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Increase in photosynthetic efficiency as a strategy of planktonic organisms exploiting deep lake layers

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SUMMARY

1. The photosynthetic efficiencies of the mixotrophic ciliate *Ophrydium naumanni* and the autotrophic dinoflagellate *Gymnodinium paradoxum* were investigated using laboratory and field experiments in Lake Moreno Oeste (41°5'S and 71°33'W, 758 m a.s.l.), in the Nahuel Huapi System (North Patagonia, Argentina).

2. The effect of different underwater light intensities on net primary production (NPP) was assessed during one summer. Additionally, laboratory experiments were carried out to obtain photosynthesis-irradiance response curves for each species.

3. *Ophrydium naumanni* and *G. paradoxum* dominated the metalimnetic (30 m depth) deep chlorophyll maximum (DCM) in the lake.

4. Despite these deep higher abundances, the cell-specific production of both species was higher at 10 m than at 30 m (DCM) depth. In addition, at 5 m depth, NPP was reduced by PAR + UV-A radiation.

5. Both species exhibited a positive NPP at very low irradiance but the mixotrophic ciliate was more efficient in exploiting the DCM irradiance level both *in situ* and at comparable light intensities in laboratory experiments. Light acclimatised *O. naumanni* showed a higher NPP at lower irradiances and photoinhibition at medium and high irradiances.

6. Under the strong wind-driven turbulence commonly found in Patagonian lakes, organisms cannot select their position in the epilimnetic water column and will be dragged to potentially harmful UV radiation levels. Thus, metalimnetic DCM colonisation by these two species represents a tradeoff between higher survival and lower cell-specific NPP.

Keywords: deep chlorophyll maxima, dinoflagellates, light availability, planktonic ciliates, ultra-oligotrophic lakes, UV radiation

Introduction

Ultraoligotrophic lakes receive low inputs of inorganic and organic nutrients from external sources. Low levels of primary production and low concentrations of relatively readily decomposable dissolved organic substrates result in low planktonic populations in a highly transparent medium. In such environments, phototrophs (autotrophs and mixotrophs) frequently develop below the surface mixed layer, producing a deep chlorophyll maximum (DCM) (Venrick, McGowan & Mantyla, 1972; Cullen, 1982; Coon *et al*., 1987; Gasol, Guerrero & Pedrós-Alió, 1992; Pilati & Wurtsbaugh, 2003). In the Andean Patagonian region, pristine ultraoligotrophic lakes have extended euphotic zones with low spectral absorption coefficients (Pérez, Queimaliños & Modenutti, 2002) and mixotrophic ciliate populations determine the chlorophyll *a* distribution in the

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water column (Modenutti, 1997; Queimaliños, Modenutti & Balseiro, 1999; Modenutti & Balseiro, 2002; Woelfl & Geller, 2002). In particular, *Ophrydium naumanni* Pejler, a freshwater pelagic ciliate with endosymbiotic *Chlorella*, has been observed at the DCM of several Andean lakes (Queimaliños *et al*., 1999; Pérez *et al*., 2002), codominating with the dinoflagellate *Gymnodinium paradoxum* Schilling (Queimaliños, Pérez & Modenutti, 2002).

Large mixotrophic ciliates (e.g. *Ophrydium, Stentor*) have been frequently described from plankton of southern-hemisphere lakes, including New Zealand (James, Burns & Forsyth, 1995), Australia (Laybourn-Parry *et al*., 1997) and South America (Woelfl, 1996; Modenutti, 1997; Woelfl & Geller, 2002). In Andean ultraoligotrophic lakes, *O. naumanni* has been observed mostly as solitary individuals (Woelfl, 1996; Modenutti, 1997; Woelfl & Geller, 2002), as was also indicated by Pejler (1962) for oligotrophic Swedish lakes. In oligotrophic lakes, mixotrophy can be viewed as an adaptive strategy that provides greater flexibility in the planktonic environment (Jones, 1994), as it may improve the access to scarce nutrients (Nygaard & Tobiesen, 1993). Furthermore, the zooplankton of such lakes is composed of small calanoids and few cyclopoids (James *et al*., 1995; Modenutti *et al*., 1998), which imposes a weak predation pressure on the protozooplankton (Balseiro, Modenutti & Queimaliños, 2001). Previous laboratory experiments revealed that *O. naumanni* has a dependence on light, as negative growth rates were obtained under continuously dark conditions (Queimaliños *et al*., 1999). In addition, particle ingestion by *O. naumanni* has also been observed to decrease under dark conditions (Modenutti & Balseiro, 2002).

The facts that *G. paradoxum* is a photoautotroph, and *O. naumanni* a mixotroph highly dependent on light, and that their highest abundances occur at the DCM implies the operation of an ecological constraint in the maintenance of such deep populations. The photosynthetic capability of heterotrophic organisms such as ciliates can be acquired by sequestering chloroplasts from ingested prey or by possession of photosynthetic cells as endosymbionts (Reisser *et al*., 1985). At the same time, plastid-sequestering oligotrichs are less efficient than those containing endosymbiotic algae (Laybourn-Parry *et al*., 1997). It could be expected that a photoautotroph organism like *G. paradoxum* would be more efficient in using light than a mixotrophic ciliate. However, the fact that *O. naumanni* has endosymbiotic *Chlorella* and dominates or codominates the DCM of Andean lakes, suggests that *O. naumanni* is efficient in fixing carbon through photosynthesis, and as efficient as a photoautotroph like *G. paradoxum*.

This study explores the different outcome of light irradiance on primary production of the two species dominating the DCM in Andean ultraoligotrophic lakes: the dinoflagellate *G. paradoxum* and the ciliate *O. naumanni*. Using laboratory and field experiments, we tested the light dependence of both species and analysed their photosynthetic efficiency responses, in order to compare the strategies of the mixotroph and the autotroph in the water column.

Methods

Study area

We conducted studies in Lake Moreno Oeste (41° 5′S and 71° 33′W, 758 m a.s.l.), which belongs to the Nahuel Huapi System (Patagonia, Argentina). Lake surface area is 6 km^2 and maximum depth is 90 m. The thermal regime is warm monomictic, remaining stratified from late November until April (spring-summer months) (Queimaliños *et al*., 1999; Modenutti, Balseiro & Queimaliños, 2000). The epilimnion of the lake has a neutral pH and a high transparency, with a euphotic zone extending to 35 m depth. Water is the major light-absorbing component, and blue light prevails in deep waters (Pérez *et al*., 2002). Conductivity values are very low (60 μS cm^{-1}) and dissolved oxygen remains at saturation levels throughout the water column. The lake is ultraoligotrophic, with total phosphorus between 2 and 4 μg L^{-1} and total dissolved phosphorus between 1 and 2 μg L^{-1}, and neither nutriclines nor oxiclines are observed (Queimaliños *et al*., 1999; Modenutti *et al*., 2000). Epilimnetic chlorophyll *a* concentration is around 0.6 μg L^{-1} and up to 3 μg L^{-1} at the deep chlorophyll maximum (Queimaliños *et al*., 1999; Modenutti *et al*., 2000). The regional climate is classified as temperate, influenced by westerly winds, with 1500 mm of annual precipitation and a mean 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.

Light and temperature profiles, chemical analysis and counting

On each sampling occasion, light vertical profiles (0–50 m) of UV bands (305, 320, 340 and 380 nm), photosynthetically active radiation (PAR) (400–700 nm) and temperature were measured using a PUV 500B submersible radiometer (Biospherical Instruments, San Diego, CA, U.S.A.). *In situ* chlorophyll *a* profiles were determined with the PUV 500B (PUV 683), calibrated against measurements in a laboratory 10-AU fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.). Water samples were obtained at 10 and 30 m depth with a 12 L Schindler-Patalas trap. A volume of 500 mL was used for laboratory chlorophyll *a* determinations and 250 mL were sampled for phytoplankton and ciliate enumeration.

In the laboratory, chlorophyll *a* was immediately determined for samples carried from the field that had been kept in darkness and thermally isolated. Samples were filtered onto GF/F filters and extracted with hot ethanol (Nusch, 1980) and measured with a 10-AU fluorometer (Turner Designs). For individual chlorophyll *a* content, six groups of 100 *O. naumanni* and 300 *G. paradoxum* were carefully picked up with a micropipette under a stereomicroscope, rinsed in 0.2 μm-filtered lake water and placed on a GF/F filter, followed by the above procedure.

Phytoplankton and ciliate samples were preserved in Lugol's iodine solution. Enumeration of cells was performed following the Utermöhl technique with an inverted microscope (Olympus IX70, Tokyo, Japan) using 50 mL Utermöhl chambers. Ciliate quantification was carried out by scanning the entire surface of the chamber at 200× magnification.

Net primary production measurements

Net primary production (NPP) was measured using the ^{14}C technique (Steeman Nielsen, 1951, 1952). Dark bottle measurements were substituted by the 'time 0' organic ^{14}C measurement by adding the isotope to the dark bottle and immediately filtering and analysing (Fanhenstiel, Redalje & Lohrenz, 1994). To measure individual primary production of *O. naumanni* and *G. paradoxum*, we performed preliminary laboratory incubations in 20 and 7 mL glass vials, which did not interfere with the wavelength spectrum higher than 320 nm, in a temperature and light controlled incubator. Lake Moreno water was filtered through 3 μm and 0.2 μm Millipore™ filter (Millipore, Betford, MA, U.S.A.) and the protists were separated under a stereomicroscope, rinsed twice in filtered lake water and added carefully to the vials filled with filtered lake water. We performed incubations for each species separately, in two densities and with the two types of filtered water, in three replicates each: 40 *O. naumanni* and 90 *G. paradoxum* in 20 mL vials, and 20 *O. naumanni* and 45 *G. paradoxum* in 7 mL vials. In addition, 20 mL of 3 μm filtered lake water was also incubated to obtain a blank for the protist measurements. Lake water was sampled at 10 and 30 m depth and was filtered through a 3 μm Millipore™ filter. Temperature and irradiance during the incubations resembled metalimnetic conditions (10 °C and 18 μmol photons m^{-2} s^{-1}). To each vial, 0.03 μCi $NaH^{14}CO_3$ mL^{-1} (Amersham Radiochemicals, Amersham, UK) were added and then incubated for 4 h. These preliminary experiments indicated that the number of protists added was suitable to give consistent results, and no marked difference was observed between 3 and 0.2 μm filtered lake water incubation.

Field study

During summer 2002–03 (December to February) four field experiments were carried out. Lake water and protists were sampled at 10 and 30 m depth on the same day 2 h before starting the incubations. Incubations were carried out, in 20 mL vials held in a frame, at 10 m (epilimnion) and 30 m depth (coinciding with the DCM). At each treatment depth, the protist species (40 *O. naumanni* and 90 *G. paradoxum* in 3 μm filtered lake water) were placed in three replicates each. In addition, lake water from 10 and 30 m depth was incubated to estimate total NPP. Filtered lake water (on 3 μm) was used as a blank for the protist measurements. On 23 February 2003, we included a third depth for incubation at 5 m using 4-mL quartz tubes with the same organisms (20 *O. naumanni* and 45 *G. paradoxum*). This incubation was run in two treatments, one exposed to full sunlight (quartz tubes) and the other only to PAR+UV-A (quartz tubes wrapped with Mylar™ foil (Dupont, Santa Barbara, CA, U.S.A.) with a cut-off at 320 nm). To each flask or tube 0.03 μCi $NaH^{14}CO_3$ mL^{-1} were added and then incubated for 4 h, symmetrically around noon.

After incubation, 1 mL aliquots were taken to check total activity. The samples were filtered using plastic disposable syringes and plastic filter holders with 0.2 μm Millipore nitrocellulose filters. Filters were acidified with 200 μL 1N HCl for 60 min. After adding 10 mL of scintillation liquid the vials were counted in a Wallac 1414 scintillation counter (Wallac, Turku, Finland).

Laboratory experiments

Photosynthesis–irradiance response (P/E) curves. We conducted a series of laboratory incubations to obtain P/E curves for both species. The experiments were carried out at 12 light intensities (from 10 to 2000 μmol photon m^{-2} s^{-1}) in an incubator filled with circulating water, with temperature control (12 ± 0.1 °C) and rotation (0.25 r.p.m.) of the incubation vials. We used 7 mL vials with 0.2 μm-filtered lake water and 20 *O. naumanni* or 45 *G. paradoxum*. Each light treatment was conducted in three replicates. In the case of *O. naumanni* we achieved two P/E curves: one with non-acclimatised individuals and the other with acclimatised ones. In the former, NPP was measured immediately after the individuals were placed in the different light treatments while in the latter the individuals were introduced 15 h prior to the measurement at each light intensity. We added 0.03 μCi $NaH^{14}CO_3$ mL^{-1} to the vials and the incubation was run for 4 h. Light intensity was measured with a Biospherical Instruments, QSL 100 sensor inside a vial. After the incubation the procedures were the same as above.

Data analysis

Field production efficiency was calculated as chlorophyll-specific production per irradiance unit of each depth. The P/E data were normalised to chlorophyll *a* and then fitted to the model described by Eilers & Peeters (1988),

$$P = \frac{I}{aI^2 + bI + c}$$

and $\alpha = \frac{1}{c}$ and $P_{\max} = \frac{1}{b+2\sqrt{ac}}$ where α is the initial slope an $P_{\max}$ is the maximal production rate. Data were fitted using Sigma Plot 2001 to perform the non-linear least-squares regression. Analysis of data was performed using Sigma Stat 2.03 statistical package and Prism 3.0 was used for comparison of slopes of linear regressions.

Results

Field study

During summer 2002–03, Lake Moreno Oeste was thermally stratified with a clear thermocline around 30 m depth, except in December when an incipient stratification was developing. Temperature ranged from 11 to 16 °C in the epilimnion and 7–8 °C in the hypolimnion. The lake had high transparency and the diffuse extinction coefficient (Kd PAR) was low and fairly constant, varying between 0.123 and 0.140 m^{-1} (Table 1). The lower limit of the euphotic zone (1% of surface PAR irradiance) was situated at about 35 m depth and included the whole of the mixed layer and the metalimnion of the lake (Fig. 1). The 1% depth of UV-B radiation at 305 nm was 6 and 8 m at 320 nm. Thus, 15–25% of the euphotic zone and 20–40% of the epilimnion received this radiation (Table 1, Fig. 1).

Epilimnetic chlorophyll *a* concentration always remained very low (0.5–1.2 μg L^{-1}). However, in the metalimnion the pigment concentration increased up to 2–5 μg L^{-1} producing a DCM (Fig. 1). This vertical heterogeneity was observed to develop through the season, and was more pronounced at mid to end summer (February) when windless conditions and

Table 1 Diffuse extinction coefficient (Kd) and depth of 1% of surface irradiance ($Z_{1\%}$) in Lake Moreno Oeste at each incubation date

Wavelength (nm)	9 December 2003		24 January 2003		6 February 2003		23 February 2003	
	Kd	$Z_{1\%}$	Kd	$Z_{1\%}$	Kd	$Z_{1\%}$	Kd	$Z_{1\%}$
305	0.875	5.3	0.873	5.3	0.776	5.9	0.757	6.1
320	0.773	6.0	0.639	7.2	0.587	7.9	0.561	8.2
340	0.617	7.5	0.479	9.6	0.447	10.3	0.417	11.1
380	0.318	14.5	0.296	15.6	0.269	17.1	0.237	19.4
PAR	0.123	37.5	0.140	32.8	0.140	33.4	0.130	35.5

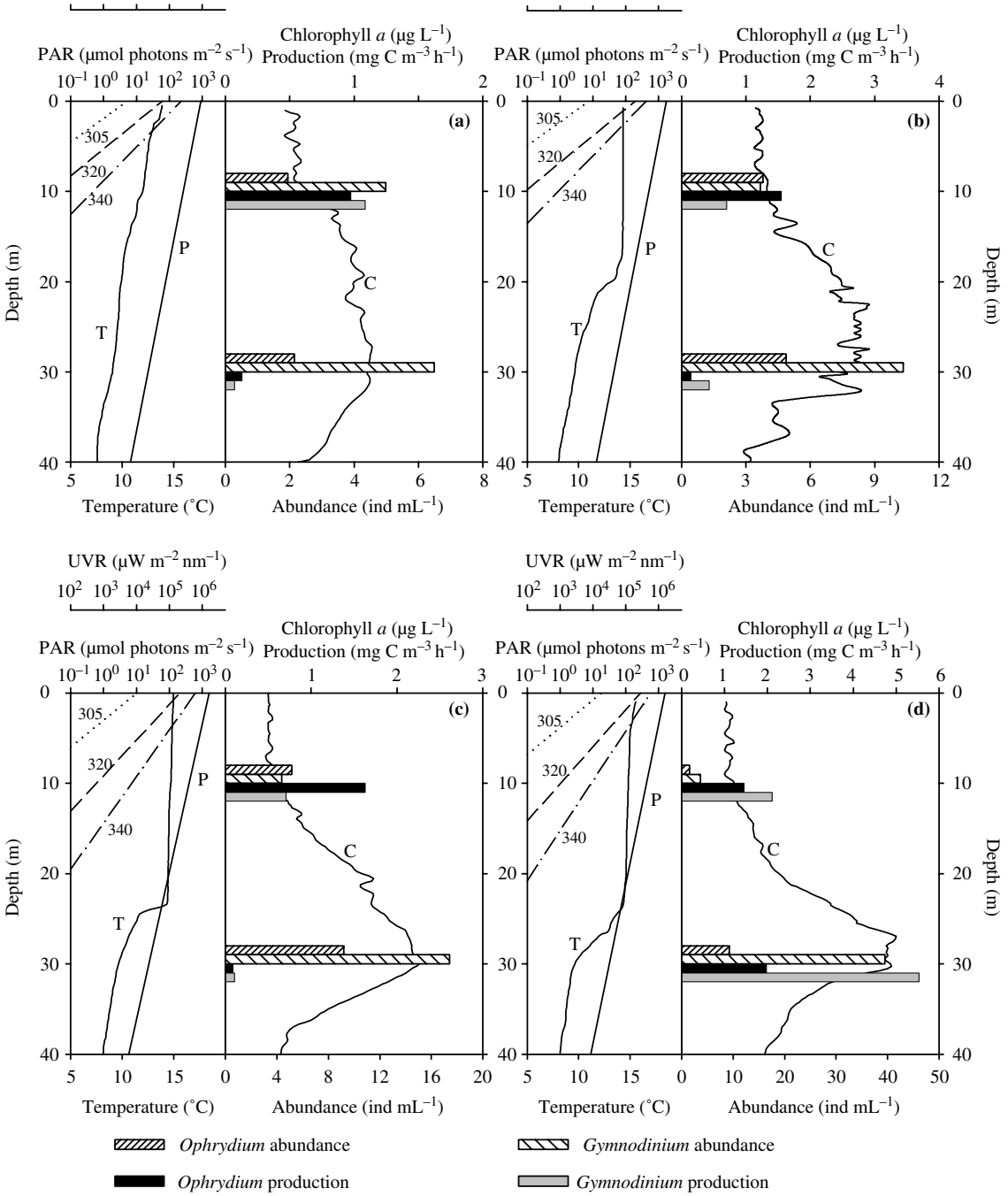

Fig. 1 Temperature (T), light [305, 320, 340 nm and PAR (P)] and chlorophyll *a* (C) vertical profiles; abundance and primary production of *Gymnodinium paradoxum* and *Ophrydium naumanni* at 10 and 30 m depth in Lake Moreno Oeste during the summer season 2002–2003. (a) December 9; (b) January 24; (c) February 6; (d) February 23.

high irradiance occurred (Fig. 1b,c). Physical conditions at this metalimnetic maximum were a temperature of 7–11 °C, no UV radiation, and 3.65–15 μmol photons m^{-2} s^{-1} of PAR irradiance (Fig. 1).

Ophrydium naumanni and *G. paradoxum* were recorded both in the epilimnion (10 m) and the metalimnion (30 m). Nevertheless, abundances were observed to increase at about 30 m depth, near the

Table 2 Individual specific production of *Ophrydium naumanni* and *Gymnodinium paradoxum* and total net primary production (NPP) in Lake Moreno Oeste during the 2002–03 summer field incubations. Values are given as mean ± SE

	9 December 2002		24 January 2003		6 February 2003		23 February 2003	
Production	10 m	30 m	10 m	30 m	10 m	30 m	10 m	30 m
O. naumanni (pg C cell^{-1} h^{-1})	500 ± 22	60 ± 21	409 ± 134	29 ± 12	315 ± 88	9 ± 2.4	564 ± 92	125 ± 33
G. paradoxum (pg C cell^{-1} h^{-1})	218 ± 10	11 ± 4	190 ± 25	41 ± 20	161 ± 11	6 ± 2	336 ± 17	82 ± 27
Total (NPP) (mg C m^{-3} h^{-1})	0.89 ± 0.11	0.11 ± 0.02	3.32 ± 0.42	0.24 ± 0.03	2.96 ± 0.22	0.50 ± 0.05	2.52 ± 0.30	3.41 ± 0.47

limit of the euphotic zone and just below the upper limit of the metalimnion (Fig. 1). Individual chlorophyll *a* content reached 0.23 ±0.04 ng Chl cell^{-1} in *O. naumanni* and 0.08 ±0.01 ng Chl cell^{-1} in *G. paradoxum*. No marked change in chlorophyll cell content was observed in the vertical profiles in any of the experiments. The contribution of the mixotrophic ciliate to total chlorophyll *a* at the DCM was between 40 and 60%, with highest values recorded in early summer (December and January); *G. paradoxum* made an important contribution (54%) in February.

The field incubations revealed that individual primary production was higher in *O. naumanni* than *G. paradoxum*. The cell-specific production of both species was higher at 10 m than at 30 m depth, indicating that the 10 m epilimnetic irradiance level was more suitable for photosynthetic activity (Table 2). Therefore, both species were light limited at the DCM level (Fig. 1). At 10 m depth, the effect of short wavelengths was minimised as UV intensity at 320 nm was <1% of that at the surface. At 5 m depth, we observed a similar (*t*-test, $P > 0.05$) decline in the chlorophyll-specific NPP values in the presence of UVB + UVA + PAR (i.e. quartz tubes) or UVA + PAR (i.e. quartz tubes wrapped with Mylar^{TM}) (Fig. 2). However, both treatments were significantly lower than the NPP at 10 m depth (ANOVA, $P < 0.005$ for both species). The lowest values were obtained for *O. naumanni* in the full sunlight treatment.

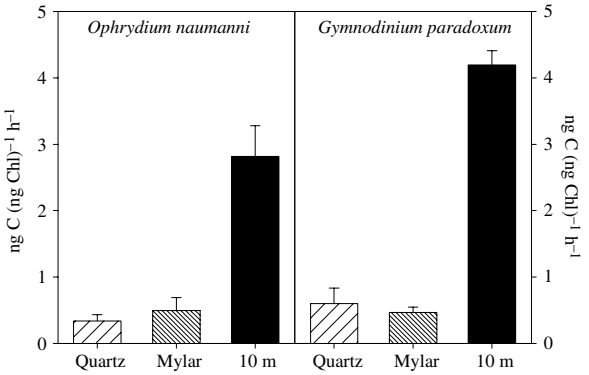

Fig. 2 Chlorophyll specific primary production of *Gymnodinium paradoxum* and *Ophrydium naumanni* at 5 m (Quartz and Mylar^{TM}) compared with that of 10 m depth in Lake Moreno Oeste (23 February 2003).

Total NPP was also higher at 10 m than at 30 m depth, reaching 2.96 ± 0.22 mg C m^{-3} h^{-1} at 10 m in February (Table 2). The contribution of the mixotrophic ciliate and *G. paradoxum* to total NPP was estimated to be between 20 and 70% through the season.

The analysis of photosynthetic efficiency (chlorophyll-specific production per irradiance unit) in relation to irradiance level revealed different trends in the two species (Fig. 3). In the field, *G. paradoxum* had consistent efficiency values independent of irradiance levels (Fig. 3), while *O. naumanni* showed a decline in efficiency as irradiance increased, being twice as efficient as *G. paradoxum* at metalimnetic irradiance levels (30 m depth) (Fig. 3). The linear regressions obtained for each species were significantly different (comparison of slopes test, $F = 34.15$, $P < 0.001$).

Photosynthesis –Irradiance response curves

In the laboratory experiments, the P/E curves showed in both species that PP increased with irradiance (Fig. 4). *Ophrydium naumanni* showed a saturation curve while *G. paradoxum* was photoinhibited at about 2000 μmol photons m^{-2} s^{-1}. The photosynthetic parameters α and *P* max were similar for the two species, although the latter was higher in *G. paradoxum* (Fig. 4).

As in the field *O. naumanni* showed a distinctive efficiency response, we carried out a second laboratory experiment with light acclimatised individuals. In this case, organisms were exposed to experimental irradiance levels for 15 h prior to the incubation, allowing *O. naumanni* to adjust to a more efficient light exploitation. The obtained P/E curve differed greatly from

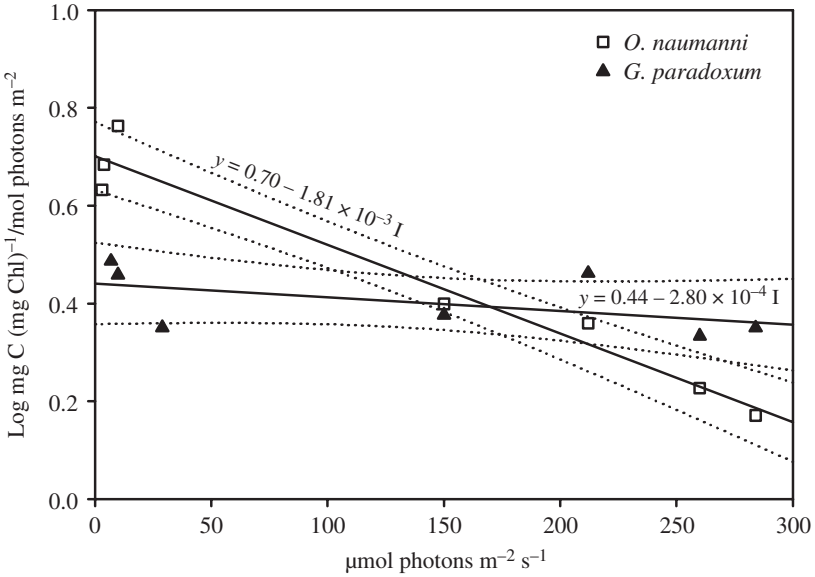

Fig. 3 Photosynthetic efficiency versus irradiance of *Gymnodinium paradoxum* and *Ophrydium naumanni* pooling all field experiments.

the previous one without acclimation, showing a sharp increase at low irradiance and a moderate photoinhibition at medium and high irradiance levels (Fig. 4). The coefficient α was considerably higher than that obtained for non-acclimatised individuals. However, *P* max decreased, confirming that the organisms were more photoinhibited.

Discussion

Our study showed that in an ultraoligotrophic, transparent lake both chlorophyll *a* concentration and the abundance of organisms reached their maxima deep in the metalimnion, although NPP per cell was lower here than in the epilimnion. Andean lakes, compared

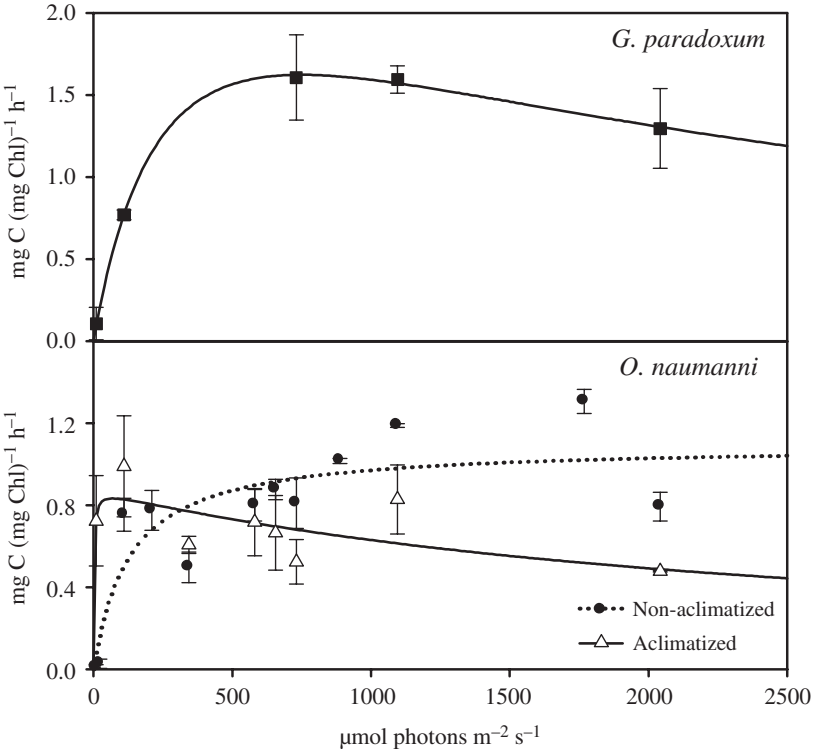

Fig. 4 Laboratory P/E curves of *Gymnodinium paradoxum* and *Ophrydium naumanni*. Model parameters: *G. paradoxum*, $\alpha = 0.0097$, $P_{max} = 1.624$; *O. naumanni* non-acclimatised, $\alpha = 0.0085$, $P_{max} = 1.094$; *O. naumanni* acclimatised, $\alpha = 0.4838$, $P_{max} = 0.832$.

with other mountain lakes (Laurion *et al*., 2000), are at the extreme of high transparency for lakes below the tree line, because of low DOC concentration (Morris *et al*., 1995). In addition, the Patagonian strong winds (>43 km h^{-1}) blow for 41% of the days of the year, resulting in very extended mixed layers (Baigún & Marinone, 1995). The upper level of the epilimnion receives high irradiance, not only PAR but also potentially hazardous shorter wavelengths (UV-B and UV-A). Photosynthetic inhibition in phytoplankton, using *in situ* techniques, has previously been observed in Patagonian waters including a small and shallow Andean lake (Villafañe, Helbling & Zagarese, 2001). In our study, at 5 m depth NPP was observed to decrease, suggesting that PAR + UV-A radiation produced photoinhibition in both species.

According to the underwater radiation characteristics, the water column can be divided into three parts, two of which are unsuitable for NPP – the upper level (0–8 m) because of harmful radiation, and the deepest level (>40 m) because it is aphotic. The intermediate level (8–40 m depth) was observed to be appropriate for NPP, although in both species the NPP per cell decreased with depth. Under this scenario, phototrophic species would be expected to perform best at the intermediate level, but they are subject to the constraint of thermal stratification. Organisms above the thermocline have a higher NPP, but mixing can carry them close to the surface. Static incubations fail to predict the performance of vertically moving individuals and may offer a distorted picture of the effects of UV in nature (Zagarese *et al*., 1998). In fact, the higher production obtained at 10 m depth was due to organisms being trapped in the incubation bottles, rather than free to be dragged to upper levels by mixing. On the other hand, organisms below the thermocline are exposed to low irradiance, although enough for positive NPP. Thus, *O. naumanni* and *G. paradoxum* living at the metalimnion, despite a lower NPP, have a lower cost in comparison with epilimnetic dragged ones. This balance would allow them to achieve higher population densities at the metalimnetic level.

In oligotrophic environments, mixotrophic ciliates appear especially favoured (Jones, 1994) as mixotrophy may improve their access to scarce nutrients (Nygaard & Tobiesen, 1993). Larger 'more autotrophic' mixotrophs are more frequent in oligotrophic systems than small mixotrophic oligotrichs, as carbon fixed via photosynthesis may be a larger proportion of the assimilated carbon (Dolan & Pérez, 2000). In previous studies, it has been shown that the primary energy source for *O. naumanni* is light, and particle ingestion was dependent itself on light availability (Queimaliños *et al*., 1999; Modenutti & Balseiro, 2002). In metalimnetic dim light, the mixotroph was able to fix carbon through photosynthesis as well as to ingest particles. Phytoplanktonic species have also been observed to be able to exploit dim light levels (Reynolds, 1984). In particular, dinoflagellates can profit at deep levels of the euphotic zone (Pollingher, 1988) and develop DCM at 75–150 m below the surface in nutrient-poor oceans (Van den Hoeck, Mann & Jahns, 1998) or near nutriclines (Kononen *et al*., 2003). Our study revealed that *G. paradoxum* was able to have positive net production at very low irradiance and in the absence of nutriclines. However, the mixotrophic ciliate *O. naumanni* was more efficient than *G. paradoxum* in exploiting the DCM irradiance level both *in situ* and at comparable irradiance in laboratory experiments (Figs 1 and 3).

The photosynthesis-light intensity models for phytoplankton assume that the probability of a unit of light hitting a photosynthetic unit remains constant as light increases (Eilers & Peeters, 1988). This would be true for *G. paradoxum* and it may be expected that the specific photosynthesis per energy unit would remain constant unless photoinhibition occurs. The results of our field experiments are in accordance with this assumption because the slope of the photosynthetic efficiency curve for *G. paradoxum* was not different from zero (Fig. 3). On the other hand, the symbiotic consortium of *O. naumanni* with *Chlorella* showed a more adaptive response to light intensity. More elongate particles absorb more light than spherical ones of equal volume (Kirk, 1994). The cell of peritrichs is highly contractile, as they have sets of functional myonemes in the oral and peristomial disc or for contracting the whole zooid (Corliss, 1979). In particular, *Ophrydium* has a very mobile neck and shows extreme variation in form depending on ontogeny and environmental conditions (Winkler & Corliss, 1965). Thus, the length of the entire cell is highly variable, allowing the endosymbiotic *Chlorella* to be arranged to optimise the light received. At low irradiance, *O. naumanni* adopt a very elongate form but high irradiance causes cell contraction (E. Balseiro, personal observation). Consequently, the ciliate can maximise the exposure of its photosynthetic cells or decrease the

efficiency with which the consortium uses light, depending on light intensity.

The two species had different P/E curves in the laboratory experiments. In phytoplanktonic species, short incubations (minutes) lead to saturation curves as photosynthetic units need time to become inactive because of excessive light (Eilers & Peeters, 1988). However, our incubations lasted 4 h, implying that for a phytoplanktonic species such as *G. paradoxum*, photoinhibition would have been measurable. Indeed, we did observe a moderate photoinhibition at irradiances around 2000 μmol photons m^{-2} s^{-1}. It seems that *O. naumanni* responds more slowly to high irradiances because the 4 h incubation resulted in a saturation curve, while photoinhibition was observed after 15 h of acclimation.

Observations suggest that locomotory activity of large ciliates (e.g. *Stentor*) and swimming effort of dinoflagellates are likely to be overridden by turbulent mixing of the water column (Pollingher & Zemal, 1981; Laybourn-Parry *et al*., 1997). Therefore, under strong wind-driven turbulence, as in Patagonian lakes, organisms cannot select their position in the epilimnetic water column. The better exploitation of dim light by *O. naumanni* could explain its success in ultraoligotrophic Andean lakes.

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