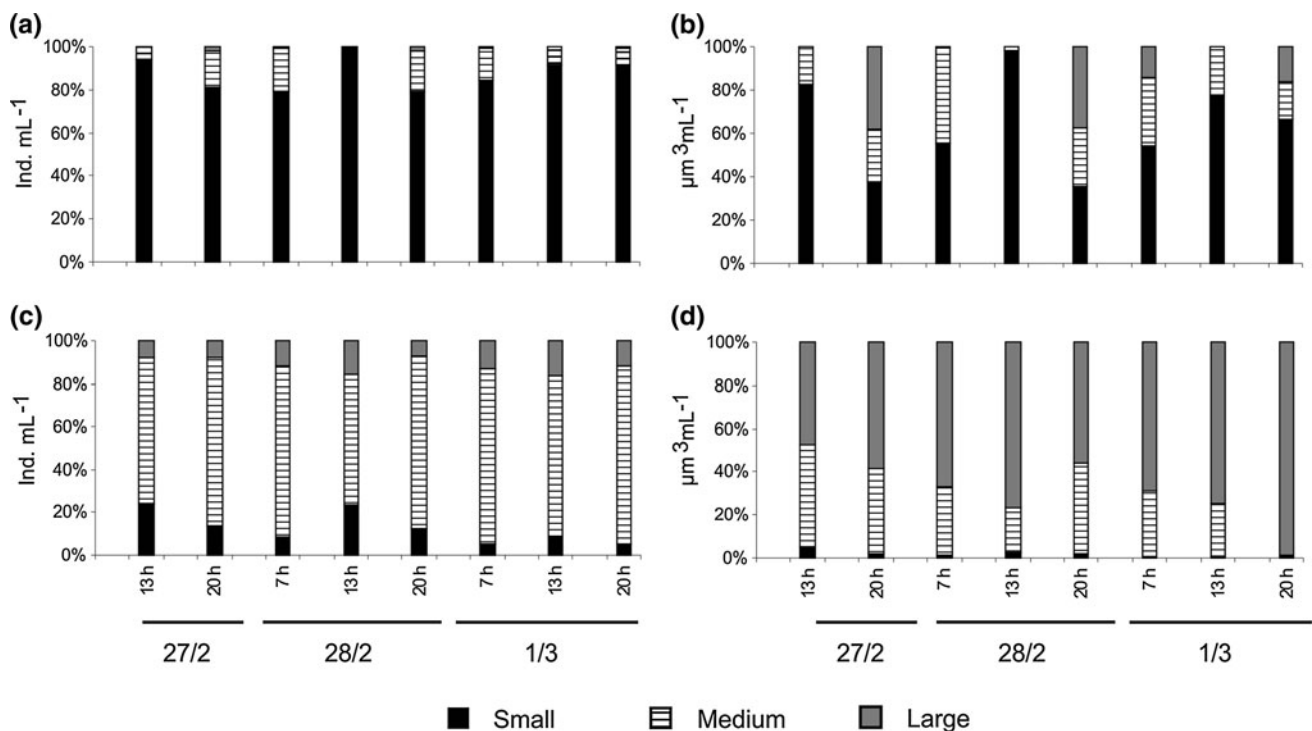
environments, while turbid, hypertrophic ones would be dominated by K-selected cyanobacterial filaments (Group III). Therefore, it is interesting to note that, in spite of being adapted to low light, high nutrient conditions, slow-growing cyanobacterial filaments usually dominate benthic communities but not planktonic ones in Antarctic ponds (Davey 1993; Vincent et al. 1993; Taton et al. 2003). On the contrary, both these eutrophic to hypertrophic shallow ponds as well as many enriched Antarctic freshwater bodies are usually strongly dominated by Group V flagellates formerly classified as C-strategists by Reynolds (1988), most probably on account of their tolerance to grazing and faster reproduction in low temperatures.

As hypothesized, short-term environmental variations (spanning for shorter times than growth rates) were not reflected in changes in the community composition, as revealed through the high SIMI index values and in accordance with Harris (1986) view that organisms filter, integrate and average the external fluctuations and respond to a time-

**Table 4** Net growth rates (*k'*) for the studied planktonic components of Musgos pond and Papúa pond

	Daily <i>k'</i> (ind. day <sup>-1</sup> )		Period <i>k'</i> (ind. day <sup>-1</sup> )
	Day 1 (day I-20 h/day II-20 h)	Day 2 (day II-20 h/day III-20 h)	Whole period (day I-20 h/day III-20 h)
<i>Papúa pond</i>			
Total >2 μm phytoplankton	0.276	-0.434	-0.079
<i>Chlamydomonas obesa</i>	0.270	-0.321	-0.025
Total <2 μm phytoplankton	-0.205	0.205	0.000
Total ciliates	-0.646	-1.085	-0.865
Large ciliates	-0.730	-0.644	-0.687
Median ciliates	-0.623	-1.053	-0.838
Small ciliates	-0.738	-1.878	-1.308
<i>Musgos pond</i>			
Total >2 μm phytoplankton	0.952	-0.278	0.337
<i>Monomastix minuta</i>	1.021	-0.277	0.372
<i>Gonium sociale</i>	-0.089	0.214	0.063
Total <2 μm phytoplankton	0.824	0.099	0.461
Total ciliates	0.777	0.413	0.595
Large ciliates	—	—	—
Median ciliates	0.860	-0.486	0.187
Small ciliates	0.760	0.556	0.658

Calculations are based on averages of two replicate data for each pond and plankton component



**Fig. 6** Relative proportion of the different ciliate size fractions (small–medium cell volume up to  $2 \times 10^3 \mu\text{m}^3$ -, medium–medium cell volume  $3.5 \times 10^3 \mu\text{m}^3$ - and large–medium cell volume  $50 \times 10^3 \mu\text{m}^3$ ) to total ciliate abundance and biovolume throughout the study

period (27/2/2003 to 1/3/2003). **a** Musgos pond abundance; **b** Musgos pond biovolume; **c** Papúa pond abundance; **d** Papúa pond biovolume. Data were obtained from two replicates at each sampling event

weighted average signal. Vincent (2000) advanced the idea that Antarctic environments subjected to wide environmental variation ranges would select for generalist microorganisms able to integrate such variations over short periods of time and that cosmopolitan species would likely possess adequate genotypes. Therefore, the communities of ponds displaying high diel variations would be expected to be dominated by such cosmopolitan taxa. All three species dominating both ponds (*Chlamydomonas obesa* in Papúa pond, *Monomastix minuta* and *Gonium sociale* in Musgos pond) have been described from other continents, although none of them is widespread across different types of environments. Nozaki and Ohtani (1992) demonstrated that an Antarctic strain of *G. sociale* had developed cold adaptation as opposed to a Japanese strain. There are a number of other examples of Antarctic microalgal species able to establish and dominate one given habitat over many years, but hardly able to thrive in nearby, apparently similar environments, as discussed by Mataloni and Vélez (2009). Therefore, it seems rather probable that many of these “generalist” species are in fact specialized in integrating variations just in those dimensions of their ecological niches likely to vary widely in Antarctica such as temperature. Comparison among genotypes and tolerance ranges of strains from Antarctica and other continents would greatly help envisaging evolutive adaptation paths of the Antarctic phycoflora.

Our third hypothesis was that at this short time scale, the microalgae would respond to environmental variations at population levels, reflected on changes in the chl *a*/abundance ratio and in the abundances of the dominant species, which should have high net reproduction rates in order to outcompete other organisms. In both ponds, the inverse relationship between the mean individual chlorophyll *a* and the abundance strongly suggested the existence of doubling events over our study period. This would be in accordance with previous results, since according to Kruk et al. (2010) average doubling time for Group V strategists is 0.89 doublings day<sup>-1</sup>. In an experiment conducted in Boeckella Lake (Hope Bay), which is also dominated by nanoflagellates, Almada et al. (2004) found algal growth consistent with doubling times of 0.8–1.8 doublings day<sup>-1</sup> given by Reynolds (1993) for C-strategists. Therefore, in view of the very high relative abundances of *C. obesa* and *M. minuta*, we expected to find positive *k'* values for both species. In Papúa pond algal densities remained almost constant over the 48-h period, though with positive *k'* values on sunny, warm day 1 and negative ones on day 2. The same decreasing trend in *k'* values was verified in Musgos pond, yet yielding a positive growth over 48 h. Growth of natural populations results from the balance between reproduction and losses by sedimentation and grazing. According to Harris (1986 and citations therein), the former would be

negligible for flagellated microalgae. Grazing by ciliates, instead, would account for the observed  $k'$  values.

The size classes of ciliates in both ponds represent distinct trophic niches, as those established by Mataloni et al. (2000a) in their study of hypertrophic Otero Lake. In this lake, different size fractions dominated over consecutive summers (Mataloni et al. 2000b; Izaguirre et al. 2001). Interestingly, the latter authors recorded a strong rise in small ciliates coupled with that of bacterio- and picophytoplankton, as well as coupled abundance peaks among median ciliates and *Monomastix minuta*. This is in accordance with the fluctuations in  $k'$  values observed in Musgos pond. On the other hand, medium and large ciliates are known to feed on nanoplanktonic Volvocales (Mataloni et al. 2000b) which would explain their very high abundances at Papúa pond. As discussed by these authors, the absence of metazooplankton in water bodies of this area allows for such high ciliate densities, since they would act as top predators in these 2-level food webs. Interestingly, Zingel et al. (2007) found that ciliates were potentially important grazers of the nanophytoplankton fraction in an Estonian shallow, turbid, naturally eutrophic lake due to a failure in metazooplankton regulation. Camacho (2006) thoroughly reviewed the experimental evidence of top-down regulation in Antarctic microbial food webs. In all studied systems, the calanoid *Boeckella poppei* acted as the top predator. According to Almada et al. (2004), experimental copepod removal positively affected the densities of nanoflagellates in Boeckella Lake. Other studies (Laybourn-Parry et al. 1996; Butler et al. 2005) focused on the cascading regulation exerted by *B. poppei* on the picoplankton via ciliates. In their conceptual model of the trophic webs in Limnopolar Lake, Rochera et al. (2011) showed that nanophytoplankton would be the food source for micro- and mesozooplankton (rotifers and copepods, respectively), while ciliates would predate on bacteria and picophytoplankton. Our results confirm the only references to regulation of autotrophic nanoflagellates by ciliates in maritime Antarctica, which are those from Otero Lake, Cierva Point.

As a general conclusion, parallel diel variation of the abiotic environment of Antarctic ponds accounted for similarities among the structure of their phytoplankton communities, which were dominated by the same type of strategists, that is, ephytoplanktonic flagellated Chlorophyta belonging to Group V sensu Kruk et al. (2010) accompanied mainly by phycocyanin-rich picocyanobacteria. Distinct taxonomic composition of these communities, in turn, followed the differences in trophic state. The three samples per day regime conducted in the present study allow a recognition that the community structure in these fluctuating ponds is stable in the short term as revealed by the SIMI index. It also successfully detected day-to-day changes in  $k'$  values of the dominant species and their

potential predators. The peculiar 2-level trophic webs of these systems, in which heterotrophic flagellates are particularly scarce, highlight the importance of ciliates as potential regulators of all phytoplankton size fractions, which deserves further investigation through controlled in situ experiments.

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