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Symbiotic association of the ciliate *Ophrydium naumanni* with *Chlorella* causing a deep chlorophyll *a* maximum in an oligotrophic South Andes lake

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Abstract. Vertical profiles of temperature, light and chlorophyll *a* concentration were examined in Lake Moreno Oeste, an oligotrophic South Andean lake (Argentina), during the warmest period of the year (November–April), when thermal stratification is characteristic. Concurrent samples for the enumeration of phytoplankton and green ciliates were taken, and the differential contribution of these fractions to total chlorophyll *a* concentration was analysed. The development of a distinctive deep chlorophyll maximum was observed during summer months. The deep chlorophyll maximum was situated near the limit of the euphotic zone and just below the upper limit of the metalimnion. The results showed that the green ciliate *Ophrydium naumanni* with endosymbiotic *Chlorella* dominated the metalimnion causing the deep chlorophyll maximum. Additional laboratory experiments revealed a strong dependence of *O.naumanni* on light. Therefore, the symbiotic association appears to be an effective exploitation of the water column in poor-nutrient–high-light ecosystems like large Andean lakes.

Introduction

The role of protozoa, in particular ciliates, in the pelagic regions of fresh waters has recently begun to be studied (Pace and Orcut, 1981; Pace, 1982; Beaver and Crisman, 1989; Müller *et al*., 1991a,b; Amblard *et al*., 1993). The concept of the 'microbial loop' (Azam *et al*., 1983) arose as a stimulus for planktologists to study the ecological linkages of planktonic protozoa. These organisms became recognized as the major consumers of microbial production (Porter *et al*., 1985). However, ciliates cannot be seen only as consumers of bacteria (Porter *et al*., 1985), since symbiotic associations with autotrophic cells appear widely distributed among them (Fenchel, 1987; Foissner, 1994). Planktonic green ciliates include a great variety of species which belong to different groups, such as holotrichs, peritrichs, oligotrichs and heterotrichs, all sharing the presence of symbiotic algae inside their cytoplasm. Some of them are facultative green ciliates since green and apochlorotic strains have been described (Reisser *et al*., 1985; Foissner, 1994).

In Andean deep oligotrophic lakes, the presence of important green ciliate populations with endosymbiotic *Chlorella* has been revealed (Modenutti, 1988, 1997; Foissner and Wolf, 1994). These assemblages are usually dominated by the peritrich *Ophrydium naumanni* Pejler and the heterotrich *Stentor araucanus* Foissner & Wolf. The presence of high numbers of *Chlorella* inside these ciliates would imply that protozoa may account for an important fraction of total chlorophyll (Chl) *a* concentration and carry significant photosynthetic potential.

We attempted to analyse vertical Chl *a* distribution in terms of the differential

contribution of phytoplankton and green ciliates along the water column, and through laboratory experiments we explored ciliate light dependence as an energy source for population maintenance.

Study site

Lake Moreno Oeste (41°5′S; 71°33′W; 758 m a.s.l.) belongs to the Nahuel Huapi system (Patagonia, Argentina). The lake has a surface area of 6 km^2 and the maximum depth is 90 m. The regional climate is classified as temperate under the influence of westerly winds, with 1500 mm of annual precipitation and a mean annual temperature of 8.7°C. The surrounding vegetation is constituted by a mixed forest of *Nothofagus dombeyi* (Mirb.) Blume and *Austrocedrus chilensis* (D. Don) Florin et Boutleje. Lake chemistry and net phytoplankton have been partially described by Izaguirre *et al*. (1990), indicating its oligotrophic condition. The thermal regime is warm monomictic with seasonal stratification from late spring to late autumn.

Method

Field methods

Sampling was carried out monthly between February and April 1997, and November 1997 and January 1998; thus, the warmest period of the year was included. A sampling point was established at the central deepest part of the basin (z = 70 m). All samplings were carried out at mid-day 1 h before astronomic noon. Sampling dates were sunny days, except on 12 March when light clouds (cirrus) were present. Temperature and light [photosynthetically active radiation (PAR), 400–700 nm] profiles from 0 to 55 m were measured with a PUV 500B submersible radiometer (Biospherical Instruments). *In situ* Chl *a* profiles (0–55 m) were determined on the basis of the natural fluorescence measured with the PUV 500B (PUV 683). Extinction coefficients for each date were calculated by regressing log-transformed light with depth. Concurrently, water samples of 12 l were obtained with a Schindler–Patalas trap from 0 to 48 m each 4 m interval or 2 m at the Chl maxima detected *in situ* by the PUV. The water obtained was transferred to 10 l polypropylene containers, which were rinsed with the water sampled at the beginning of the collection. Containers were kept in darkness and immediately carried to the laboratory (30 min after collection).

Laboratory methods

In the laboratory, 250 ml of the sampled water at each depth were fixed with acid Lugol solution for phytoplankton and *O.naumanni* counting. Three litres were filtered through a GF/F filter at ~20 mmHg, and the filter was used for Chl *a* determination. Chlorophyll *a* concentration was measured by extraction with hot 90% ethanol following Nusch (1980). Corrections for phaeophytin *a* were performed by acidification with HCl. In November, December and January,

phosphorus concentrations were determined on 250 ml of unfiltered lake water for total phosphorus (TP) and a similar volume of filtered water (GFC) was used for total dissolved phosphorus (TDP). The samples were digested with potassium persulphate at 125°C at 1.5 atm for 1 h. Concentrations were analysed through the ascorbate–reduced molybdenum blue method.

Phytoplankton and *O.naumanni* densities were quantified with an inverted microscope using 50 ml Utermöhl chambers. The limit between nano- and net phytoplankton was considered as 20 μm greatest axial linear dimension (GALD). At least 30 cells of each phytoplankton species were measured and cell biovolume was calculated by approximation to appropriate geometric figures. The preservation of *O.naumanni* in the samples was very good, but to ensure their identification during the counting, we followed the Lugol fixation procedure under a microscope in order to assess the fixed *Ophrydium* shape. Symbiotic *Chlorella* diameter and mean number for each *Ophrydium* were quantified in live ciliate specimens under direct microscopy. Symbiotic *Chlorella* biovolume results from multiplying individual *Chlorella* biovolume by the mean number of *Chlorella* per *Ophrydium* times *Ophrydium* density.

Linear simple regression analysis and forward stepwise regression analysis between spectrophotometric Chl *a* concentration as dependent variable and the different biovolume fractions as independent variables were carried out. In all the statistical analysis, normality and homoscedasticity were tested and values were log transformed when necessary.

Experimental methods

In order to test *O.naumanni* light dependence, two series of laboratory experiments were performed in February and December 1997. The experiments lasted 7 days (February) and 12 days (December), and they were conducted in a growth chamber at 14°C and a 14:10 h light:dark photoperiod; light intensity inside the chamber was 39.0 μE m^{-2} s^{-1}. These conditions closely resembled those observed in the summer epilimnion of the lake (20 m). The cultures were run in 10 ml test tubes which were rotated on a turntable at 2 r.p.m. Before starting the experiments, all the vessels and test tubes were sterilized (121°C, 1 atm, 20 min). Four treatments, with five replicates each, were tested: (i) 10 ml of lake water filtered through a 0.45 μm pore membrane filter (in order to remove particulate matter); (ii) 10 ml of lake water filtered through a 0.45 μm pore membrane filter wrapped with aluminium foil to remove light; (iii) 10 ml of lake water filtered through a plankton net of 35 μm mesh (in order to remove zooplankton); (iv) 10 ml of lake water filtered through a plankton net of 35 μm mesh wrapped with aluminium foil to remove light. Each treatment was started with five individuals of *O.naumanni*. They were counted and the water was replaced with fresh medium every 2–4 days, in sterilized test tubes. Results of these experiments were expressed as growth rates:

$$r = \frac{LnN_{t+1} - LnN_t}{t}$$

Results

The lake remained stratified during the entire study period, except in November (mid-spring) when the stratification was incipient. In all the stratified period, the mixing layer was broad with the thermocline below 30 m depth (Figure 1). Epilimnion temperatures ranged from 11°C in November to 17°C in March (late summer), while the hypolimnion remained at 7.6°C.

Daily surface PAR irradiance varied during the sampling season, with maximum and minimum values observed in November–January and February–March, respectively (Table I). The diffuse extinction coefficient (K_d) was low and fairly constant, varying between 0.120 and 0.142 m^{-1}, with maximum values during November (mid-spring) (Table I). The euphotic zone was extended up to 38 m, including the whole mixing layer within it (Figure 1).

TDP concentrations were always very low with no remarkable differences along the water column (Table II). On the contrary, TP showed a slight increase which correspond to maximum values in bioseston (Chl *a* concentrations), always remaining between 2 and 4 µg l^{-1} (Table II). Dissolved organic carbon (DOC) was low (0.41–0.69 mg l^{-1}) (D.Morris personal communication), and no remarkable shifts were noted along the water column.

Vertical profiles of Chl *a* obtained through the natural fluorescence of the PUV showed maximum values always near the limit of the euphotic zone, just below the upper limit of the metalimnion. Direct measurements of Chl *a* showed the same pattern (Figure 2). The epilimnetic Chl *a* concentration was always <1 µg l^{-1}, while the metalimnetic maximum reached 1.5–2 µg l^{-1} (Figure 2). Distinctive deep Chl maxima were observed during summer months (January, February and

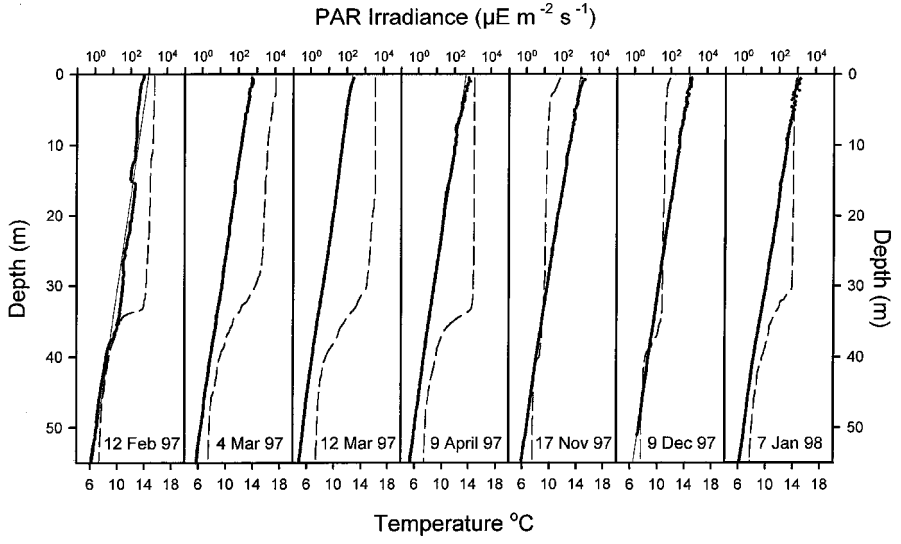

Fig. 1. Vertical profiles of temperature (dashed line) and log-transformed light penetration (PAR) (solid line and dots) in Lake Moreno Oeste.

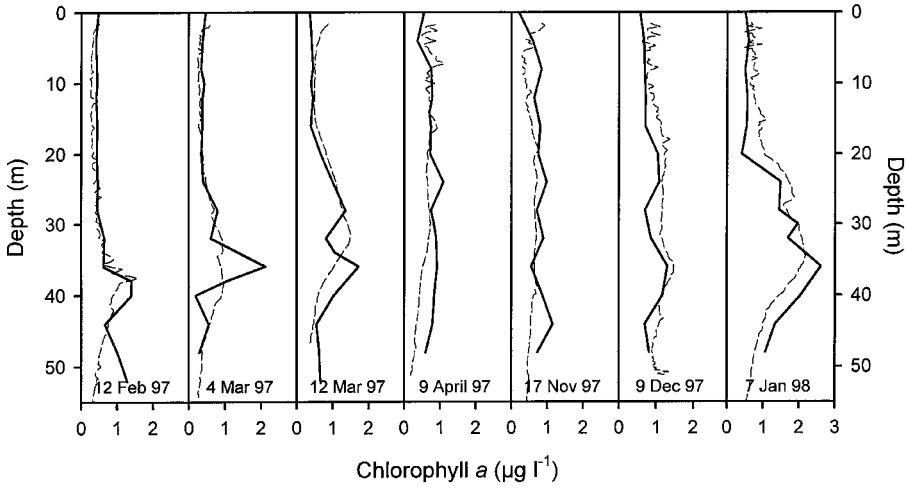

Fig. 2. Vertical profiles of Chl *a* concentration in Lake Moreno Oeste. Solid line, spectrophotometric chlorophyll; dashed line, natural fluorescence chlorophyll.

Table I. Light conditions of Lake Moreno Oeste in each sampling date. K_d is the diffuse extinction coefficient, I_0 is the surface PAR irradiance (µE m^{-2} s^{-1}), I_{zDCM} is the PAR irradiance at the DCM (deep chlorophyll maximum) (µE m^{-2} s^{-1}). In April and November, DCM were not distinctive, so I_{zDCM} are not included

	14 Feb.	4 March	12 March	9 April	17 Nov.	9 Dec.	7 Jan.
K_d	0.120	0.131	0.125	0.133	0.142	0.129	0.127
I_0	5.5×10^2	5.5×10^2	3.0×10^2	5.0×10^2	1.5×10^3	1.2×10^3	1.5×10^3
I_{zDCM}	7.12	3.65	3.98	–	–	10.00	5.64

Table II. Total dissolved phosphorus (TDP) and total phosphorus (TP) from the three depth strata (epi-, meta- and hypolimnion) in Lake Moreno Oeste, during spring (November, December) and summer (January)

		17 Nov.	9 Dec.	7 Jan.
TP (µg l^{-1})	Epilimnion	2.4	2.7	3.1
	Metalimnion	2.1	2.6	3.7
	Hypolimnion	2.5	2.9	4.1
TDP (µg l^{-1})	Epilimnion	1.3	1.7	1.1
	Metalimnion	1.5	1.3	1.2
	Hypolimnion	1.3	1.4	1.9

March, sunny and cloudy days), while during autumn (April) and spring (November) Chl *a* was almost evenly distributed along the water column (Figure 2). These summer deep Chl maxima received at noon from 3.65 to 10 µE m^{-2} s^{-1} of PAR (Table I).

Phytoplankton cell abundance was low, according to the oligotrophic condition of the lake. The minimum value was registered during November at 0 m, with 209

cells ml^{-1}, while the maximum abundance occurred during summer at 12 m, reaching 1984 cells ml^{-1} (Figure 3). The community was dominated by nanoplanktonic species (<20 µm GALD) constituting >98% of total cell abundance. The prymnesiophycean *Chrysochromulina parva* Lackey (3–5 µm GALD), followed by the cryptophycean *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky (8–10 µm GALD) largely dominated nanoplankton. The dinoflagellate *Gymnodinium* aff. *varians* (10–12 µm GALD) was present in all samplings, but at low densities. Net phytoplankton was constituted by *Dinobryon divergens* Imhof (colonies >40 mm), followed by *Gymnodinium paradoxum* Schilling (37–39 µm GALD). Nevertheless, this fraction did not account for an important contribution in terms of cell abundance (0–23 cells ml^{-1}).

On the other hand, the ciliate assemblage was constituted by the peritrich *O.naumanni* and a number of unidentified oligotrichs. *Ophrydium naumanni* constituted 50–90% of total ciliate density and was present over all the period, reaching a maximum of 17 ind. ml^{-1} at or below 30 m depth in January, February and March (summer) (Figure 3). Each ciliate contained 250 *Chlorella* on average, ranging between 79 and 424, but with a sharp mode at 250. *Chlorella* diameter was estimated at 5 µm; therefore, the effective photosynthetic biovolume of each ciliate was estimated by multiplying *Chlorella* biovolume by the number of *Chlorella* per ciliate.

The biovolume of the different photosynthetic cell fractions showed different patterns along the water column (Figure 4). Total photosynthetic biovolume was considered as the sum of nano- and net phytoplankton, and symbiotic *Chlorella* biovolume. Its maximum values were observed during summer with peaks below

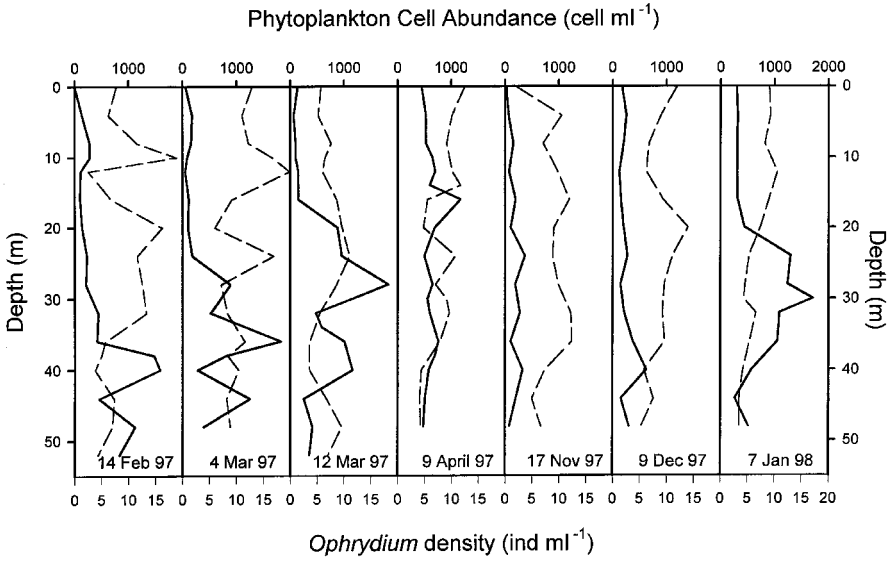

Fig. 3. Phytoplankton (dashed line) and *O.naumanni* (solid line) cell abundance along the water column in Lake Moreno Oeste.

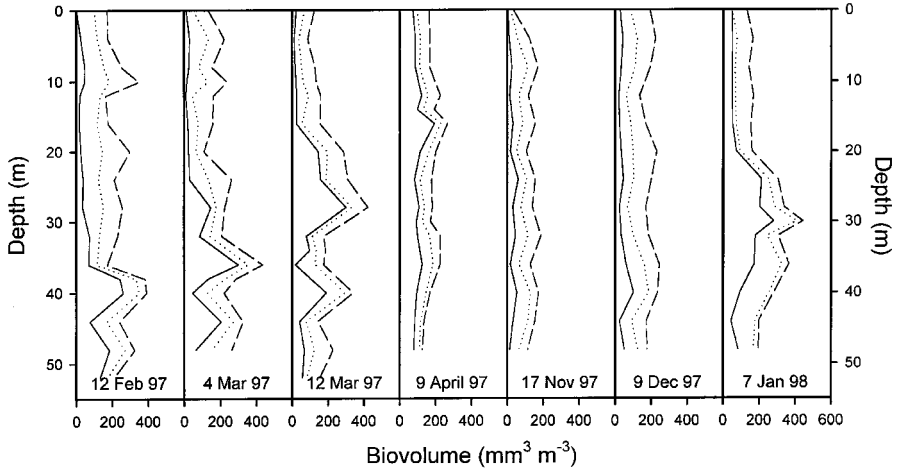

Fig. 4. Cumulative biovolumes of the different photosynthetic fractions along the water column in Lake Moreno Oeste. Dashed line, nanoplankton; dotted line, net phytoplankton; solid line, endosymbiotic *Chlorella*.

30 m depth (Figure 4). However, it is noticeable that total photosynthetic biovolume was clearly determined by the symbiotic *Chlorella* (Figure 4). Nanoplanktonic biovolume showed a rather even distribution in the water column. Net phytoplankton biovolume also showed an increase below 30 m depth (Figure 4; 7 January 1998, 40 m) due to an increase in density of *G.paradoxum*.

Chlorophyll *a* concentration was analysed in relation to the biovolume of the different photosynthetic fractions, being the pigment concentration significantly related to each fraction (Table III). However, when analysed separately, not all fractions showed direct relationships. *Ophrydium naumanni* symbiotic *Chlorella* biovolume was found to account for the highest explained variance (Table III) and to be directly related to Chl *a* (Figure 5). The forward stepwise regression analysis showed that the effective ciliate photosynthetic biovolume was the first variable included and accounted for 38% of Chl *a* variance. Then, nano and net phytoplankton biovolume were included to the model, and each variable increased in 4% the explained variable (Table IV). In this analysis, each fraction is related to previously unexplained variance; therefore, all of them resulted in positive relationships (Table IV).

Laboratory experiments revealed a marked dependence of *O.naumanni* on light conditions. In both experiments, the response of *O.naumanni* to treatment conditions was similar. In all treatments without light (aluminium foil covered), high mortality rates (highly negative increase rates) of the ciliates were observed within the first 3 days of experimentation. Beyond the fourth day, there were no individuals recorded in the experimental tubes (Figure 6). In illuminated treatments, those with water filtered through 35 μm mesh always showed positive increase rates and higher values than those with water filtered through a 0.45 μm pore filter (Figure 6). These results may indicate a positive effect of particulate

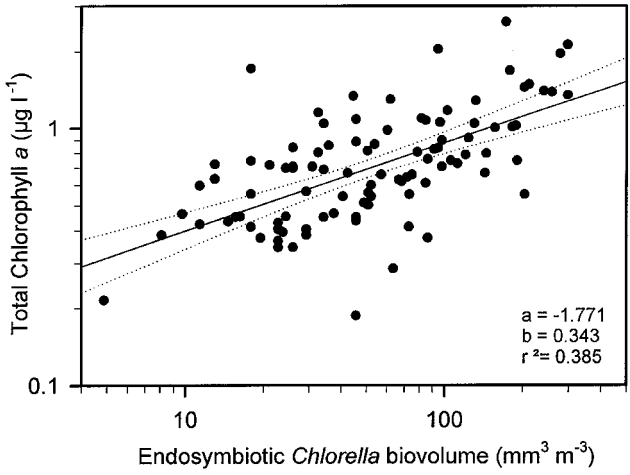

Fig. 5. Relationship between Chl *a* concentration and endosymbiotic *Chlorella* biovolume.

Table III. Linear simple regression analysis between chlorophyll *a* as dependent variable and biovolumes of symbiotic *Chlorella* (SCB), net phytoplankton (NeB) and nanoplankton (NaB). Variables were log transformed

Regression	r^2	*P*	Slope	Origin
Chl *a* – SCB	0.384	<0.001	0.343	–0.326
Chl *a* – NaB	0.101	<0.005	–0.373	0.518
Chl *a* – NeB	0.055	<0.05	0.181	–0.469

Table IV. Summary of the forward stepwise regression between Chl *a* as dependent variable and biovolumes of symbiotic *Chlorella* (SCB), net phytoplankton (NeB) and nanoplankton (NaB). Variables were log transformed

Step	Variables entered	Variables removed	*R*	R^2	ΔR^2	Variables in model	*P*
1	Log SCB	–	0.620	0.385	0.3846	Log SCB	<0.0001
2	Log NaB	–	0.656	0.430	0.0459	Log NaB	0.0053
3	Log NeB	–	0.688	0.474	0.0433	Log NeB	0.0063

matter on *O.naumanni* increase rates. However, we cannot ensure that treatments with water filtered through 0.45 µm were free from bacteria, since when *Ophrydium* individuals were added or transferred to new medium a drop of lake water was added too.

Discussion

The results obtained showed that during the summer stratification period Lake Moreno Oeste has a deep Chl maximum. This maximum was situated below the thermocline and near the 1% level of PAR. Similar deep Chl maxima have been

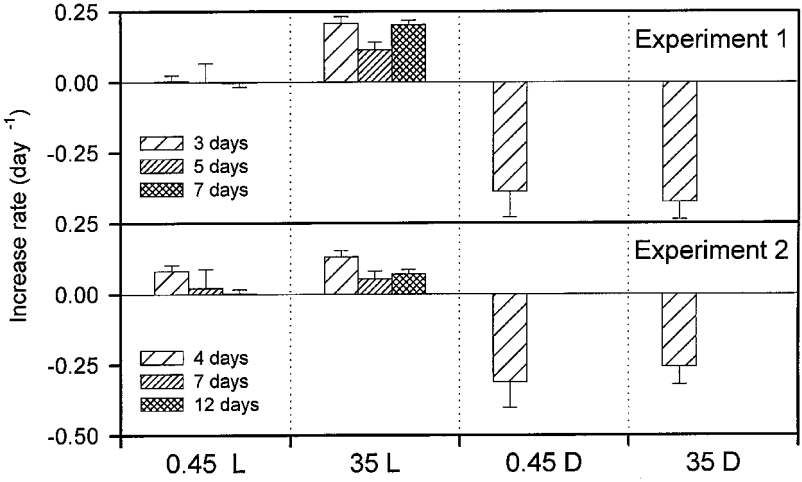

Fig. 6. Increase rates of *O.naumanni* in laboratory experiments under the four treatments (0.45 L; 0.45 D; 35 L; 35 D). Experiment 1, February 1997; Experiment 2, December 1997. 0.45 L, lake water filtered through 0.45 μm pore membrane filter with light; 0.45 D, lake water filtered through 0.45 μm pore membrane filter wrapped with aluminium foil (dark); 35 L, lake water filtered through a plankton net of 35 μm mesh size with light; 35 D, lake water filtered through a plankton net of 35 μm mesh size wrapped with aluminium foil (dark).

recorded both in freshwater and marine ecosystems (Coon *et al*., 1987; Jackson *et al*., 1990; Estrada *et al*., 1993; McManus and Dawson, 1994; Gervais *et al*., 1997). In fresh waters, the trophic state of the lake determines the possibility of developing this maximum in deep layers, since only oligotrophic clear lakes may have the appropriate light climate allowing such a maximum below the mixed layer. On this basis, in Andean oligotrophic lakes, a deep Chl maximum can be predicted, but this feature had not been previously recorded.

In oligotrophic lakes, diatoms, green algae and cyanobacterial picoplankton have been found dominating deep waters (Coon *et al*., 1987; Shortreed and Stockner, 1990; Gervais *et al*., 1997). By contrast, in Lake Moreno Oeste we found distinctive deep Chl maxima dominated by ciliated protozoa with symbiotic *Chlorella*. In the epilimnion of the oligotrophic Lake Tanganyika and of the oligomesotrophic Lake Pavin, significant green ciliate populations have also been reported, and may lead to a notable overestimation of the phytoplankton biomass if evaluated on the basis of Chl content (Hecky and Kling, 1981; Amblard *et al*., 1993). Mixotrophic ciliated taxa, in particular large-size oligotrichs, have been found developing preferentially in oligotrophic waters (Beaver *et al*., 1988) where they can represent up to 50% of all ciliate biomass (Hecky and Kling, 1981; Amblard *et al*., 1993). In Andean lakes, a distinctive assemblage of large ciliates (>50 μm) constituted by a peritrich (*O.naumanni*) and a heterotrich (*Stentor araucanus*) has been previously reported (Modenutti, 1997). These two species were found in oligotrophic or ultraoligotrophic large lakes (>5 km^2), where they form large populations. Our data on Lake Moreno Oeste indicate that

O.naumanni dominates the ciliate assemblage and determines the deep Chl maximum near the 1% level of PAR. This is the first description of a natural situation where a dense population of a mixotrophic ciliate causes such a deep Chl maximum.

The results of our experiments showed a strong dependence of *O.naumanni* on light, since we observed that the species cannot survive under dark conditions. Nevertheless, the mixotrophic nature of this ciliate may be evident in the two alternative light treatments (with and without particulate matter). In the treatment with lake water filtered through 35 μm mesh, *O.naumanni* showed higher growth rates than in treatments with water filtered through 0.45 μm. The mixotrophic nature of ciliates having endosymbiotic algae gives them a competitive advantage by increasing their trophic efficiency (Hallock, 1981; Pace, 1982; Beaver *et al*., 1988). Symbiosis between phagotrophic and photosynthetic organisms would be especially favoured in oligotrophic waters, where a closed nutrient cycle within the symbiotic association would confer advantages to both members of the association (Fenchel, 1987).

Under high-light–low-nutrient environments, an autotrophic organism might excrete much of its carbon fixed through photosynthesis (Sterner *et al*., 1997). The advantage of *O.naumanni* having endosymbiotic *Chlorella* would lie in the fact that it may be able to profit from this organic carbon excreted by the algae directly into its cytoplasm. If a large proportion of fixed carbon is excreted, then ciliates containing these algae would be able to have an organic carbon source in a high-nutrient-limited environment. Lake Moreno Oeste has an extended euphotic zone (K_d = 0.12 m^{-1}, or Secchi disk 18 m) and very low nutrient concentration (TP < 4 μg l^{-1}, TDP < 2 μg l^{-1}). Under these conditions, the ciliate would obtain reduced carbon and the algae would receive mineral nutrients along the water column. Another advantage for the algae may be the reduced grazing on them. If this is so, endosymbiotic *Chlorella* would not need to counterbalance mortality losses as do other free-living algae. However, direct predation on *Ophrydium* cells, which would cause *Chlorella* mortality, has not yet been observed.

Owing to the closed nutrient cycle in a high-nutrient-limited environment, *Ophrydium* may adjust to an appropriate depth to balance light climate with nutrient availability. The importance of light quality for species selection in the deep Chl maximum has been shown in marine ecosystems (Wood, 1985; Glover *et al*., 1986). In fresh waters, Gervais *et al*. (1997) showed that in oligotrophic Lake Stechlin, picocyanobacteria were pre-adapted to 1% PAR irradiance (in the range 500–600 nm) by the presence of phycoerythrin. Unfortunately, we did not measure different light qualities along the water column, and there is no evidence that in green ciliates species selection occurs due to light quality.

Probably, a result of the mentioned advantages of the symbiotic association is the high contribution of endosymbiotic *Chlorella* biovolume to total photosynthetic biovolume (Figure 4). On the other hand, *O.naumanni* clearly dominated the zooplankton assemblage in terms of individual density (personal observation). Therefore, this association appears to be an effective exploitation of the water column in poor-nutrient–high-light ecosystems, like Andean large lakes.

As was shown, in Lake Moreno Oeste the effective photosynthetic biovolume

of *Ophrydium* may determine the Chl *a* distribution. Consequently, primary production would not be equally available for all consumers, as a large part of it is trapped within ciliate cytoplasm. Whether this organic matter is then consumed by a predator and re-entered into the traditional food web is as yet unknown. Under these circumstances, some models which refer to epilimnetic Chl *a* concentration (Quirós, 1990; Baigún and Marinone, 1995) must be viewed with care since these would not reflect either free-living algal biomass or the deep Chl *a* concentration.

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