

# *Daphnia* distribution in Andean Patagonian lakes: effect of low food quality and fish predation

Esteban Balseiro · Beatriz Modenutti ·  
Claudia Queimaliños · Mariana Reissig

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**Abstract** Food quality in terms of carbon (C):phosphorus (P) ratio can constrain the success of highly demanding P herbivores as *Daphnia*. North Andean Patagonian lakes are ultraoligotrophic with low nutrient concentrations and well-developed euphotic zones. We investigated the distribution of the large *Daphnia commutata* in relation with food quality ( sestonic C:P ratio) and predation risk in these lakes. The predation risk was estimated based on the fish species present and their relative eye diameter and transparency of the lake. The C:P ratios in the lakes were high, varying from 350 to >1,200. The lakes with *D. commutata* had significantly lower C:P ratio than those without these daphnids. On the other hand, those lakes where *Daphnia* is present have the lower predation risk than those where *Daphnia* is absent. In addition, we carried out growth experiments with neonates and natural seston of three lakes with different C:P ratio. The growth rates were inversely related with C:P of the food. Food quality and predation risk together determined the success or failure of large *Daphnia* populations in these Andean clear ultraoligotrophic lakes.

**Keywords** Stoichiometry Planktivory C/P ratio Oligotrophic lakes Predation risk Vertical migration Light climate

## Introduction

Aquatic ecosystem structure and processes are primarily determined by the inputs of light and nutrients, both in absolute and relative terms. Recent studies have demonstrated that the phytoplankton primary production, in terms of elemental ratios, may be determined by the light levels and nutrient inputs (Urabe and Sterner 1996; Sterner et al. 1997). At the same time, these inputs control the efficiency of transfer of carbon and energy from the bottom to the top of foodweb in lakes (Sterner et al. 1997). At high light levels the uptake of C and P may be desynchronized causing the increase in the C:P ratios (Hessen et al. 2002). Thus, when availability of solar energy is high relative to P, the seston would assimilate relatively more carbon than phosphorus. On the contrary, C:P ratios tend to be lower under low light and unlimiting P concentrations (Urabe and Sterner 1996; Sterner et al. 1997).

In daphnids, which are commonly the most important grazers of lakes, phosphorus requirements for somatic growth are high, whereas freshwater phytoplankton is frequently phosphorus deficient (Hessen 1992; Sterner 1993). Phytoplankton in lakes often show very high C:P ratio, compared with

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E. Balseiro (✉) · B. Modenutti · C. Queimaliños  
M. Reissig  
Laboratorio de Limnología, CONICET – Centro Regional  
Universitario Bariloche, Universidad Nacional del  
Comahue, Quintral 1250, Bariloche 8400, Argentina  
e-mail: balseiro@crub.uncoma.edu.ar

consumers (Elser and Hassett 1994), and this could lead to low food-chain production and limit phosphorus for growth of daphnids (Sterner and Hessen 1994; Hessen 1997; Sterner et al. 1997, 1998; Hessen and Faafeng 2000). Food quality limitation due to insufficient P content is predicted to occur for *Daphnia* species when food atomic C:P ratio exceeds 300 (Urabe et al. 2002). Resource C:P ratios >300 are common in lakes, leading to the prediction that *Daphnia* should often experience P limitation in nature (Sterner and Schulz 1998; Brett et al. 2000).

Light also affects the coexistence of planktivorous fish and large *Daphnia*, since the presence of a deep-water refuge for avoiding predation under cover of darkness may favour their coexistence (Wright and Shapiro 1990; Tessier and Welser 1991). Therefore, it can be assumed that extremely transparent lakes will have increasing risk of fish predation. Consequently, high-light:low-nutrient environments can be predicted as unfavourable for *Daphnia* growth due to poor food quality mainly due to insufficient P, and to fish predation pressure.

North-Patagonian Andean lakes (40°–42°S) are extremely transparent and have very low nutrient concentrations (Morris et al. 1995; Markert et al. 1997; Modenutti et al. 2000). Based on Sterner et al. (1997) light-nutrient model it was estimated that these lakes have extremely high C:P ratios in seston (Balseiro et al. 2004). At the same time, the absence of *Daphnia* in many of these lakes is remarkable (Modenutti et al. 1998). However, in a few Andean lakes the presence of large *Daphnia* (*D. commutata*, reported in earlier studies as *D. middendorffiana*) has been observed (José de Paggi and Paggi 1985; Pizzolón et al. 1995; Modenutti et al. 2003; Balseiro et al. 2004). High illuminated habitats are related

with a relatively higher probability of attack by visual predators. Thus, in these lakes with both autochthonous and exotic fishes large *Daphnia* should avoid the illuminated layers during daytime (Reissig et al. 2004).

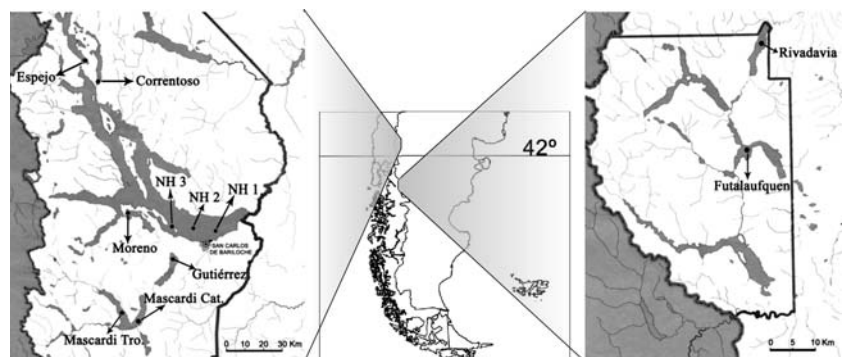
Under this scenario, the presence of large *Daphnia* in Andean lakes would be constrained by a low food quality (high C:P ratio) and high visual predation risk. This prevailing situation led us to test the food quality and the predation hypotheses in the presence-absence of large *Daphnia*. We performed a field summer survey for comparing the deep stratified lakes with and without *D. commutata*, and to identify trends in the presence of *Daphnia*. In addition, we used a *Daphnia* juvenile growth assay to test how food quality limitation varied in lakes that differed in C:P ratios.

## Material and methods

### Field study

This study was carried out in eight large Andean lakes of glacial origin with deep basins ( $Z_{\max} > 100$  m) and located between 40°40' S and 42°49' S and 71°38' W and 71°44' W (North Patagonia, Argentina) (Fig. 1). The lakes are included in the Nahuel Huapi National Park (Lakes Correntoso, Espejo, Nahuel Huapi, Moreno Oeste, Gutiérrez and the two arms of lake Mascaradi, Tronador and Catedral), and Los Alerces National Park (Lakes Rivadavia and Futalauquen). The climate in the region is temperate, cool with an annual precipitation of 1,500 mm and a mean annual temperature of 8.7 °C (Paruelo et al. 1998). The surrounding vegetation

**Fig. 1** Study Site. Lakes of Nahuel Huapi National Park (left panel) and Los Alerces National Park (right panel). NH 1, NH 2 and NH 3 correspond to Nahuel Huapi 1, 2 and 3; Mascaradi Tro. to Mascaradi Tronador and Mascaradi Cat. to Mascaradi Catedral



is constituted by a mixed forest of *Nothofagus dombeyi* (Mirb.) Blume and *Austrocedrus chilensis* (D. Don) Florin et Boutleje.

The lakes exhibit a warm, monomictic thermal regime, with stable thermal stratification during late spring and summer. Dissolved oxygen concentration remains at ~100% saturation level all along the water column and transparency is extremely high with very low extinction coefficients ( $K_{d\text{ PAR}} = 0.10\text{--}0.16\text{ m}^{-1}$ ) (Morris et al. 1995). Lake Mascardi has higher  $K_d$  values ( $0.22\text{ m}^{-1}$ ) (Morris et al. 1995) because it receives the upper Río Manso with opaque waters (with glacial clay) discharged by glaciers from Tronador Mountain (Chillrud et al. 1994; Modenutti et al. 2000). As a consequence, the transparency increases from the western arm Tronador to the eastern arm Catedral (Modenutti et al. 2000).

All lakes have a mixture of native and exotic fishes. The autochthonous assemblage has some differences among the studied lakes, while introduced exotic salmonids, *Salmo trutta* L., *Salvelinus fontinalis* (Mitchill) and *Oncorhynchus mykiss* (Walbaum), do not show such differences between them (Macchi et al. 1999).

Each of the eight lakes (11 sampling sites) was sampled once during summer 2003 (January 13–February 26) under stable thermal stratification. Samples were obtained in a central sampling point located at the deepest part of each lake basin. Lake Nahuel Huapi was sampled in three sampling points (Nahuel Huapi 1, 2 and 3) and Lake Mascardi in two (Mascardi Catedral and Mascardi Tronador) (Fig. 1). All sampling were carried out at mid-day, 1 h before astronomical noon.

Vertical profiles of temperature, Photosynthetically Active Radiation (PAR, 400–700 nm), and *in situ* chlorophyll *a* distribution were measured with a PUV 500B submersible radiometer (Biospherical Instruments). Water samples of 12 l were obtained with a Schindler–Patalas trap from 5, 10 and 30 m depth, in Lake Nahuel Huapi 40 m depth. They were then transferred to 5 l polypropylene containers (HCl washed), which were kept in dark and thermally isolated, and immediately carried to the laboratory. Zooplankton of each lake was sampled with vertical tows from 0–10–30–50 m performed with a Bongo net of 48 and 202  $\mu\text{m}$  mesh size with closing mechanism.

At the laboratory, direct measurements of chlorophyll *a* concentration were carried out by filtering

500 ml of lake water of each depth onto GF/F Whatman filters. Chlorophyll *a* concentration was determined fluorometrically with a Turner AU 10 Fluorometer by extraction with hot 90% ethanol following Nusch (1980). PUV vertical profiles of Chlorophyll were adjusted to these direct measurements.

A volume of 300 ml of lake water from 5, 10 and ~30 m depth (in Nahuel Huapi at 40 m depth) was filtered through pre-combusted GF/F Whatman filters in order to assess the elemental composition of the seston of each lake. Filters were dried at 60°C and stored at 20°C until analysis. Total sestonic carbon (TSC) was analyzed on a Carlo Erba 1112 CHN elemental analyzer. Total phosphorus (TP) and total particulate phosphorus (TPP) were analyzed with persulphate digestion followed by molybdate reaction (APHA 1989).

Crustacean zooplankton were examined under stereomicroscope in 5 ml Bogorov chambers. Body size of a minimum of 30 *D. commutata* was measured under microscope with a graduate eyepiece.

#### Laboratory experiments

Growth rates of *Daphnia* neonates were measured in laboratory under different natural lake seston. The daphnids used were sampled from Lake Mascardi (Catedral) four days earlier. Lake water was sampled from 20 m depth with a Ruttner bottle and at the laboratory, it was gently filtered through 80  $\mu\text{m}$  mesh net size. Egg carrying females were carefully sorted under dissecting microscope and placed in beakers with filtered lake water. During the next day, all neonates and non-egg carrying females were discarded, and after 24 h of this procedure, neonates (<24 h old) were selected for starting the experiment. The experiment was carried out with water from lakes (Mascardi Catedral, Gutiérrez and Correntoso) with different C:P ratios. Experiments were run in an incubator at 15°C (epilimnion temperature of lakes) and 14:10 (light:dark) photoperiod. Freshly collected water from each lake was filtered through 80  $\mu\text{m}$  mesh net size. A total of 500 millilitre of filtered water of each lake was analyzed for C:P ratios (100 ml for TPP and 400 ml for total sestonic carbon (TSC).

The body area of animals (at <24 h) was measured by taking lateral images of each animal, and calcu-

lating it by using Image-Pro Plus, (Media Cybernetics) software, following Acharya et al. (2004). Non-injured neonates were then transferred to 50 ml Erlenmeyer ground stopper flasks filled with the corresponding filtered lake water. The flasks were completely filled to decrease the risk of neonates getting caught in the surface tension. The animals were moved to freshly filtered lake water every 24 h using a clean 5 ml pipette. Animals were measured every 48 h. Experiments lasted for 4 days, and were run in 20 replicates. Animals from the different treatments were dried at 60°C for C content analysis and treated as seston samples.

### Data analysis

Diffuse attenuation coefficients of PAR (400–700 nm) ( $K_d$  PAR) for each lake were calculated by regressing log-transformed (ln) light with depth. The visual predation risk (PR) was calculated for the native fish assemblage based on the water transparency ( $K_d$ ) and a relative visual acuity of each fish species. The latter variable was estimated on the Relative Eye Diameter (RED), which was obtained from literature measurements (Ringuélet et al. 1967) as the ratio of the eye diameter to headlength. This measure was considered as an estimate of the visual capability of the fish, based on the fact that larger eye lens (relative to head size) would imply larger optic tectum, and higher visual acuity (Guthrie and Munts 1993). For each lake, all RED values (one for each native fish species present) were obtained. The PR was estimated as the ratio of the maximum RED in the lake and the corresponding  $K_d$  (max RED/ $K_d$ ). Larger eyes or more transparent lakes (lower  $K_d$ ) would define higher risk.

Migration distance of daphnids was estimated for each lake, based on PAR intensity and the vertical day and night distribution of *D. commutata* in Lake Rivadavia. We used Lake Rivadavia data because is the only one of this set with available analysis of zooplankton diel vertical migration (Reissig et al. 2004). We assumed that *Daphnia* vertical distribution in each lake would be at depths that have equivalent light intensities of those observed in lake Rivadavia. Mid-day PAR intensity measured with the PUV, at the level of *D. commutata* maximum abundance during day and night (58 and 0.27  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively), was used to estimate the day

and night depth distribution of *Daphnia* in each lake. The difference between these two depths was assumed as the distance that *Daphnia* would have migrated in each lake.

Growth rates of *Daphnia* neonate experiments, were estimated as the proportional change in the body area (without the tail spine) as

$$GR \delta \text{day}^{-1} = \frac{1}{t} \ln \left( \frac{f.a.}{i.a.} \right) = t$$

where f.a. and i.a. are final and initial areas, expressed in  $\text{mm}^2$ ,  $t$  is time in days.

Statistical significance of differences were tested through ANOVA. Data were log transformed when needed to fulfil normality and homoscedasticity.

## Results

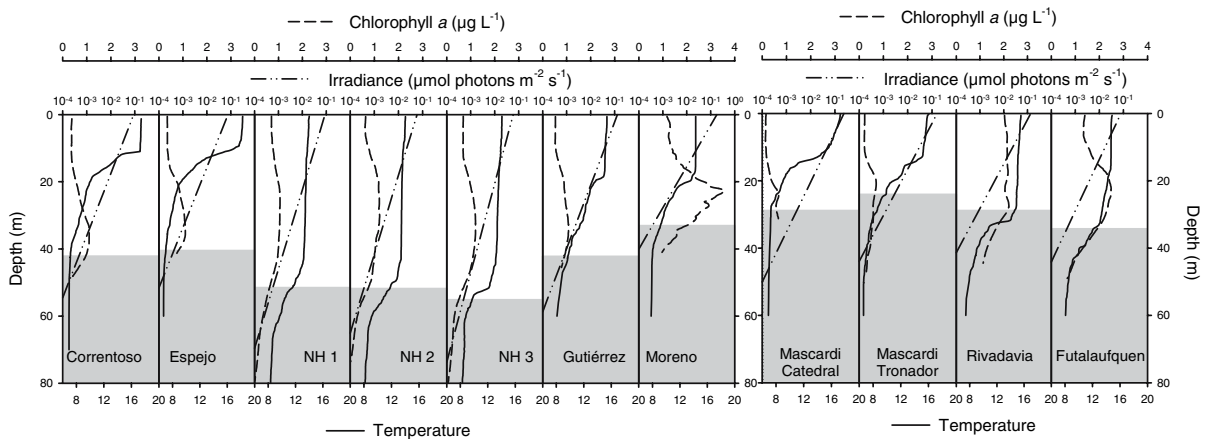
### Between lakes comparison

The lakes were all thermally stratified and had large euphotic zones, reaching 55 m for the large lake Nahuel Huapi (Fig. 2, Table 1). The relation between thermocline depth and  $Z_{1\% \text{ PAR}}$  differed among lakes. In lakes Correntoso, Espejo, Gutiérrez, Moreno and Mascardi the upper layers of the hypolimnion were included in the euphotic zone. In Lakes Rivadavia and Futalaufquen, euphotic zone was restricted to upper part of the epilimnion, whereas in Lake Nahuel Huapi, both zones almost overlapped and were very deep (Fig. 2).

Chlorophyll *a* concentration from 5, 10 and 30 m depth ranged from 0.25 to 2.35  $\mu\text{g l}^{-1}$ . However, we did observe noticeable differences along the water column with the development, in many lakes, of deep chlorophyll maxima (DCM) (Fig. 2).

As expected, TP concentration was in all cases very low (less than 0.19  $\mu\text{mol l}^{-1}$ ) (Table 1), and did not show marked differences in the vertical profile (Table 1 standard errors). TSC as an average of 5, 10 and 30 m depth, ranged from 27 to 63  $\mu\text{mol l}^{-1}$ . In some lakes, we observed slight increases of the C concentration at 30 m depth, especially those where a clear DCM developed (Correntoso, Espejo, Moreno and Mascardi).

The sestonic C:P atomic ratio were high in all lakes and values above 500 at certain depths were observed (except Lake Mascardi Cathedral 5 m



**Fig. 2** Vertical profiles of temperature (solid line), chlorophyll *a* (dashed line) and irradiance (dash-dot-dash line). Shaded area represents aphotic zone. Left group: lakes without *Daphnia*, right group: lakes with *Daphnia*

**Table 1** Features of Andean lakes studied during summer 2003

Lake	$Z_{1\% \text{ PAR}}$ (m)	$Z_{\text{therm}}$ (m)	$K_d$ ( $\text{m}^{-1}$ )	TPP ( $\mu\text{g l}^{-1}$ )	TP ( $\mu\text{g l}^{-1}$ )	TSC ( $\mu\text{g l}^{-1}$ )	C:P ratio (atomic)		
							5 m	10 m	30 m
Correntoso	42	12	0.110	1.209 ± 0.186	3.069 ± 0.124	479.4 ± 0.024	1,098	659	1,484
Espejo	40	11	0.114	1.209 ± 0.093	3.224 ± 0.155	472.6 ± 13.644	846	951	1,236
Nahuel Huapi 1	52	40	0.089	2.325 ± 0.155	4.805 ± 0.310	643.2 ± 24.216	692	620	860
Nahuel Huapi 2	52	40	0.088	2.356 ± 0.062	4.836 ± 0.093	640.8 ± 22.008	743	740	630
Nahuel Huapi 3	55	40	0.083	2.108 ± 0.093	4.526 ± 0.155	565.1 ± 44.448	673	801	604
Gutiérrez	42	22	0.111	1.395 ± 0.155	3.782 ± 0.093	602.6 ± 29.952	1,448	1,254	793
Moreno Oeste	33	22	0.141	3.007 ± 0.434	5.766 ± 0.341	750.5 ± 46.104	732	687	549
Mascardi Catedral	29	18	0.166	1.426 ± 0.124	3.565 ± 0.186	327.7 ± 70.056	343	713	671
Mascardi Tronador	24	20	0.195	1.581 ± 0.031	3.875 ± 0.031	410.2 ± 14.976	713	625	673
Rivadavia	29	35	0.159	3.193 ± 0.186	5.828 ± 0.155	716.1 ± 56.640	605	646	485
Futalaufquen	34	38	0.136	2.387 ± 0.155	4.929 ± 0.062	641.1 ± 41.460	598	788	688

Total phosphorus (TP), total particulate phosphorus (TPP) and total sestonic carbon (TSC) concentrations are average from 5, 10 and 30 m depth.  $Z_{1\% \text{ PAR}}$  = euphotic zone depth,  $Z_{\text{therm}}$  = thermocline depth

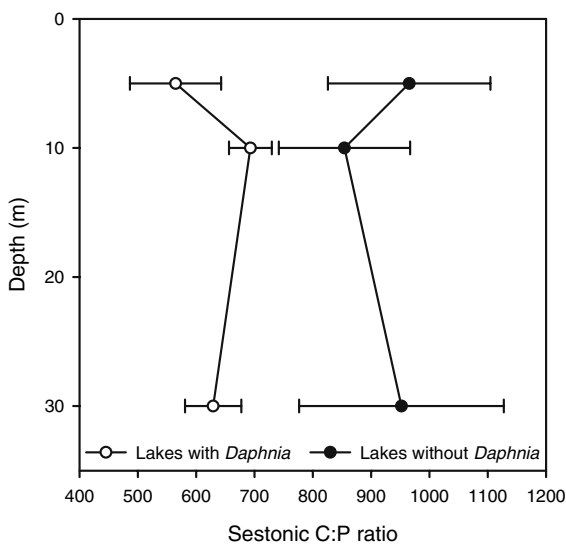
C:P = 343) (Table 1). In our dataset, seven sites lacked *Daphnia* whereas in four it was present (Table 2). The sestonic C:P ratio of lakes with and without *Daphnia* differed significantly (C:P with *Daphnia* < C:P without *Daphnia*) (two way ANOVA,  $F_{(1,27)} = 8.245, P = 0.008$ ) while no significant trends were observed with depth (Fig. 3).

*Daphnia commutata* was present in lakes Mascardi (Tronador and Catedral), Rivadavia and Futalaufquen with abundances around 3–5 ind  $\text{m}^{-3}$  (Table 2). However, the adult female sizes differed among lakes, being the largest in lake Rivadavia, and smallest in Mascardi (both arms) (Table 3). These

lakes showed comparatively low C:P ratios (mean range for water column, 574–691) and only lake Moreno (mean C:P = 653) lacking *Daphnia* was included within this range. In the other lakes, the cladocerans present were *Ceriodaphnia dubia* (Richard) (0.6 mm body length) and *Bosmina longirostris* (O.F.Müller) and *B. chilensis* Daday (both averaging 0.35–0.40 mm in body length) (Table 2). In all lakes, copepods were dominated by small and slender calanoids, *Boeckella gracilipes* (Daday) and *B. michaelsoni* (Mrázek), both of 0.7 mm total body length. In lakes Rivadavia and Futalaufquen the presence of another large crustacean, the predaceous

**Table 2** Crustacean zooplankton present (P) in the studied lakes during summer 2003

	<i>Daphnia commutata</i>	<i>Ceriodaphnia dubia</i>	<i>Bosmina longirostris</i>	<i>Bosmina chilensis</i>	<i>Boeckella gracilipes</i>	<i>Boeckella michaelsoni</i>	<i>Parabroteas sarsi</i>
<i>Lakes</i>							
Correntoso		P	P	P	P		
Espejo		P	P	P	P		
Nahuel Huapi 1		P	P	P	P		
Nahuel Huapi 2		P	P	P	P		
Nahuel Huapi 3		P	P	P	P		
Gutiérrez		P	P	P	P		
Moreno Oeste		P	P	P	P		
Mascardi Catedral	P	P	P	P	P		
Mascardi Tronador	P	P	P	P	P		
Rivadavia	P		P	P		P	P
Futalaufquen	P		P	P		P	P

**Fig. 3** Mean vertical profiles of sestonic C:P atomic ratio of lakes with and without *Daphnia*. Horizontal lines are 1 standard error**Table 3** *Daphnia commutata* adult size (mm)

Lake	Mean size	Maximum size	S.E.
Mascardi (both arms)	2.04	2.24	0.04
Rivadavia	2.22	2.68	0.05
Futalaufquen	2.16	2.64	0.04

calanoid *Parabroteas sarsi* Daday (3.08 mm body length) was recorded (Table 2).

The risk of visual predation would depend on the amount of light and the capability of the visual predator in detecting their prey. The amount of light in the water column in the studied lakes is high considering that the diffuse extinction coefficient ( $K_d$ ) varied between  $0.08 \text{ m}^{-1}$  in lake Nahuel Huapi (without *Daphnia*) and  $0.19 \text{ m}^{-1}$  in Mascardi Tronador (with *Daphnia*) (Table 1). However, all lakes, except Moreno, without *Daphnia*, showed larger euphotic zones ( $>40 \text{ m}$ ) than those with *Daphnia* (Fig. 2). The RED was used as an approach of the visual acuity of the fishes present in each lake. The RED of autochthonous patagonian adult fishes varied between 16 (*Percichthys trucha* (Cuvier & Valenciennes)) and 33 (*Galaxias maculatus* Jennyns) (Table 4). The latter is absent from lakes Rivadavia and Futalaufquen (Table 4). Combining both variables, we observed that the estimated predation risk corresponded well with the presence or absence of *Daphnia*. Lakes with PR lower than 200 have *Daphnia*, while in those with values higher than 240 *Daphnia* is absent (Fig. 4).

In lakes where *D. commutata* was present, it was found during daytime in deeper layers ( $>30 \text{ m}$ ). In Lake Rivadavia the daphnids performed vertical migrations, reaching 5 m depth after dawn (Reissig

**Table 4** Presence of autochthonous fishes in the Andean lakes studied and their corresponding Relative Eye Diameter (RED)

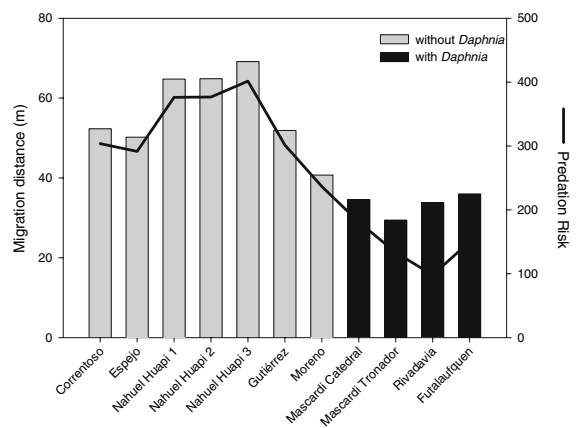
RED	<i>Galaxias maculatus</i>	<i>Galaxias platei</i>	<i>Aplochiton zebra</i>	<i>Odonthestes hatcheri</i>	<i>Percichthys trucha</i>	Literature source
	33	18	20	18	16	Ringuelet et al. (1967)
<i>Lakes</i>						
Correntoso	P	P			P	Cussac (pers. Comm.).
Espejo	P	P		P	P	Ruzzante et al. (2003)
Nahuel Huapi 1	P	P		P	P	Cussac (pers. comm.)
Nahuel Huapi 2	P	P		P	P	Cussac (pers. comm.)
Nahuel Huapi 3	P	P		P	P	Cussac (pers. comm.)
Gutiérrez	P	P				Barriga et al. (2002)
Moreno Oeste	P	P		P	P	Milano et al. (2002)
Mascardi Catedral	P	P				Milano et al. (2002)
Mascardi Tronador	P	P				Milano et al. (2002)
Rivadavia		P	P	P	P	Ruzzante et al. (2003)
Futalaufquen		P	P	P	P	Cussac (pers. comm.)

et al. 2004). Based on these data and on the extinction coefficient of each lake, we estimated the migration distance that *D. commutata* should have covered if present in all lakes (Fig. 4). This distance varied from 30 to 35 m in lakes Mascardi, Rivadavia and Futalaufquen, to more than 65 m in the case of Lake Nahuel Huapi. Lake Moreno showed the lowest expected migration distance of those lakes where *Daphnia* is absent (Fig. 4).

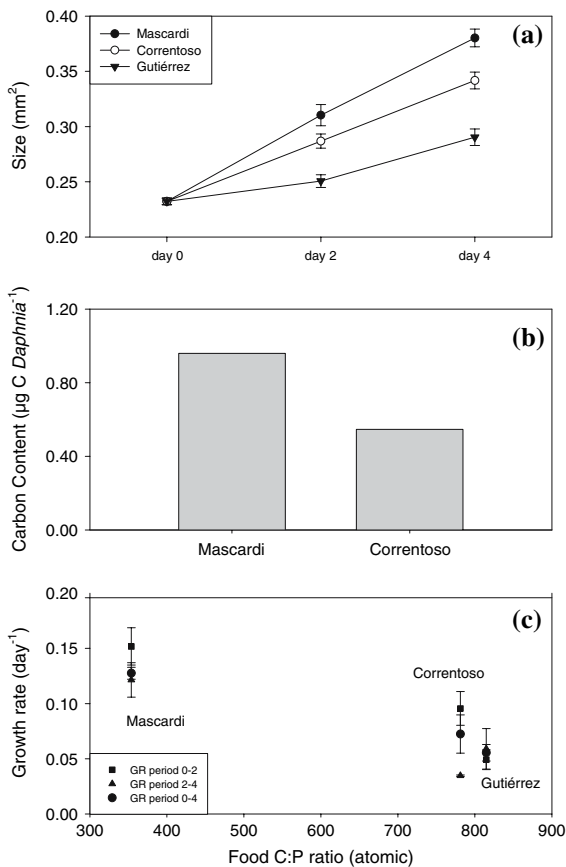
Experimental studies

The filtered (80 μm) seston used as food from the three different lakes did not differ in C content (23, 25 and 22 μmol l<sup>-1</sup> in lakes Mascardi, Correntoso and Gutiérrez respectively), but it did in C:P ratio (354, 781 and 815, respectively). The growth rates of *D. commutata* differed among the treatments (Fig. 5a). Neonates fed with seston of lake Mascardi grew better than those fed on seston from Lake Correntoso and Gutiérrez, in both two- and four-day experiments (ANOVA *P* < 0.001). Also carbon content per *Daphnia* differed among these treatments

(Fig. 5b, carbon content determination of *Daphnia* from Gutiérrez treatment failed). The observed difference in growth between treatments was not due to differences in C content of the food, as all treatments resulted in similar C content (mean ± S.E. 12.24 ± 0.513 μmol C l<sup>-1</sup>, ANOVA *P* > 0.05).



**Fig. 4** Estimated migration distance (vertical bars) and predation risk (solid line) in each of the studied lakes



**Fig. 5** Experimental growth assay. (a) Size of *Daphnia* in each of the treatments at initial, intermediate and final date. (b) Carbon content of individual *Daphnia* at the end of the experiment, Gutiérrez C estimation failed. (c) Growth rate as a function of the food C:P ratio

In our experiments, *D. commutata* growth rates were negatively correlated with the sestonic C:P ratio of the different filtered lake water used as food (Fig. 5c). Under higher C:P condition (Lake Correntoso and Gutiérrez) growth rates were extremely low and the individuals were starved. We observed that at day 4, the individuals reared with this lake water became very transparent and limb movements slowed down.

## Discussion

Our results support the hypothesis that the presence of large *Daphnia* in Andean lakes would be constrained by low food quality and high visual predation

risk. The C:P ratios in the studied lakes were always above 300, the threshold value for *Daphnia* P limitation (Urabe et al. 2002). In addition, the extremely transparent habitats (all  $K_d < 0.19 \text{ m}^{-1}$ ) would expose the large zooplankton to high visual predation pressure.

Among autochthonous fishes, only the patagonic silverside *Odonthestes hatcheri* (Eigenmann) and the Galaxiids are reported as planktivorous (Macchi et al. 1999). In particular, *Galaxias maculatus* is planktivorous throughout its lifespan, and can move from littoral to pelagic and from subsurface to 50 m depth (Barriga et al. 2002). In addition, its visual acuity seems to be high (Table 4) and it is able to efficiently consume small zooplankton (Reissig et al. 2003). On the contrary, *G. platei* Steindachner is planktivorous only in its early stages, as juveniles and adults are benthic (Milano et al. 2002). The absence of *O. hatcheri* in lake Mascardi (both arms) and of *G. maculatus* in lakes Rivadavia and Futalaufquen seems to contribute to the success of large *Daphnia* in these systems. Lakes Moreno and Futalaufquen appear to be very similar in most of their features (Table 1). The former, however, lacks *Daphnia*, and the presence of *G. maculatus*, increasing the predation risk (Fig. 4), may be the key in this difference.

The coexistence of planktivorous fish and *Daphnia* during summer depends on the presence of a deep-water refuge (Wright and Shapiro 1990; Tessier and Welser 1991). In such systems like the Andean lake Rivadavia, *Daphnia* avoids fish predation by migrating to surface waters at night, and deeper, dark layers during mid-day (Reissig et al. 2004). This migration reduces the probability of attack at the cost of decreasing net energy gain (Lampert 1993; De Robertis 2002). However, Williamson et al. (1996) showed that resources from a metalimnetic peak in Chl *a* supported better zooplankton reproduction than resource from surface waters. This suggestion would imply that *Daphnia* might successfully exploit the DCM of Andean lakes. Nevertheless, at daytime *D. commutata* occupies layers below 30 m depth that has  $<0.27 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , and this light intensity layer is in all lakes much deeper than the observed DCM (Fig. 2). Thus, the observed wider euphotic zones of lakes lacking *Daphnia* imply that it needs to migrate to reach at least the DCM layer (Fig. 2). However, in Lake Rivadavia, where Chl *a* is homogeneously distributed in the euphotic zone,



*D. commutata* migrates to 5 m depth during night (Reissig et al. 2004) instead of ascending only up to 20–25 m where Chl *a* is as abundant as at 5 m depth (Fig. 2). Based on this behaviour, we estimated that *D. commutata* should have migrate, in most lakes lacking *Daphnia*, a distance that resulted twice as high as for Lake Rivadavia (Fig. 4, grey bars).

The energetic disadvantage of vertical migration would be enhanced in a low quality food gradient. Many studies have shown that food quality is often more important than food quantity for grazers (Gulati and DeMott 1997; Sterner and Schulz 1998). Thus, DCM would imply an increase of food quantity but not a corresponding increase of food quality. In a study on four stratified Michigan lakes (two oligotrophic and two eutrophic), *Daphnia* growth improved with depth corresponding with a decrease in C:P ratio (DeMott et al. 2004). In Andean lakes we did not observe a general trend in the C:P ratio with depth, although lakes with *Daphnia* showed always lower ratios all along the water column (Table 1, Fig. 3).

High C:P ratios are associated with high light-phosphorus ratios (Sterner et al. 1997), so, as observed in our lakes, migration distances should increase as C:P increases. This implies a greater predation evasion effort with lower food quality. In addition, our experiments showed that Lakes Correntoso and Gutiérrez, lacking *Daphnia*, have food-quality conditions that may not support *Daphnia* growth. The food C concentrations in the three tested lakes were similar, but not the P, or C:P ratios. Some workers who used *Daphnia* growth assays with P supplement found evidence for P-limited growth in both hypereutrophic (DeMott et al. 2001) and oligotrophic lakes (Elser et al. 2001). *Daphnia* growth has been shown to correlate well with algal P content when food P content is below threshold levels (Urabe and Watanabe 1992; Sterner et al. 1993; Gulati and DeMott 1997). In addition, Acharya et al. (2004) indicate that variations in P content affect the growth rate of *D. galeata* and *D. pulicaria* through the ribosomal RNA content, since increase in growth rate requires elevated allocation of P to RNA-rich ribosomes. The food concentration in all studied Andean lakes can be considered very low, and low food quantity also increases the threshold for P limitation (Sterner 1997), that makes the bottleneck narrower. It seems that some of the lakes lacking *Daphnia*, like

Lake Moreno, are potentially capable to support daphnids, while others like Lake Correntoso seems to have too poor food quality. Stoichiometric theory predicts that C:P ratios >300 would result in P limitation for *Daphnia* (DeMott and Gulati 1999; Urabe et al. 2002). Our experiments, with C:P 350–820, showed a negative relationship between C:P and growth rates. Similar C concentration in all treatments, indicate the importance of P limitation.

On the other hand, it has been shown that low food quality, in terms of C:P ratio, increases the respiration rates in *Daphnia* to compensate for the excess of C (Darchambeau et al. 2003). As a result, in very transparent lakes, with low food quality and high C:P ratio, species like large *Daphnia*, with increased respiration rates, would not afford the high energy consuming vertical migration to avoid visual predation. Therefore, the persistence of a high P-demanding species populations are the outcome of food quality and visual predation pressure that can change the balance from success to failure.

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## References

- Acharya K, Kyle M, Elser J (2004) Biological stoichiometry of *Daphnia* growth: An ecophysiological test of the growth rate hypothesis. *Limnol Oceanogr* 49:656–665
- American Public Health Association (APHA) (1989) Standard methods for the examination of water, sewage, and wastewater. American Public Health Association, Washington, D.C
- Balseiro EG, Queimaliños CP, Modenutti BE (2004) Grazing impact on autotrophic picoplankton in two south andean lakes (Patagonia, Argentina) with different light:nutrient ratios. *Rev Chil Hist Nat* 77:73–85
- Barriga JP, Battini MA, Macchi PJ, Milano D, Cussac VE (2002) Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South Andes. *N Z J Mar Freshwater Res* 36:345–359
- Brett MT, MullerNavarra DC, Park SK (2000) Empirical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. *Limnol Oceanogr* 45:1564–1575
- Chillrud SN, Pedrozo FL, Temporetti PF, Planas FH, Froelich PN (1994) Chemical weathering of phosphate and

- germanium in glacial meltwater streams: effects of subglacial pyrite oxidation. *Limnol Oceanogr* 39:1130–1140
- Darchambeau F, Faeovig PJ, Hessen DO (2003) How *Daphnia* copes with excess carbon in its food. *Oecologia* 136:336–346
- De Robertis A (2002) Small-scale spatial distribution of the euphausiid *Euphausia pacifica* and overlap with planktivorous fishes. *J Plankton Res* 24:1207–1220(14)
- DeMott WR, Gulati RD (1999) Phosphorus limitation in *Daphnia*: evidence from a long term study of three hypereutrophic Dutch lakes. *Limnol Oceanogr* 44:1557–1564
- DeMott WR, Gulati R, VanDonk E (2001) *Daphnia* food limitation in three hypereutrophic Dutch lakes: evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnol Oceanogr* 46:2054–2060
- DeMott WR, Pape BJ, Tessier AJ (2004) Patterns and sources of variation in *Daphnia* phosphorus content in nature. *Aquatic Ecol* 38:433–440
- Elsner JJ, Hassett RP (1994) Stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystem. *Nature* 370:211–213
- Elsner J, Hayakawa K, Urabe J (2001) Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. *Ecology* 82:898–903
- Gulati RD, DeMott WR (1997) The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. *Freshw Biol* 38:753–768
- Guthrie DM, Muntz WRA (1993) Role of vision in fish behaviour. In: Pitcher TJ (ed) *Behaviour of teleost fishes*. Chapman & Hall, London, UK, pp 89–128
- Hessen DO (1992) Nutrient element limitation of zooplankton production. *Am Nat* 140:799–814
- Hessen DO (1997) Stoichiometry in food webs—Lotka revisited. *Oikos* 79:195–200
- Hessen DO, Faafeng BO (2000) Elemental ratios in freshwater seston: implications for community structure and energy transfer in food webs. *Arch Hydrobiol Spec Issues Adv Limnol* 55:349–363
- Hessen DO, Faerovig PJ, Andersen T (2002) Light, nutrients, and P:C ratios in algae: grazer performance related to food quality and quantity. *Ecology* 83:1886–1898
- José de Paggi S, Paggi JC (1985) Zooplankton de los cuerpos de agua preexistentes en el área del Embalse Amutui Quimei (Cuenca del Río Futaleufu). *Neotropica* 31:119–131
- Lampert W (1993) Phenotypic plasticity of the size at 1st reproduction in *Daphnia*—the importance of maternal size. *Ecology* 74:1455–1466
- Macchi PJ, Cussac VE, Alonso MF, Denegri MA (1999) Predation relationships between introduced salmonids and the native fish fauna in lakes and reservoirs in northern Patagonia. *Ecol Freshw Fish* 8:227–236
- Markert B, Pedrozo F, Geller W, Friese K, Korhammer S, Baffico G, Diaz M, Wolf S (1997) A contribution to the study of the heavy-metal and nutritional element status of some lakes in the southern Andes of Patagonia (Argentina). *Sci Total Environ* 206:1–15
- Milano D, Cussac VE, Macchi PJ, Ruzzante DE, Alonso MF, Vigliano PH, Denegri MA (2002) Predator associated morphology in *Galaxias platei* in Patagonian lakes. *J Fish Biol* 61:138–156
- Modenutti BE, Pérez GL, Balseiro EG, Queimaliños CP (2000) Relationship between light availability, chlorophyll a and total suspended solid in a glacial lake of South Andes. *Verh Int Ver Limnol* 27:2648–2651
- Modenutti B, Queimaliños C, Balseiro E, Reissig M (2003) Impact of different zooplankton structures on the microbial food web of a South Andean oligotrophic lake. *Acta Oecol Int J Ecol* 24:S289–S298
- Modenutti BE, Balseiro EG, Queimaliños CP, Añón Suárez DA, Diéguez MC, Albariño RJ (1998) Structure and dynamics of food web in Andean lakes. *Lakes Res Manage* 3:179–186
- Morris DP, Zagarese HE, Williamson CE, Balseiro EG, Hargreaves BR, Modenutti BE, Moeller R, Queimaliños C (1995) The attenuation of UV radiation in lakes and the role of dissolved organic carbon. *Limnol Oceanogr* 40:1381–1391
- Nusch EA (1980) Comparison of different methods for chlorophyll and phaeopigment determination. *Arch Hydrobiol Beih Ergeb Limnol* 14:14–36
- Paruelo JM, Beltran A, Jobbágy E, Sala O, Golluscio R (1998) The climate of Patagonia: general patterns and controls on biotic processes. *Ecol Austral* 8:85–101
- Pizzolón L, Santinelli N, Marinone MC, Menu-Marque SA (1995) Plankton and hydrochemistry of Lake Futalaufquen (Patagonia, Argentina) during the growing season. *Hydrobiologia* 316:63–73
- Reissig M, Queimaliños CP, Balseiro EG (2003) Effects of *Galaxias maculatus* on nutrient dynamics and phytoplankton biomass in a North Patagonian oligotrophic lake. *Environ Biol Fishes* 68:15–24
- Reissig M, Modenutti B, Balseiro E, Queimaliños C (2004) The role of the predaceous copepod *Parabroteas sarsi* in the pelagic food web of a large deep Andean Lake. *Hydrobiologia* 524:67–77
- Ringuelet RA, Aramburu RH, Alonso A (1967) Los peces argentinos de agua dulce. Comisión de Investigación Científica de la Provincia de Buenos Aires, Buenos Aires
- Ruzzante DE, Walde SJ, Cussac VE, Macchi PJ, Alonso MF, Battini M (2003) Resource polymorphism in a Patagonian fish *Percichthys trucha* (Percichthyidae): phenotypic evidence for interlake pattern variation. *Biol J Linn Soc* 78:497–515
- Sterner RW (1993) *Daphnia* growth on varying quality of *Scenedesmus*—mineral limitation of zooplankton. *Ecology* 74:2351–2360
- Sterner RW (1997) Modelling interactions of food quality and quantity in homeostatic consumers. *Freshw Biol* 38:473–481
- Sterner RW, Hessen DO (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. *Ann Rev Ecol Syst* 25:1–29
- Sterner R, Schulz K (1998) Zooplankton nutrition: recent progress and a reality check. *Aquatic Ecol* 32:261–279
- Sterner R, Hagemeyer D, Smith W (1993) Phytoplankton nutrient limitation and food quality for *Daphnia*. *Limnol Oceanogr* 38:857–871
- Sterner RW, Clasen J, Lampert W, Weisse T (1998) Carbon:phosphorus stoichiometry and food chain production. *Ecol Lett* 1:146–150

- Sterner RW, Elser JJ, Fee EJ, Guildford SJ, Chrzanowski TH (1997) The light:nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. *Am Nat* 150:663–684
- Tessier AJ, Welser J (1991) Cladoceran assemblage, seasonal succession and the importance of a hypolimnetic refuge. *Freshw Biol* 25:85–93
- Urabe J, Watanabe Y (1992) Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnol Oceanogr* 37:244–251
- Urabe J, Sterner R (1996) Regulation of herbivore growth by the balance of light and nutrients. *Proc Natl Acad Sci* 93:84–65
- Urabe J, Kyle M, Makino W, Yoshida T, Andersen T, Elser JJ (2002) Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. *Ecology* 83:619–627
- Williamson CE, Sanders RW, Moeller RE, Stutzman PL (1996) Utilization of subsurface food resources for zooplankton reproduction: Implications for diel vertical migration theory. *Limnol Oceanogr* 41:224–233
- Wright D, Shapiro J (1990) refuge availability: a key to understanding the summer disappearance of *Daphnia*. *Freshw Biol* 24:43–62