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ORIGINAL PAPER

Responses of a Maritime Antarctic lake to a catastrophic draining event under a climate change scenario

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Abstract The limnological features of Lake Boeckella, the main water body of Esperanza/Hope Bay (Antarctic Peninsula), were evaluated over a 16-year period, under a climate change context evidenced by the increasing air temperature trend reported for this region for the last 50 years. We analyzed the physicochemical and phytoplankton data of the lake obtained from 1991 to 2007 during the austral summers. At the beginning of January 2001, a sudden water level drop (~3 m) occurred in Lake Boeckella as a consequence of an extremely high water discharge to the sea. This was triggered by the progressive thawing of the permafrost in the basin of the system. After this disturbance, nutrients, conductivity, chlorophyll *a* (Chl *a*) and picoplankton density showed strong peaks. The pre-draining and post-draining periods showed significant differences for most of the limnological variables analyzed. Secchi disk depth significantly decreased throughout the study period, resulting in a thinner euphotic layer. Chrysophyceae and Volvocales dominated the >2 µm phytoplankton fraction in the lake, but from 2004 onwards, other small-sized eukaryotic algae (3–5 µm) also became very abundant. Autotrophic picoplankton showed a significant peak during the summer when the water level decreased. A shift in their composition was observed through the study period: in 1998, picocyanobacteria were numerically dominant; from 2002 onwards, picoeukaryotes increased and became dominant in 2004. This study suggests that climate change may trigger the thawing of the permafrost in the catchments of Maritime Antarctic lakes, leading to catastrophic draining events, which favor natural eutrophication processes.

Keywords Catastrophic draining event · Lake · Phytoplankton · Permafrost · Maritime Antarctica · Climate change

Introduction

Two climatic zones are recognized in the Antarctic Peninsula: the polar maritime zone in the western side and the polar continental zone in the east (Martin and Peel 1978). While temperature inter-annual variability is high, mean annual air temperatures of the Antarctic Peninsula generally range between −3 and −10°C in the western side along the 63°S to 73°S transect and between −5 and −17°C in the east coast along a similar transect (Vaughan and Doake 1996).

Over the last century, climate change has occurred in the Antarctic Peninsula and associated archipelagos. This region has experienced one of the most rapid air temperature increases on Earth: about 2°C on average (King 1994; Smith et al. 1996; King and Harangozo 1998; Skvarca et al. 1998; Vaughan et al. 2003; Convey et al. 2009; Turner et al. 2009). This rapid warming is associated with the instability of some Antarctic Peninsula ice shelves (Ingólfsson et al.

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2003). In particular, an increasing air temperature trend was reported for Esperanza/Hope Bay, located at the north end of the Antarctic Peninsula (Convey 2006). Deviations in precipitation patterns are also associated with climate change. Modeling approaches have predicted a general increase in precipitation in the Antarctic coastal zone (Krinner et al. 2007). The studies reviewed by Convey (2006) support this prediction for Maritime Antarctica.

An important direct effect of the increase in air temperature is the thawing of the permafrost. This renders major consequences in the biogeochemical composition of fresh waters due to the immediate release of easily leached compounds that can be transported to streams and lakes (Lyons and Finlay 2008 and citations therein). The permafrost may also contain considerable stocks of ancient organic matter that can be released during melting (Quesada et al. 2006).

Different studies acknowledge lakes as good sentinels of global climate change, as they rapidly sense environmental variations (Adrian et al. 2009 and citations therein). Lakes are also integrators, as their sediments constitute archives of past responses to climate change (Williamson et al. 2009). In Antarctica, long-term investigations conducted at Signy Island (Quayle et al. 2002, 2003) have shown a decline in the permanent ice cover, coinciding with an almost 1°C rise in summer air temperatures since the 1950s. These studies showed that mean winter chlorophyll *a* (Chl *a*) and dissolved reactive phosphorus (DRP) concentrations have significantly increased in several oligotrophic lakes of this region. Likewise, in the Arctic, important changes associated with the climate warming have been reported for Alaskan lakes (Engstrom et al. 2000), where waters have become enriched in dissolved organic carbon due to changes in watershed vegetation and soil conditions. Corcoran et al. (2009) reported changes in nutrients, cations, Chl *a* and invertebrates in wetlands from the boreal forest of Northeast Alaska, and studies in Northern Siberia have indicated that soil- and permafrost-bound dissolved organic carbon and nutrients are apparently being released into rivers and lakes (Neff et al. 2006). Global warming also results in shifts in the timing of ice formation and thawing (Magnuson et al. 2000).

The lakes located at Hope Bay (Antarctic Peninsula) were surveyed by our research group from 1991 until 2007. These studies provided taxonomic and ecological baseline information on the planktonic and epilithic communities of the lakes and streams of the region (Vinocur and Izaguirre 1994; Tell et al. 1995; Vinocur and Pizarro 1995; Izaguirre et al. 1998, 2003; Pizarro et al. 2002, 2004). In particular, Lake Boeckella, the main water body at Hope Bay, was intensively studied during several austral summers (Izaguirre et al. 1993, 1996, 2003; Allende and Izaguirre 2003; Unrein et al. 2005).

In the present study, we analyzed the changes in the limnological features and phytoplankton community in Lake Boeckella throughout the above-mentioned 16-year period (1991–2007). We assessed the responses of the lake to the catastrophic draining disturbance occurred during the 2001-austral summer, under the frame of a warming scenario in Hope Bay.

Study site

Hope Bay is located at the northern end of the Antarctic Peninsula (63°23′S; 56°59′W), in an area of cold moist maritime climate (Fig. 1). This region encompasses numerous shallow lakes of which Lake Boeckella is the largest (Izaguirre et al. 1998). Most of these lakes receive water from melting glaciers and snowfields during the summer period. Lake Boeckella is placed in a fluvio-glacial depression dammed by moraine sediments, which at the south-western margin are covered by a thick layer of guano derived from a nearby penguin (*Pygoscelis adeliae*) rookery. Soil profiles in the lake's catchment show considerable quantities of phosphate in different chemical forms as a result of present and past bird activities—relict soils—(Tatur 1989). Lake Boeckella is the main source of drinking water for the Argentinean Esperanza Station. It is situated at an altitude of 49 m a.s.l., 650 m away from the seashore. It receives melting water from Mount Flora and a nearby glacier and has a natural outlet to the sea. The historical morphometric data of the lake before 2001 are maximum depth 4 m; mean depth 1.84 m; surface area 67,454 m^2; volume 124,097 m^3 (Izaguirre et al. 1993). It is usually ice-free during the whole austral summer (December to March) and exhibits a cold polymictic mixing regime. According to our previous studies, it can be classified as meso-eutrophic (Izaguirre et al. 1998, 2003).

Catastrophic disturbance in Lake Boeckella

At the beginning of January 2001, a sudden and remarkable water level drop (~3 m) occurred in Lake Boeckella overnight, owing to the progressive thawing of the permafrost in the lake's basin, which caused an extremely high water discharge to the sea (Izaguirre and Almada 2001). Therefore, the lake's surface area and volume diminished, and some islands appeared. The remaining lake volume was about 22,923 m^3 (ca. 19% of its original volume). Since the water supply of the Esperanza Station was at risk, and in order to restore the original water level, a dam was built at the mouth of the outlet from 2001 to 2002. Once dammed, the lake recovered the historical water levels; its present volume is about 140,000 m^3 (Ermolin 2003). The disturbance event, of catastrophic magnitude, may be linked to a

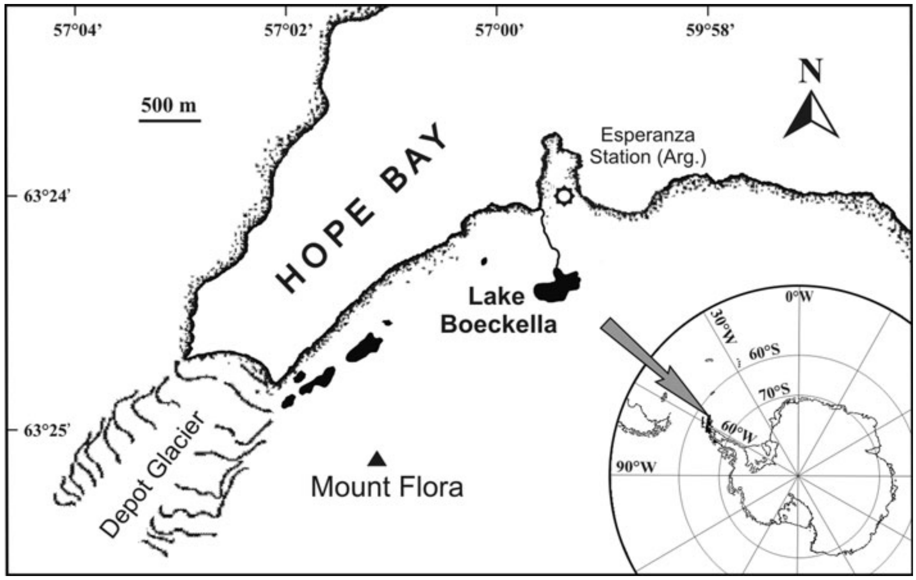

Fig. 1 Map of Hope Bay showing the location of Lake Boeckella

regional process of air temperature increase that has been going on for the last 50 years in the region.

Materials and methods

We studied Lake Boeckella during seventeen austral summers (in general January–February) from 1991 to 2007. In most cases, we collected the samples weekly throughout the summer. Due to logistic constraints, we did not measure all the variables on all the occasions.

We measured several physical and chemical variables sub-superficially at a single sampling point where the maximum depth was about 2 m. We measured temperature, pH, conductivity and dissolved oxygen with Hanna HI8314 and HI8033 portable meters (Hanna Instruments, USA) and estimated transparency with a Secchi disk. We determined phosphate, nitrate + nitrite and ammonium concentrations using a Hach® DR/2010 spectrophotometer and their corresponding reagent kits (the detection limit for all nutrients was of 0.001 mg l^{-1}). Samples for phytoplankton chlorophyll (Chl *a*) and nutrient analyses were filtered through Whatman GF/F. We determined Chl *a* concentrations, corrected for phaeopigments, by spectrophotometry, both before and after acidification (HCl 0.1 N), using hot ethanol (60–70°C) as a solvent (Nusch 1980) and used the equations by Lorenzen (1967) for the calculations.

We took sub-surface phytoplankton samples for quantitative analyses of the >2 µm size fraction and preserved them with acidified 1% Lugol's iodine solution, and counts were performed using an inverted microscope according to Utermöhl (1958). From 1998 to 2007, samples for the estimation of picophytoplankton (fraction <2 µm) were also obtained and preserved with glutaraldehyde 2% (final concentration), and counts were carried out using epifluorescence microscopy. 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). We examined each filter for pigment autofluorescence under 1,000× magnification, using a Zeiss Axioplan microscope equipped with an HBO 50 W 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).

Additionally, in the 2003 and 2004 austral summers, we took samples for flow cytometry analyses; 4 ml of lake water was fixed immediately with cold 10% glutaraldehyde (1% final concentration), left in the dark for 10 min at room temperature and then stored at −70°C. A FacsCalibur (Becton & Dickinson) flow cytometer equipped with a blue laser (15 mW) Argon-ion laser (488 nm emission) and a red laser (635 nm) diode was used. At least 30,000 events were acquired for each sample. Fluorescent beads (1 µm, Fluoresbrite carboxylate microspheres, Polysciences Inc., Warrington, PA) were added at a known density as internal standards. Data were analyzed with the Paint-A-Gate software (Becton & Dickinson). In order to analyze the changes in physical, chemical and biological variables related to the catastrophic natural disturbance occurred in 2001, we compared the data from the pre-draining period (1991–2000) and the post-draining period (2001–2007) using the Mann–Whitney (M–W) rank-sum non-parametric test (Zar 1999).

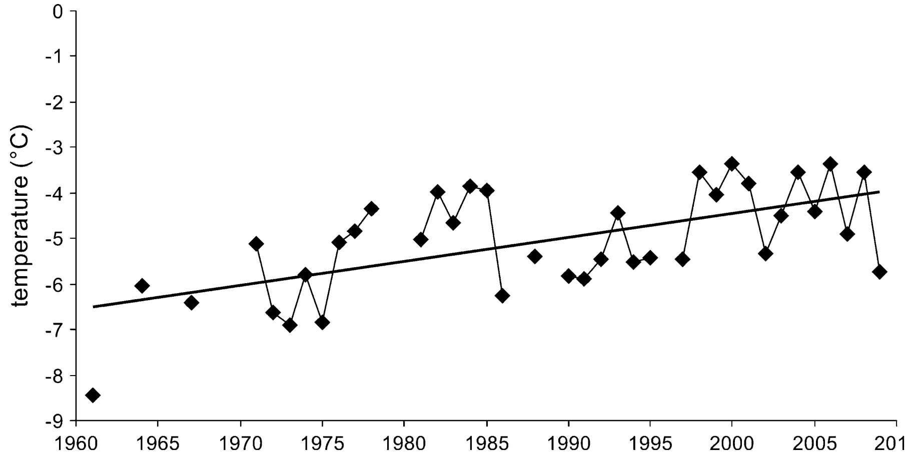

Fig. 2 Time series of annual mean temperature at Hope Bay. Data provided by the National Meteorological Service of Argentina

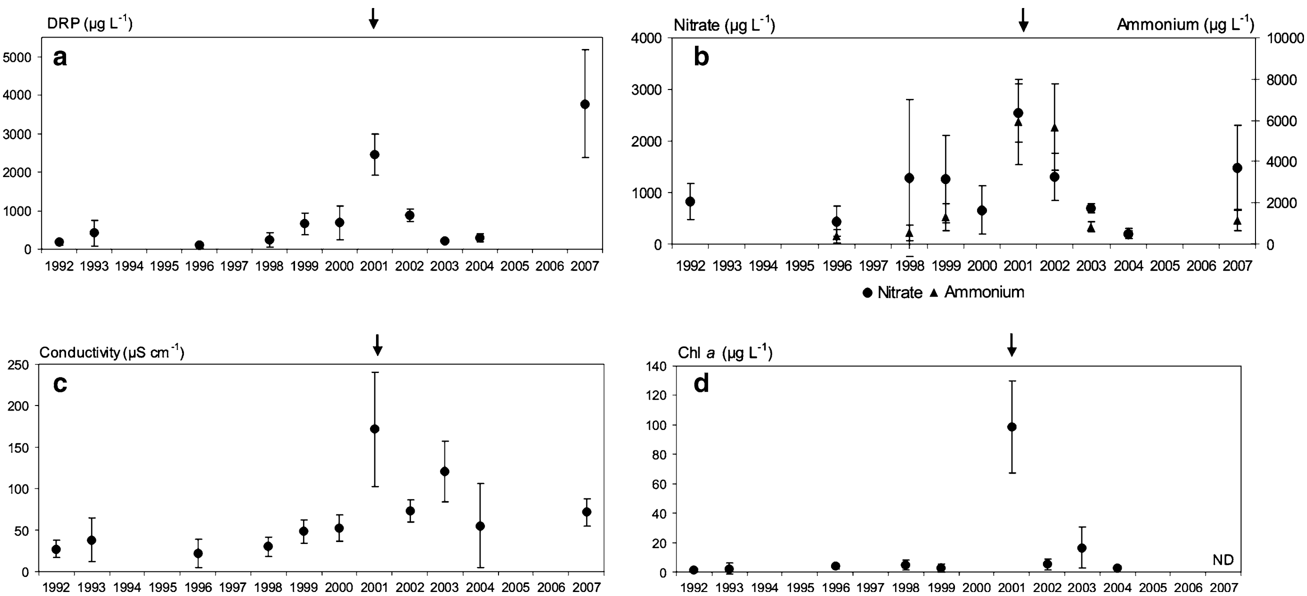

Fig. 3 Variations in summer mean values of **a** dissolved reactive phosphorus (DRP); **b** nitrate and ammonium; **c** conductivity; **d** phytoplanktonic chlorophyll *a* in Lake Boeckella over the 16-year period studied. The *arrows* indicate the year of the draining event. *ND* No data

Results

According to the data provided by the National Meteorological Service of Argentina, a significant increasing trend of annual mean air temperature ($P < 0.0001$; $n = 37$; $R^2 = 0.4$) was observed at Hope Bay from 1961 to 2009 (Fig. 2).

Throughout this 16-year period, Lake Boeckella underwent important changes in its physical and chemical variables. Dissolved reactive phosphorus (DRP) increased one order of magnitude from 1992 (mean value 177.5 µg l^{-1}) to 2007 (mean value 3,775 µg l^{-1}) (Fig. 3a), and differences between pre-draining and post-draining periods were significant (U_{M-W} 129.5; $P = 0.000005$).

In contrast, the dissolved inorganic nitrogen forms showed no increasing trend. However, a strong peak of ammonium concentration was recorded in 2001, when the water level dropped. Values remained high until 2002 (Fig. 3b). While ammonium concentrations generally ranged between 29 and 2,300 µg l^{-1}, in 2001–2002 it increased from 3,700 to 8,000 µg l^{-1}. Both nitrates and ammonium showed significant differences between pre-draining and post-draining periods (nitrates: U_{M-W} 242.5, $P = 0.034$; ammonium: U_{M-W} 124.0, $P = 0.0005$). Nitrate concentrations showed little inter-annual variability. Their concentrations fluctuated within each summer period associated with the thaw-freeze cycles (data not shown), with values varying from 53 to 4,853 µg l^{-1} for the whole study period. Nitrates concentrations were always much lower than those of ammonium. Mean summer values of the ammonium/nitrate ratio ranged between 0.85 and 1.16 prior to the disturbance, reached their highest values in 2001 and 2002 (2.57–4.51) after the water level drop and then decreased (0.93–3.14).

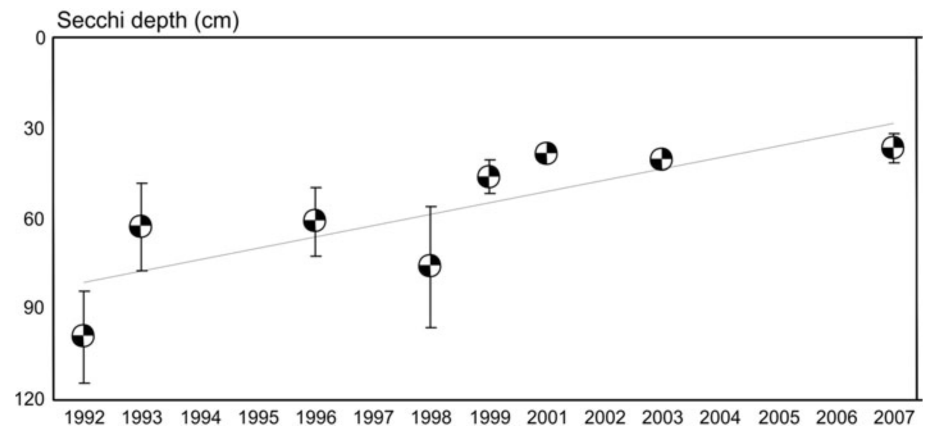

Fig. 4 Variation in Secchi disk depth in Lake Boeckella throughout the time. The *arrow* indicates the year of the disturbance event

Water conductivity significantly increased from 1992 (mean value 27 µS cm^{-1}) to 2007 (mean value 72 µS cm^{-1}) (Fig. 3c) with values sharply rising after the disturbance episode in 2001 (103–278 µS cm^{-1}). The M–W test showed significant differences between the pre-draining and post-draining periods ($U_{M–W}$ 43.0; $P = 0.000005$).

Phytoplankton chlorophyll (Chl *a*) concentration (Fig. 3d) before the water level drop varied from undetectable to 12.3 µg l^{-1}. During the 2001 disturbance, Chl *a* attained maximum values (77.1–152.4 µg l^{-1}) and then decreased in the post-disturbance summers (1.45–32.66 µg l^{-1}). Likewise, Chl *a* concentration was significantly lower in the pre-draining period than in the post-draining period ($U_{M–W}$ 69.0; $P = 0.00008$).

Water transparency significantly decreased ($P < 0.00001$; $n = 53$; $R^2 = 0.42$) throughout this 16-year study. In 1992, Secchi depth varied between 76 and 120 cm, which determined that the light penetration down to the bottom of the lake encompassed more than 80% of its surface. Conversely, in the last years of the study, values decreased two to three times (30–43 cm), resulting in a thinner euphotic layer (Fig. 4). Water transparency during the pre-draining period was statistically higher than during the post-draining period ($U_{M–W}$ 9.0; $P = 0.0000001$).

Dissolved oxygen and pH did not show inter-annual variability. Oxygen concentrations were always very high, ranging from saturation to oversaturation levels (9–16 mg l^{-1}; mean value 12.8 mg l^{-1}); pH values varied from 5.7 to 7.2 (mean value 6.9).

Phytoplankton >2 µm abundance showed the typical temporal fluctuations of the Maritime Antarctic lakes, associated with the timing of the thaw-freeze cycles. Minimum values usually occurred during the ice-melting episodes because of the dilution effect and the increase in water discharge. Phytoplankton peaks were mainly represented by flagellates and were usually detected either at the beginning of the austral summer, when the lake was still covered by ice, or in late summer, concomitantly with an increase in the retention time of the lake. In spite of these summer fluctuations, the long-term analysis from 1991 to 2007 evidenced an enhancement of phytoplankton abundance through time. Mean phytoplankton abundances increased from a range of 145 to 4,975 ind. ml^{-1} in the pre-draining period (1991–2000) to a range of 5,322 to 25,975 ind. ml^{-1} in the post-disturbance period (2001–2007). This difference was significant ($U_{M–W}$ 85.0; $P = 0.00001$) (Fig. 5a). Phytoplankton >2 µm was dominated by Chrysophyceae (mainly *Ochromonas* spp.) and Volvocales (mainly *Chlamydomonas* spp.) until 2003. From 2004 onwards, a high abundance of small eukaryotes (3–5 µm), probably belonging to Chlorococcales, was also recorded in the lake and accounted for the increase in total phytoplankton density (Table 1). These changes implied a shift in the proportion of mixotrophic to strictly autotrophic taxa, being the latter more abundant during the last austral summers.

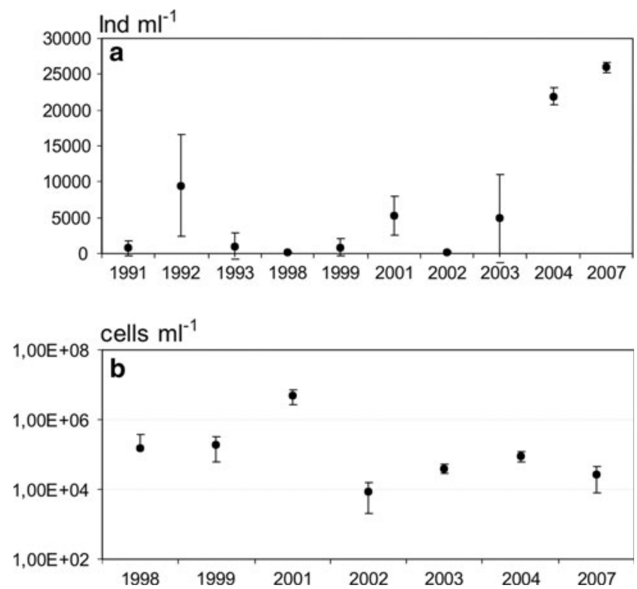

Fig. 5 Variation in summer mean phytoplankton abundances in Lake Boeckella throughout the study period. **a** Phytoplankton >2 µm; **b** Autotrophic picoplankton

Table 1 Phytoplankton composition before and after the draining event

	More abundant phytoplankton taxa (nanoplankton fraction)	Cyanobacteria species richness	Chlorophyta species richness	Bacillariophyceae species richness	Chrysophyceae species richness	Species richness of other groups	Number of species from the epilithon[a]	Autotrophic picoplankton
Before draining (1991–2000)	*Ochromonas* spp. *Chlamydomonas* spp.	31	16	14	5	3	34	Mainly Pcy (more 90%)
After draining (2001–2007)	*Ochromonas* spp. *Chlamydomonas* spp. small chlorococcal algae	10	9	12	5	2	18	Pcy and Peuk (2003–2007 very abundant)

[a] Considering total richness, it indicates the number of species from the benthos

Total phytoplankton richness decreased after the draining event. During the pre-draining period, many tychoplanktonic species contributed to phytoplankton richness. These came from the benthic community, which was well developed in the lake until 2001 (e.g., several filamentous cyanobacteria such as *Leptolyngbya* spp. and *Phormidium* spp., *Tribonema* spp., *Prasiola* spp., and many diatoms species, mainly of the genera *Luticola*, *Pinnularia*, *Achnanthes* and *Nitzschia*), as recorded by Vinocur and Pizarro (1995). After the disturbance, the contribution of organisms from the benthic community to the pelagic samples was much lower (Table 1). Autotrophic picoplankton (APP) densities varied from 1.30×10^4 to 6.9×10^5 cells ml^{-1} during 1998 and 1999. In 2001, during the water level drop, APP markedly increased, reaching a maximum of 6.98×10^6 cells ml^{-1}. In the subsequent summers, APP densities recovered their historical values (0.41×10^4–1.09×10^5 cells ml^{-1}) (Fig. 5b). Thus, APP abundance was similar in the pre-draining and the post-draining periods (U_{M-W} 126; $P = 0.114$). Interestingly, APP showed a shift in their composition over time (Table 1). In 1998, APP were completely dominated by picocyanobacteria (Pcy), whereas in summer 2003, an increase in picoeukaryotes (Peuk) occurred, and from then onwards, Peuk became numerically dominant (>80%).

Discussion

The main changes in limnological features observed in Lake Boeckella over the study period were associated with the dramatic draining event that took place in the austral summer 2001. The sudden decrease in the hydrometric level occurred because of the gradual thawing of the permafrost in the lake catchment. This, in turn, resulted in a fast loss of a huge volume of water through the discharge. Consequently, a marked increase in nutrients, conductivity values, Chl *a* and APP abundances occurred owing to a concentration effect. In 2002, a year after this disturbance event, the permafrost in the area of Lake Boeckella was characterized by Ermolin (2003); according to his estimations, the permafrost in this area was ca. 80–100 m thick, and the thaw layer below the lake was 2.5–3.5 m thick. Different authors have reported that one of the direct effects of climate warming in polar regions is the thawing of permafrost (Quesada et al. 2006; Lyons and Finlay 2008 and citations therein).The permafrost melting in the catchment of Lake Boeckella may be linked to the increasing air temperatures at Hope Bay over the last decades.

The changes observed in Lake Boeckella in several variables (water transparency, conductivity, nutrient concentrations and phytoplankton abundance) indicate an increased eutrophication. Quayle et al. (2002) showed that the rise of ca. 1°C in summer air temperatures during the last 50 years has caused a marked increase in nutrients and Chl *a* in lakes of Signy Island. The alterations in nutrient concentrations as well as in their ratios occur because of changes in terrestrial export related to climatic influences on weathering rates, precipitation and runoff (Adrian et al. 2009).

The increased conductivity and nutrient values observed in Lake Boeckella over the 16-year period studied may be related to a higher runoff during rainy summers in the last decades. Literature reports an increase in precipitation for some coastal areas of the Antarctic Peninsula (Turner et al. 1997), and models predict increasing precipitations for this region in the twenty-first century (Krinner et al. 2007). At Hope Bay, the soils have high phosphate load due to present and past penguin activities (Tatur 1989). This nutrient can be released during permafrost melting and transported by runoff to the lakes. In other Maritime Antarctic regions, the enrichment of the water bodies due to the increasing runoff in rainy summers has been previously reported (Quayle et al. 2002).

The remarkable shift in the Pcy to Peuk ratio seems associated with the decrease in the water transparency of the lake. Different authors have reported the preference of Peuk for low light levels (Pick and Agbeti 1991; Callieri 2007). In a five-year study conducted in Lake Balaton, Vörös et al. (2009) observed the predominance of Peuk in winter, which were able to grow under the ice cover. These authors suggested that Peuk would be better competitors than Pcy at low light and low temperatures.

The decrease in water transparency in Lake Boeckella further resulted in a diminished proportion of the bottom surface available for photoautotrophic organisms. Although historical data on the biomass of algal mats are not available for Lake Boeckella, observations of the benthic material collected by divers of the crew of Esperanza Station in our first campaigns showed that, prior to 2001, the lake bottom was almost entirely covered by dense microbial mats. Hence, the contribution of epilithic taxa to the phytoplankton samples (tychoplankton) was high during the pre-draining period (Vinocur and Pizarro 1995), resulting in a higher phytoplankton richness. Conversely, epilithon biomass after the draining period was very low in Lake Boeckella (Pizarro et al. 2004) and comparatively lower than in nearby lakes. Such a poor benthos development may be linked to a decrease in water transparency, which caused low light conditions at the bottom. Moreover, because of the water level drop, the littoral areas remained exposed and dried during a longer period. In Lake Boeckella, the decrease in transparency is likely associated with a higher phytoplankton development coupled with increased input of inorganic and organic matter by runoff. A higher runoff mediated by an increased thawing in the catchment of the lake would be feasible under a warming scenario.

Shallow oligotrophic lakes in Maritime Antarctica are characterized by low phytoplankton biomass and well-developed algal mats (Priddle 1980; Hawes 1990; Izaguirre et al. 1998). However, the influence of sea animals progressively triggers natural eutrophication, hence turning lakes more turbid. The increase in phytoplankton biomass occurs concomitantly with the decline in the biomass of algal mats (Hawes 1990; Butler 1999; Izaguirre et al. 2003). Interestingly, the shift in the dominant algal community in Lake Boeckella may be explained within the framework of the Alternative Equilibria Hypothesis (Scheffer et al. 1993); this model was first proposed to explain the alternative equilibria between clear and turbid shallow lakes in relation to phytoplankton and submerged macrophytes. Later on, Libouriussen and Jeppesen (2003) proposed a new approach to this model based on the study of the benthic microalgae and phytoplankton in turbid and clear shallow lakes. They demonstrated that, in clear lakes, benthic microalgae were the dominant primary producers, whereas, in turbid lakes, the dominance was almost exclusively pelagic.

On the other hand, in relation to the eutrophication process that is taking place in Lake Boeckella, an increase in the biogenic source of nutrients should be dismissed, since, according to data reported by Carlini et al. (2007), the number of penguin breeding pairs at Hope Bay decreased by 37.4% from 1995 to 2005, probably as a consequence of climate change (lower availability of food during winter). Hence, a higher washing seems an important driver of the limnological changes observed in Lake Boeckella.

The long-term response of lake dynamics in relation to climate change is complex in systems influenced by human impact (Lyons et al. 2006). Ellis-Evans et al. (1997) reported the effects of anthropogenic influence in Antarctic lakes, which were evidenced by changes in several physical and chemical variables in a lake from Larsemann Hills, as a consequence of the installation of a station. In Esperanza Station at Hope Bay, the human influence on Lake Boeckella has remained quite similar since 1980 and has been restricted to water extraction for human consumption. The volume of water removed every year is of about 2.88×10^3 m^3 $year^{-1}$. This extraction is compensated by the water inputs from the melting streams and rainfalls in summer, when the hydrometric level may increase ca. 0.5 m (Ermolin 2003).

Lakes are sentinels of climate change (Adrian et al. 2009; Williamson et al. 2009), and, particularly, both Arctic and Antarctic lakes are proving to be sensitive to climate warming (Laybourn-Parry and Vincent 2008). The impacts of these changes on the freshwater ecosystems still need to be assessed. Our data obtained over a 16-year period suggest that the rapid warming over the last 50 years could have triggered the changes observed in Lake Boeckella. Our study shows how climate change renders accelerated natural eutrophication of lakes in Maritime Antarctica.

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