



Factors regulating summer phytoplankton in a highly eutrophic Antarctic lake

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Received 2 December 1998; in revised form 21 April 2000; accepted 9 May 2000

Key words: Antarctica, lakes, phytoplankton, ecology, grazing

Abstract

Lakes from Maritime Antarctica are regarded as systems generally inhabited by metazoan plankton capable of imposing a top-down control on the phytoplankton during short periods, while lakes from Continental Antarctica lacking these communities would be typically controlled by scarcity of nutrients, following a bottom-up model. Otero Lake is a highly eutrophic small lake located on the NW of the Antarctic Peninsula, which has no metazoan plankton. During summer 1996, we studied the density, composition and vertical distribution of the phytoplankton community of this lake with respect to various abiotic variables, yet our results demonstrated neither light nor nutrient limitation of the phytoplankton biomass. Densities of heterotrophic nanoflagellates (HNAN) and ciliates from three different size categories were also studied. Extremely low densities of HNAN ($0\text{--}155 \text{ ind. ml}^{-1}$) could be due to feeding competition by bacterivore nanociliates and/or predation by large ciliates. A summer bloom of the phytoflagellate *Chlamydomonas* aff. *celerrima* Pascher reached densities tenfold those of previous years ($158.10^3 \text{ ind. ml}^{-1}$), though apparently curtailed by a strong peak of large ciliates (107 ind. ml^{-1}) which would heavily graze on PNAN (phototrophic nanoflagellates). Top-down control can thus occur in this lake during short periods of long hydrologic residence time.

Introduction

Due to the short food chains present, Antarctic lakes have long been considered as very simple systems in comparison to similar environments from other continents. From the point of view of classical food webs, Antarctic lakes may be regarded as 'two level' systems, composed of primary producers and crustacean grazers (Hansson, 1992). However, increasingly attention is being paid to the composition and significance of the microbial food webs that dominate all Antarctic freshwater environments (Ellis-Evans, 1996; Laybourn-Parry et al., 1997).

The structure of phytoplankton communities of shallow lakes from the Antarctic Peninsula is considered to be largely determined by nutrient limitation, unless they are influenced by heavy nutrient inputs

from surrounding animal colonies (Izaguirre et al., 1993; Ellis-Evans, 1996). In this maritime region, most lakes have a number of crustacean and rotifer components (metazoan plankton), which can potentially impose top-down control on planktonic communities (Laybourn-Parry et al., 1996). In contrast, continental Antarctic systems contain few, if any, grazing metazoans, and control is therefore minimal, so these systems are entirely driven by bottom-up forces and the dynamics of the microbial loop (Laybourn-Parry, 1997).

Located on the NW side of the Antarctic Peninsula, Otero Lake is a very small shallow eutrophic lake, fed both by snow melt and runoff from Gentoo penguin colonies, and also heavily influenced by the presence of a large number of skuas within the catchment. Concentrations of nutrients do not appear to limit algal biomass capacity during summer (Mataloni

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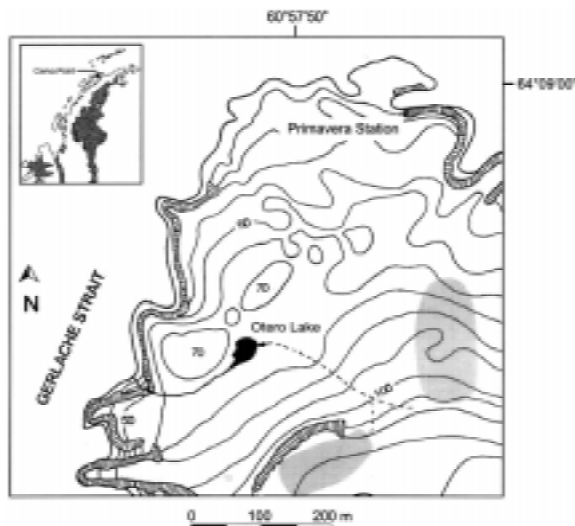


Figure 1. Map of Cierva Point, showing the location of Otero Lake and Primavera Station. Shaded areas indicate Gentoo rookeries

et al., 1998). Whilst the lake lies towards the top end of trophic status seen in maritime lakes, it does not have a metazoan component, and in this respect is more comparable to continental lake environments. Absence of metazoan plankton, on the other hand, would oppose the hypothesis of some grazing control being exerted on phytoplankton. In this paper, we investigate the processes influencing variations in microalgae in this water body by studying a number of abiotic variables and the abundances of some microheterotrophic components of the protozoan plankton (nanoflagellates and ciliates).

Materials and methods

Study area

Otero Lake is a small (area 248.8 m², maximum depth 3.2 m) water body located 500 m away from Argentinian Primavera Station, (61° 58' 00" W, 64° 09' 14" S), on the northwestern section of the Antarctic Peninsula (Figure 1). Unusually favourable microclimatic features of this area which have led to its nomination by the Scientific Committee of Antarctic Research (SCAR) as Site of Special Scientific Interest No. 15 are detailed in Mataloni et al. (1998).

The lake catchment encompasses a large area mainly occupied by Gentoo penguin (*Pygoscelis papua*) rookeries interspersed with snowfields. The latter melt during summer, and are the main source

of water entering Otero Lake with a high load of ornithogenic nutrients. Together with the melting of the snowbank forming the northern shore, this enlarges the volume of the lake during the main thawing period, as well as the discharge through the single outflow to the sea. Water level is then about 30 cm higher than during the ice cover period.

Sampling

One sampling station was established in Otero Lake during summer 1996. Weekly samples were taken at three depths: surface, depth of the Secchi disk, and bottom. Temperature and pH were measured *in situ* with a Luftman P-400 combined electronic meter, and conductivity with an Altronix conductimeter. The Winkler titration method was used to calculate dissolved oxygen concentration.

Water samples for Chlorophyll *a* and nutrient analyses were taken in acid-washed PVC flasks and filtered through Whatman GF/C filters. These were immediately stored at -20 °C for transport to Buenos Aires, where Chlorophyll *a* concentrations were calculated as detailed in Izaguirre et al. (1998). Dissolved phosphate analyses were performed on the filtered samples following the method of Mackereth et al. (1978). Nitrate concentrations were estimated using the Cadmium Reduction method, while the Phenate method was used for ammonium (APHA-AWWA-WPCF, 1975).

Qualitative plankton samples were collected by passing a 15 µm pore net through the open water in order to get a larger concentration of algae. Fresh algae were observed by means of a Zeiss Laboval compound microscope and drawn using a camera lucida. The floristic composition was the same as detailed in Mataloni et al. (1998). Quantitative plankton samples were taken in PVC flasks and preserved with 1% Lugol's iodine solution. Estimations of algal densities were performed on an inverted microscope following Utermöhl (1958). Subsamples were allowed to sediment in 10 ml chambers for at least 24 h, and then a number of fields was counted in each of them, until counting error was below 20% (Venrick, 1978). The same method was used for counting heterotrophic nanoflagellates (HNAN) and ciliates. Lugol's iodine is considered to cause more cell distortion of ciliates, therefore making identification to species level more difficult, yet it is also considered best for preserving abundance (Laybourn-Parry et al., 1997). Although ciliates were not taxonomically identified, three size categories

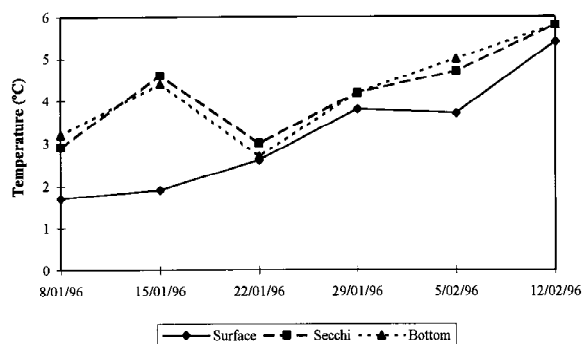


Figure 2. Temperature values for Otero Lake during summer 1996.

were distinguished according to cell volume (CV): small (CV up to $2 \cdot 10^3 \mu\text{m}^3$), medium sized (CV $2\text{--}5 \cdot 10^3 \mu\text{m}^3$) and large (CV $20\text{--}80 \cdot 10^3 \mu\text{m}^3$). Small ciliates did not show any algal content, while medium- and large ciliates showed an average number of 3 and 25 cells, respectively. These were photographed with a Zeiss camera attached to a Zeiss Axioplan microscope (bright field, $1000\times$). Cell volumes of ciliates, HNAN and the two main PNAN of the phytoplankton were calculated by using the nearest geometrical shape.

Results

Abiotic features

Ice cover of the lake was already incomplete on the first sampling date (8 January), but a weak inverse thermal stratification was maintained until ice-out on 22 January. Between this date and the beginning of February, wind and sunny days contributed to the dramatic thawing of the surrounding snowfields, increasing the inflow to the lake and favouring the mixing of the water column. A very cold period before 5 February is evidenced by the formation of a 1 cm-thick ice layer completely covering the lake surface, and the subsequent thermal stratification (Figure 2). As in former seasons, both volume of the lake and discharge through the outflow peaked during the period of maximum snowfield thawing. Although discharge measurements have not been made in this study, it is known that the hydrologic residence time can be as short as 2.4 days during this period (Mataloni, unpubl.). In contrast, it is negligible during cold periods when both inflow and outflow of the lake freeze, or after the thawing period in dry summers, when rainfall in the catchment is scarce.

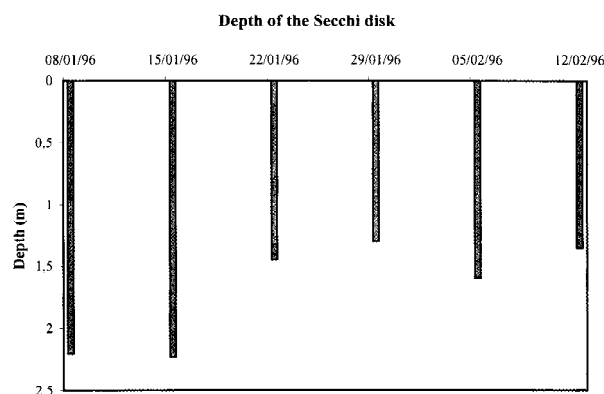


Figure 3. Depth of the Secchi disk at the sampling site.

Conductivity reflected the thawing of the ice cover of the lake with low values from 8 to 15 January ($84.7\text{--}106 \mu\text{S cm}^{-1}$). Later, thawing of surrounding snowfields contributed high amounts of organic debris and sediments to the lake, while wind-mixing accounted for higher, even values along the water column ($135.7\text{--}136.6 \mu\text{S cm}^{-1}$ on 29/1). This fact also explains the lower transparency during the open water period (Figure 3), while stratification conditions are associated with higher transparency. Nevertheless, solar radiation reached the bottom of the lake all summer long. Dissolved oxygen was close to supersaturation ($14.4\text{--}16.8 \text{ mg l}^{-1}$) during the whole summer. pH, in turn, was mildly acid ($6\text{--}6.7$), showing a decreasing trend throughout the study.

Concentrations of nutrients seem to follow the same dynamics as other dissolved and suspended compounds, with temporal curves throughout the summer broadly following that of conductivity. Dissolved reactive phosphorus (DRP) has a very stable distribution in the water column ($1058\text{--}1250 \mu\text{g l}^{-1}$) except for one lower value at the surface on 15 Jan ($806 \mu\text{g l}^{-1}$), probably due to the low P content in the thawing ice cover. Nitrogen compounds ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) also show a similar pattern (Figure 4), except for the comparatively lower value at the bottom on 5 February, concurrent with an algal bloom at this depth. In general, nitrate showed a trend to increase over time, while concentrations of ammonia were more fluctuating and tended to decrease over the summer.

Biotic features

The taxonomic composition of the phytoplanktonic community was overall almost identical to the one described by Mataloni et al. (1998). Algal flora of

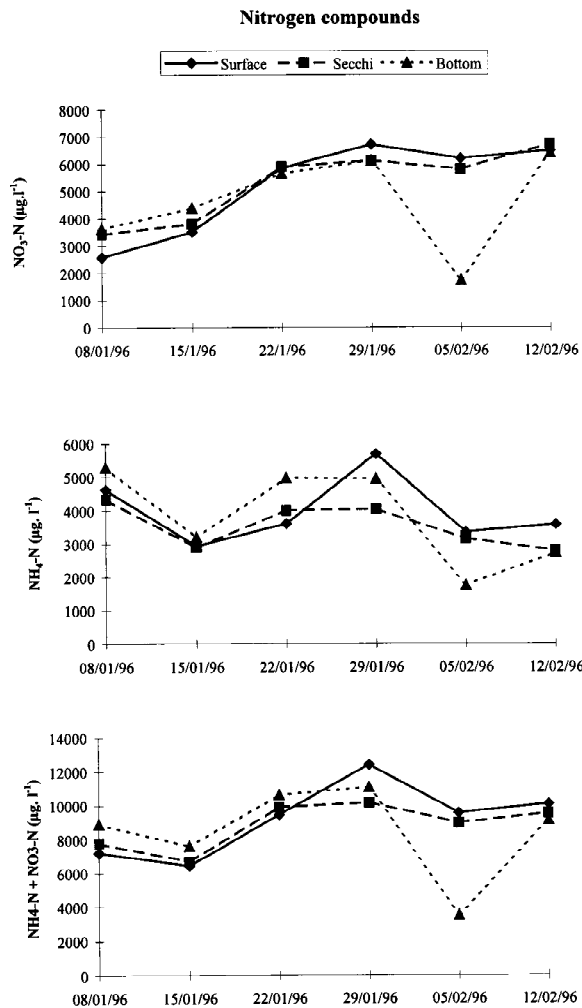


Figure 4. Concentrations of nitrates (NO₃-N), ammonium (NH₄-N) and dissolved nitrogen (NO₃-N + NH₄-N) in Otero Lake.

Otero Lake is dominated by flagellated Chlorophyta throughout the summer. During the maximum period of thaw in surrounding snowfields, a number of cryobiontic taxa are incorporated in the lake (mainly *Raphidonema* spp. and resting stages of *Chloromonas* and *Desmotetra* spp.), and mixing contributes to resuspend diatoms in the water column. Nevertheless, in spite of the high species richness found by these authors (74 taxa), between 70.8 and 99% of the total phytoplankton abundance was due to *Chlamydomonas* aff. *celerrima* Pascher, while a flagellated Chrysophycean accounted for most of the rest. These two species together represented between 89.6 and <100% of the total phytoplankton density, thus allowing us to estimate the biovolume of phototrophic nanoflagellates.

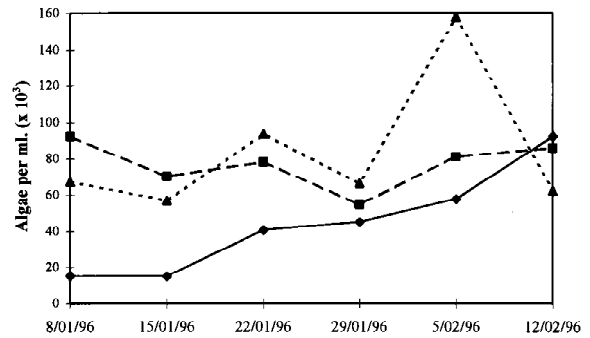


Figure 5. Phytoplankton densities in Otero Lake.

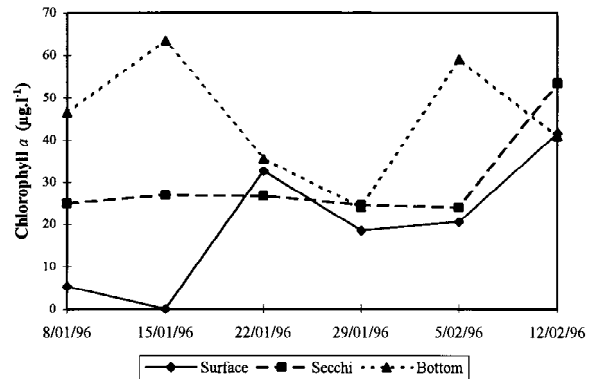


Figure 6. Chlorophyll-*a* concentrations at the three sampling depths.

Algal densities varied distinctly at the three sampling depths (Figure 5). Surface samples showed very low initial values with a clear trend to increasing densities through the summer, while higher, fluctuating values were observed at both Secchi disk depth and bottom. On 5 February, a bloom of *Chlamydomonas* aff. *celerrima* occurred at the bottom, reaching maximum densities tenfold higher than those previously recorded (Mataloni et al., 1998). Although this species was previously recorded by these authors as *Chlamydomonas subcaudata* Wille, it could be in fact new for science (Mataloni & Pose, in press) and will be subjected to detailed study for identification at species level.

Chlorophyll-*a* values roughly reflected changes in algal density (Figure 6), except for a maximum value of 63.5 µg l⁻¹, recorded at the bottom on 15 January, which was coupled with the lowest algal density at that depth.

Heterotrophic nanoflagellates showed densities of 0–155 ind. ml⁻¹, highest values being recorded at the surface at the beginning of the ice break. Total densities of ciliates reached 273 ind. ml⁻¹. Small ciliates

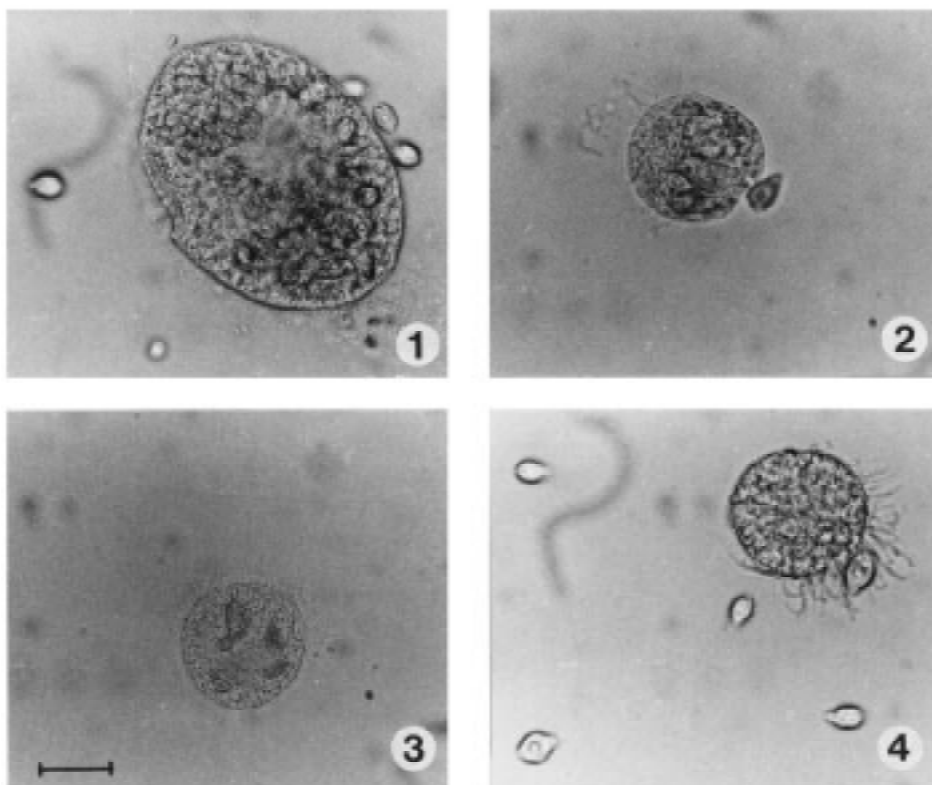


Figure 7. Individuals of *Chlamydomonas* aff. *celerrima*, free-living and captured inside large (1) and medium sized (2, 3, 4) ciliates. The scale bar is 10 μm in all cases.

varied from 0 to 63 ind. ml^{-1} , medium size ones ranged from 0 to 91 ind. ml^{-1} , and densities of large ciliates varied between 0 and 107 ind. ml^{-1} during a strong peak at the bottom which followed that of algae on 5 February. Microphotographs of both medium and large size ciliates (Figure 7: 1–4) containing a number of cells still intact showed that they are in fact retaining a significant number of *Chlamydomonas* aff. *celerrima*. A rough calculation based on the average number of algae observed in ciliates from both sizes shows that this accounted for about 5% of the total density of this alga at the bottom on 12 February.

Figure 8 shows the variation in biovolumes for both photo- and heterotrophic nanoflagellates, as well as for ciliates from all three size categories. Here, the accumulation of biovolume in the PNAN compartment is evidenced, while HNAN and small ciliates have small biovolumes throughout the study. Medium and large ciliates show an increasing trend over the summer. In particular, late increases in the volume of large ciliates on 29 January at Secchi disk and bottom depths, and that of large ciliates at the bottom

(12 February) are coupled with drops in the PNAN biovolumes.

No metazoan plankton have been observed in this water body, but examination of samples of the cyanobacterial mat covering the surface of the sediments revealed the presence of rotifers, nematodes and tardigrades in the benthic community of Otero Lake.

Discussion

Temperature, conductivity and transparency values reflected switches between stratification and mixing conditions during the sampling period. These switches were due to the melting of the lake ice cover in early summer, the incorporation of organic debris into the lake during the period of maximum thawing of surrounding snowfields, and the freezing of the lake surface during a short cold period. Data recorded from different depths in this study were consistent with the description of these processes given by Mataloni et al. (1998). Abundant dissolved oxygen and a slightly

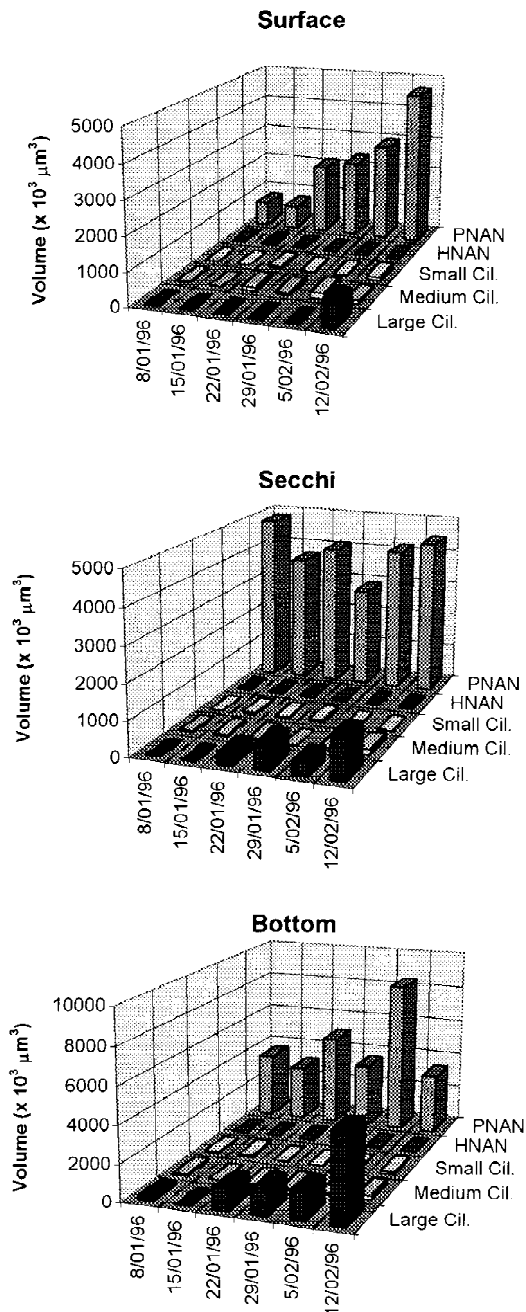


Figure 8. Biovolumes of phototrophic (PNAN) and heterotrophic nanoflagellates (HNAN), and ciliates from all three size categories at each sampling depth.

acid pH range were also in accordance with previous records (Mataloni et al., 1998).

High concentrations of $\text{PO}_4\text{-P}$, $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ throughout the study indicate that nutrients are not limiting algal biomass capacity of the lake. Although

the drop in nitrogen concentrations at the bottom on 5 February seems to be caused by the bloom of *Chlamydomonas* aff. *celerrima*, amounts of bioavailable N never fall below $3000 \mu\text{g l}^{-1}$. They thus reflect a high algal uptake of a plentiful resource. In particular, the decreasing trend in $\text{NH}_4\text{-N}$ concentrations along the summer suggest that this is the preferred nitrogen source for the algae, as previously discussed by Hawes (1983).

The phytoplanktonic community was clearly dominated by the eutrophilous *Chlamydomonas* aff. *celerrima*, which reached densities tenfold those of previous years. Whilst frequent observations of division stages confirm its activity during the whole study period, its density at the time of the early ice cover break was already higher than during the bloom of the previous summer (Mataloni et al., 1998) and reached six times this number during the bloom. Increases in density between the first sampling date and the bloom were about 5.5 and 7.4 times for seasons 92/93 and 94/95, respectively. This would indicate that development of massive blooms of this species depends on conditions prior to the ice cover break rather than distinct summer growth. The time of the season in which the bloom takes place would relate to climatic conditions leading to longer hydrologic residence times. The bloom proceeded at the end of late-thawing 92/93 season, in which relatively dry and cold conditions lead to a slow thawing of the surrounding snowfields, and in the middle of 94/95 season, between a strong thawing period and the onset of an unusually rainy season, which diluted the planktonic community and increased the outflow (Mataloni et al., 1998; Mataloni, unpubl.)

Abundance of nutrients and light availability in the water column account for the higher initial algal densities at the bottom and Secchi disk depths, while a more diluted community can be observed at the surface. Although the three depths show different variations in algal concentrations over the whole summer, stratification conditions coincide with more distinct phytoplankton abundances in the water column, while mixing events taking place shortly before the 29 January and 12 February contributed to a more even vertical distribution of the community. This variety of conditions is reflected, in turn, by the Chlorophyll-*a* concentrations. The exception to this is a peak of Chlorophyll-*a* recorded at the bottom on 15 January. A high density of the picoplanktonic fraction, which was not evaluated in this study, could be the cause for this peak. Hawes (1990) reported that five water bodies

showing a wide range of trophic conditions from Signy Island were dominated by a pico-cyanobacterium in terms of Chlorophyll-*a*. Such small taxa were detected in the qualitative analysis of samples from Otero Lake. Although the Utermöhl method does not allow for realistic counting of these organisms, we can say that they were not dominant.

Abundances of heterotrophic nanoflagellates were near the lower end of the typical range across a trophic continuum, as given by Laybourn-Parry (1997). Densities of these organisms in Otero Lake are comparable to the ones recorded by the latter author for oligotrophic Crooked Lake, Vestfold Hills, in continental Antarctica. Also similarly, highest HNAN densities for the summer were recorded in surface samples at the beginning of the season. Nevertheless, abundances of these organisms were unexpectedly low for a very eutrophic system such as Otero Lake. According to Sorokin (1999), nanociliates up to $5 \cdot 10^3 \mu\text{m}^3$ feed mostly on bacteria and picoplanktonic algae. In this study, this was true for those small ciliates up to $2 \cdot 10^3 \mu\text{m}^3$, while large ones proved able to feed on particles the size of HNAN. These facts could impose a double restriction on the growth of flagellates: Competition for food with nanociliates and predation pressure from large ciliates. Fenchel (1987) observed that bacterivorous ciliates seem only to be competitive at fairly high densities of bacteria, which is not unlikely in this system. Studies on the abundance and dynamics of the bacteria serving these organisms as an energy source will help greatly in discerning both effects.

The remarkably high overall density of ciliates recorded here (up to 273 ind. ml^{-1}) is difficult to compare even with the most eutrophic Antarctic lakes we have found in the literature. Heywood Lake reached 6 ind. ml^{-1} (Laybourn-Parry, 1997) and heavily eutrophized No Worries Lake, 20 ind. ml^{-1} (Ellis Evans et al., 1997). Laybourn-Parry et al. (1997) attributed the unexpectedly large ciliate community in Lake Fryxell to their slow growth rate or to a highly productive, heavily grazed food source. Also, the absence of metazoan plankton would release ciliates from grazing pressure, thus allowing them to reach high densities, as observed by Sorokin (1999). A combination of these causes could be operating in Otero Lake, especially regarding large ciliates, since they steadily increased from undetectable numbers to very high concentrations over the whole summer, with density peaks following those of *Chlamydomonas* aff. *celerrima*.

Mixotrophic ciliates have been reported from a number of lakes in Antarctica, some of them har-

bouring symbiotic zoochlorellae (Laybourn-Parry et al., 1997). Advantages of this association would be a closed nutrient cycle within the consortium in very oligotrophic waters (Amblard et al., 1993), or the internal production of photosynthetic oxygen in anoxic environments (Finlay & Esteban, 1998), yet neither of these is the case in Otero Lake. Therefore, whilst grazing rates have not been measured in this study, it is strongly likely that ciliates are actively feeding on PNAN.

Laybourn-Parry et al. (1997) pointed out that lakes from maritime Antarctica are generally inhabited by crustaceans and rotifers which are capable of exerting a top-down control on the phytoplankton community, while lakes from continental Antarctica lack metazoan plankton, thus being entirely driven by bottom-up forces relating to scarcity of nutrients. This point of view makes Otero Lake a very special environment, since it is located in the maritime Antarctica, has very eutrophic features, yet lacks metazoan zooplankton. Priddle et al. (1986) proposed three possible causes for phytoplankton loss: sedimentation, grazing and loss to the outflow. The latter would have been the cause for the ending of the bloom occurred during 94/95 wet season in Otero Lake (Mataloni et al., 1998; Mataloni, unpubl.), yet it is the strong increase in the density of large ciliates which seems to have curtailed the bloom of *Chlamydomonas* aff. *celerrima* in the present study, as evidenced by the microphotographs. Present results thus suggest that grazing by protozoan plankton could be, in fact, exerting a top-down control on the phytoplankton of Otero Lake during periods of long residence time.

Morphological diversity of ciliates in Otero Lake was extremely low, in coincidence with observations of Laybourn-Parry (1997) for similar lakes in Signy Island. According to this author, the low ciliate diversity displayed by these lakes could be due to the short time during which they have existed. Albeit a similar situation could occur in Otero Lake, a large local diversity of rare and encysted ciliates could exist in this water body, which would readily fill the vacant niches created under a spectrum of changing environmental conditions, as shown by Finlay & Esteban (1998). A similar 'propagule bank' has been observed relating soil colonizing algae in Cierva Point (Mataloni et al., 2000), and is likely to exist in other Antarctic environments. Studies on the structure and dynamics of the various microbial communities over a number of years is recommended in order to fully understand the func-

tioning of the microbial loop in this and other unstable habitats subjected to climatic change.

Acknowledgements

This project has been supported by the University of Buenos Aires-Conicet - Instituto Antártico Argentino. We are grateful to the personnel of Base Antártica Primavera for their logistic support during field work. Helpful comments from J. Laybourn-Parry and an anonymous referee on an earlier manuscript were much appreciated.

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