

Pelagic communities and ecosystem processes in Andean Patagonian lakes

Esteban Balseiro and Beatriz E. Modenutti

Laboratorio de Limnología, Depto. Ecología, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Unidad Postal Universidad, 8400 Bariloche, Argentina.

Abstract. *Limiting nutrients, nitrogen and phosphorus, are of crucial importance in the structure and dynamics of freshwater plankton. Oligotrophic lakes are nutrient limited environments and therefore their plankton dynamics depends mostly on internal mechanisms of recycling. The plankton dynamics and food web structure of Andean lakes were analysed linking the biogeochemical cycles and classic food web ecology. As in other oligotrophic waters, the producer trophic level of Andean lakes is formed by a phytoplankton dominated by small cells. A particular feature of these lakes is that the herbivorous zooplankton is restricted to rotifers and small crustaceans with body length < 1 mm. The direct effect of grazing decreases nanoplanktonic cells abundance but, the indirect effect of zooplankton (through nutrient recycling) results in an increase in netphytoplankton, particularly diatoms. Changes in the zooplankton constitution over the annual cycle may change the nutrient supply ratio. The copepod *Boeckella gracilipes* decreased P limitation lowering the N:P ratio whereas the dominance of the cladoceran *Bosmina longirostris* increased the N:P ratio and therefore increased P limitation during summer. In addition, predation by larvae of the autochthonous fish *Galaxias maculatus* change the quality and quantity of grazers since their predation on *Boeckella nauplii* provokes the failure of the summer cohort of the copepod. Consequently, zooplankton composition and the elemental ratios of recycled nutrients change. These results suggest that top-down and bottom-up effects of pelagic food webs cannot be easily separated.*

Introduction

The current view on pelagic communities is that the potential production at each trophic level is determined by available nutrients. During the last decade, this limitation by resources, named “bottom-up control”, was confronted with the control by predators (“top-down control”). In the former, carbon transfer from primary producers to higher levels determines the size of each level and the length of the food web. The latter states that a given trophic level will depend on predation pressure from the upper level (McQueen et al. 1989). In this scenario, predators will lower herbivore densities, and as a consequence, herbivory over primary producers will be lowered. Based on this view, and following the trophic cascade model (Carpenter et al. 1985), food web manipulation has been tested as a tool for eutrophication control (Gulati et al. 1990). Many observations confirm a strong effect of fishes on zooplankton size, but the link from fishes to phytoplankton is less clear (Gulati et al. 1990). In this sense, phosphorus appears as an important nutrient not only for lake productivity but also for community composition and food web organisation.

Classical food web models are based on the upward of energy from producers to predators. Although pioneering works recognised the importance of the flow of nutrients in food webs (Lotka, 1925), only in recent years was the role of nutrient recycling conceived as a structuring component of ecosystems (Hessen 1997). Stoichiometric studies of freshwater zooplankton demonstrated that elemental ratio in producers and consumers often mismatch, and so, this difference would affect nutrient release by excretion (Hessen and Andersen 1992). Therefore, the links between

biogeochemical cycles and classic food web ecology has surged as a new view of the role of nutrient cycling on aquatic food web regulation (Sterner and Hessen 1994).

In this contribution, we analyse the structuring of pelagic food webs in Andean lakes of the Bariloche region (41° S). This analysis was based on our own experimental data on nutrient flux rates, recycling by excretion, and interaction with predators. Since these oligotrophic lakes have low nutrient concentrations and slow rates of external supply, nutrient availability would depend on internal processes in the food web.

Pelagic communities in Andean lakes

Andean lakes, located between 39°S and 54°S in the Andean valleys, are of glacial origin and reach depths frequently greater than 100 meters. They are extremely transparent due to their oligotrophic condition and have an extended euphotic zone up to 50 meters (see Modenutti et al. 1998). Plankton assemblages of lakes in the Bariloche region (41° S), where our experimental work was carried out, have a very simple structure. The pelagic food web has four main trophic levels: producers, herbivores, planktivores, and piscivores (although the two latter ones are facultative).

Producers are represented by a phytoplankton in which nanoplanktonic flagellated cells (less than 20 µm in length) dominate over net phytoplankton (Queimaliños 1997). Thus, cell size distribution is shifted to small cells, a common feature of oligotrophic waters (Capblancq 1990). An additional mixotrophic level has been recently noted (Modenutti 1997, Modenutti et al. 1997). This assemblage is dominated by large ciliates (> 100 µm) that have stable associations with symbiotic green algae (*Chlorella*) and reach up to 2000 cells per ciliate (Modenutti 1988, Foissner and Wölf 1994). The species are restricted to large lakes (> 5 km²), where they develop important populations within the extended euphotic zone (40-50 m) (Modenutti 1997). The trophic linkages of this mixotrophic level are not yet understood.

Herbivorous zooplankton is characterised by the dominance of rotifers and small crustaceans (< 1 mm body length). This is a striking feature of Andean lakes since in temperate lakes of the Northern Hemisphere, zooplankton has a wider size range that depends on fish predation pressure (Brooks and Dodson 1965). Cladocerans are represented by species of the genus *Bosmina* and *Ceriodaphnia*. Copepods are mainly calanoids of the genus *Boeckella* since cyclopoid copepods are quite underrepresented numerically. *Boeckella gracilipes* Daday has a widespread distribution among lakes and is dominant in the pelagic zone below 20-30 m depth during daytime.

Interactions between zoo- and phytoplankton include direct losses of algae by consumption but, at the same time, zooplankters release phosphorus and nitrogen mainly as dissolved compounds of N and P available for algal uptake (Peters 1975, Lehman 1984, Sterner 1989). Release of nutrients by zooplankton is often the most important source of dissolved nutrients during stratification periods (Lampert and Sommer, 1997). Therefore, like other herbivores, zooplankton not only acts as predator in the classic sense but it also has an effect on competition among producers (Elser et al. 1988).

Nanoplanktonic producers constitute the main food resource for zooplankton and, consequently, niches at the herbivore level highly overlap (Matveev and Balseiro 1990). After experimentally increasing zooplankton biomass, we observed that grazing decreased nanoplankton abundance and consequently shifted the nano-net phytoplankton ratio (Queimaliños et al. 1998). Through this experimental manipulation, we obtained opposite responses of the nanoplanktonic flagellate *Chrysochromulina parva* Lackey and the netphytoplankter diatom, *Aulacoseira granulata* (Ehr) Simonsen. The heavy grazing on nanoplanktonic cells decreased *C. parva* abundance and *A. granulata* was released from resource competition, and benefited from the nutrients (P) recycled by zooplankton (Queimaliños et al. 1998). This highlights the importance of grazing as a direct limiting factor for *C. parva* abundance and the indirect effect through nutrient recycling on the development of net phytoplankton. Diatoms depend not only on N and P but also on available silica. Since, silica concentration in Andean lakes is higher than in other lakes of the world (Dfaz and Pedrozo 1993),

under heavy grazing a development of diatoms is expected, though silica is not recycled by grazers (Queimaliños et al. 1998).

The level of planktivores is represented by invertebrate and vertebrate predators. Remarkably, the most important North Hemisphere invertebrate predators, such as the Diptera *Chaoborus* and the Cladocera *Leptodora* are absent. However, a water mite (*Limnesia patagonica* Lundbald) and two calanoid copepods (*Boeckella gibbosa* Brehm and *Parabroteas sarsi* Daday) are present. Nevertheless, these organisms are not widespread since their presence is restricted to particular lakes. Water mites prey over rotifers and cladocerans (Balseiro 1992), the predaceous calanoid *Parabroteas* consumes a great variety of prey including rotifers, cladocerans, and copepods (Balseiro and Vega 1994, Vega 1995), while *Boeckella gibbosa* eats rotifers at the end of its development (Modenutti 1993).

Vertebrate planktivory is mainly exerted by fish larvae and juveniles of Galaxiidae and Atherinidae (Modenutti et al. 1993, Cervellini et al. 1993). During a spring-summer period, fish larvae preferred copepod nauplii whereas juveniles fed on cladocerans (Modenutti et al. 1993). In particular, larvae and juveniles of *Galaxias maculatus* Jennyns affected the copepod *B. gracilipes* causing the failure of its summer cohort (Modenutti et al. 1993).

The highest trophic level is poor in species. There are very few piscivorous fishes. Only one native species, the Patagonian perch (*Percichthys colhuapiensis* Mc Donagh), has been reported as piscivorous in adult stages. However, exotic salmonids, in particular species of *Salmo* and *Salvelinus* that are often considered as piscivorous have been introduced (Quirós 1998).

The recent focus on the role of the microbial food web in aquatic environments has changed the concept of the functioning of the pelagic ecosystems. Bacteria, algal and protozoan components of the so-called microbial loop (Azam et al. 1983) have extremely rapid turnover rates. In oligotrophic waters, most production is accounted by this small fraction of organisms (Capblancq 1990) which convert, both by autotrophy and heterotrophy, soluble organic and inorganic nutrients to particulate biomass. Therefore, studies on non-traditional taxons or trophic levels, such as the ciliate communities in Andean lakes, will contribute to a new and more accurate understanding of the planktonic food web in these environments. For example, it has been recently demonstrated that the green ciliate *Ophrydium naumanni* Pejler determines the chlorophyll a distribution in a deep oligotrophic Andean lake (Queimaliños et al. 1999).

Element cycling and stoichiometry

The transfer of matter and energy between trophic levels has been classically viewed as a transfer of carbon. In classical ecological theory, the amount of carbon fixed by producers would determine the energy available for consumers. Thus, environments with limited resources for consumers would have low carbon concentration. Recently, it has been shown that the elemental composition of carbon, nitrogen and phosphorus of different zooplankters may differ greatly between species, but not within them (Hessen 1990, Andersen and Hessen 1991, Hessen and Lyche 1991, Sterner et al. 1992, Sterner and Hessen 1994, Urabe et al. 1995).

In terms of food limitation, this new point of view shifted the food limitation from C or organic matter to a more specific elemental limitation (Hessen and Andersen 1992). Thus, the elemental C:N:P ratio of the ingested food became more important than the absolute amount of ingested C. This means that in a system where stoichiometry of phytoplankton is highly variable, but that of its consumers (zooplankton) is not, limitation may change from C to other element according to the particular elemental ratio of the consumers and their resource. As a rule, phytoplankton has a P:C ratio much lower than zooplankton's. Within zooplankton, this ratio increases from copepods to cladocerans and *Daphnia* is the endpoint of this distribution with highest P:C ratio (Hessen 1990). As a consequence assimilation efficiency of C of different species will depend on the differences between their specific P:C ratio and that of their food. Assimilation efficiencies for the different elements will then depend on specific internal ratio compared to that of the food ratio. Thus, the

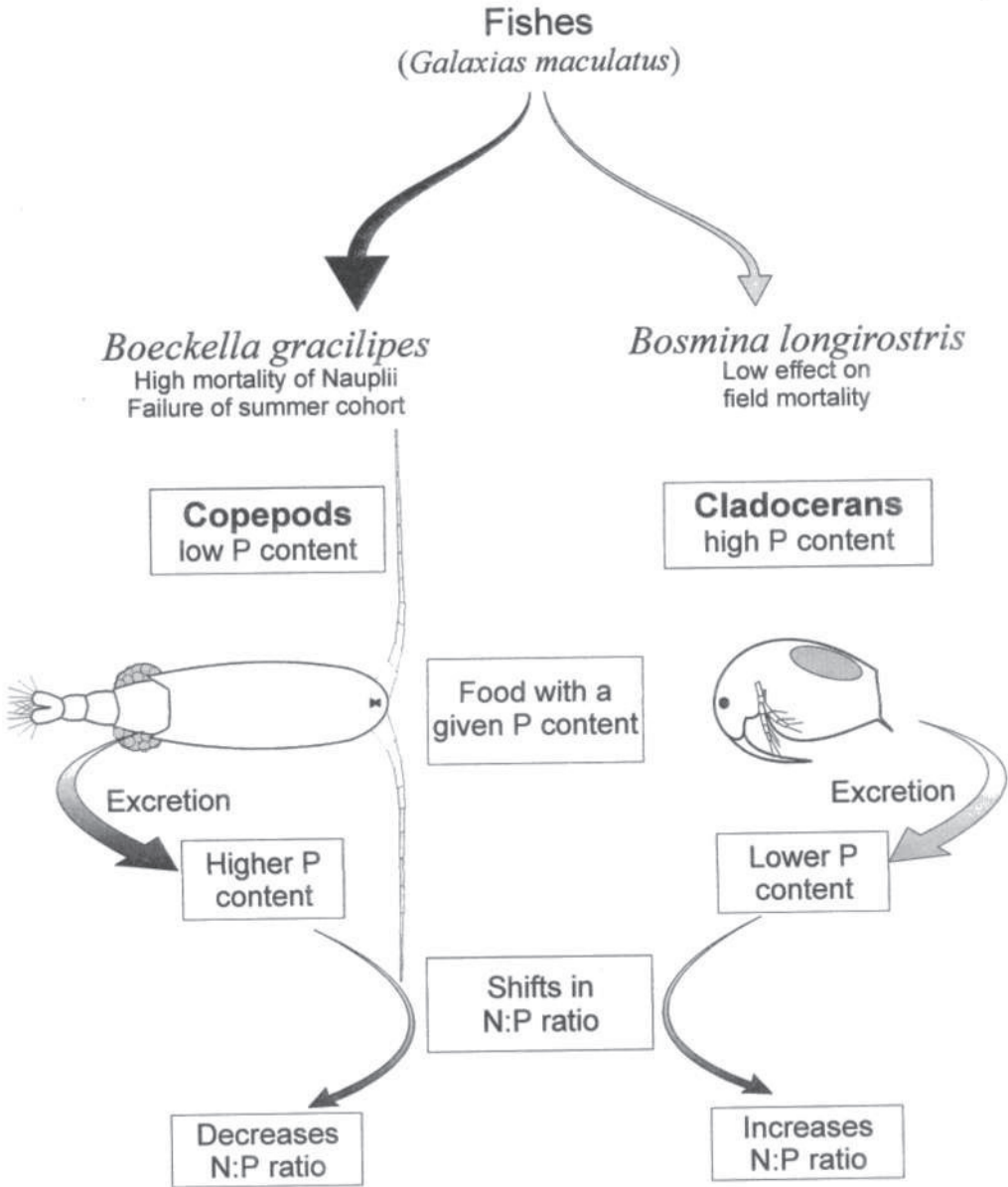


Figure 1. Relationship between intermediate and upper levels in Andean pelagic food web and the resulting N:P ratios. Based on Modenutti et al (1993) and Balseiro et al (1997).

assimilation of non-limiting elements will be lowered to maintain internal ratios with the limiting one. Since zooplankton has a P:C ratio higher than that of phytoplankton, it has been shown that C is no longer the limiting element (Hessen 1997).

It has been hypothesised that excretion greatly varies according to elemental composition of both the food and the grazer. With grazers that have a P:C ratio higher than that of phytoplankton, the direct and indirect effects (grazing and nutrient cycling) will force the grazers to retain more P and lower the assimilation of C. The phytoplankton will be more P-limited and the P:C ratio of algae lowered (Sterner 1990). When grazing on this algae, the difference between P and C assimilation by

consumers will be increased. However, different zooplankton constitution will recycle elements at different ratios and may drive the system to a stronger P limitation (Sterner and Hessen 1994). In oligotrophic lakes, where phytoplankton production is heavily nutrient limited, the zooplankton excretion is the primary short-term nutrient supply. Andean lakes, as other oligotrophic waters, promote a strong nutrient limitation for phytoplankton growth and, in consequence, resource competition will be enhanced. Under this condition, an increase of the rates of turnover of nitrogen and phosphorus can be expected indicating a faster internal recycling in oligotrophic waters (Capblancq 1990). However, the specific release rate of each element will depend on zooplankton constitution, so changes in it can produce changes in this elemental limitation.

In Andean lakes, zooplankton succession is characterised by a change in the dominance from the calanoid copepod *Boeckella gracilipes* in winter and spring to the cladoceran *Bosmina longirostris* in mid summer (Balseiro and Modenutti 1990, Balseiro et al. 1992). The N:P ratio of excretion changes according to this species replacement (Balseiro et al. 1997). A field incubation experiment showed that *Boeckella gracilipes* lowered the N:P ratio and decreased P limitation, whereas *Bosmina longirostris* increased this ratio and therefore increased P limitation during summer (Balseiro et al. 1997)

Under visual fish predation, zooplankton size structure shifts to smaller sizes (Brooks and Dodson 1965). This shift in size spectrum changes the effect of grazing on producers, since larger grazers have higher clearance rates (Top-Down effect) (Hall et al. 1976, Carpenter et al. 1987). However, changes in zooplankton constitution due to fish predation would affect the recycling of elements. Hessen (1997) predicts that top-down effect is no longer restricted to a matter of competition outcome and grazing intensity of zooplankton, but changes in elemental limitation would also derive from this predation as a consequence of species replacement. In Andean lakes, Modenutti et al. (1993) showed that fish larvae of *Galaxias maculatus* affect zooplankton through predation on copepod nauplii, and consequently, the summer cohort of the copepod *Boeckella gracilipes* fails. On the other hand, Balseiro et al. (1997) demonstrated that the different zooplankton constitution of spring and summer, is associated with nutrient recycling shifts from lower to higher N:P ratio. The fact that fish predation drives the summer zooplankton to a low copepod proportion may be in part responsible for the observed shift in elemental ratio available for producers (Figure 1). This means that the failure of the summer copepod cohort would affect the recycled nutrient ratio for algal growth. The effect of predation on the species composition of zooplankton affects the system in two ways. On the one hand, lowering one species, competition for resources will be affected in both consumers and producers' levels through changes in grazing pressure on the different phytoplankton species. On the other hand, the shift in zooplankton constitution changes the nutrient supply causing a stronger phosphorus limitation during summer.

Conclusions

In this contribution, we pointed out the importance of zooplankton constitution in nutrient recycling *via* excretion in oligotrophic Andean waters. The influences of both predators and nutrient availability are perhaps equally strong at the zooplankton-phytoplankton level and produce interactions that are hardly understood. As it has been shown, fish predation changes not only the quality and quantity of grazers, but also the elemental ratios of recycled nutrients. In consequence, the outcome of direct and indirect effect of grazers would depend greatly on the species involved both at the consumer and producer levels. At this point, it is clear that the consequence of any manipulation of the food web (intentionally or not) is not straightforward. Stoichiometric effects may be expected at all levels of the food web, with feedback mechanisms that cannot be easily separated (Hessen 1997). In addition, this point of view constitutes another argument against the strict top-down or bottom-up view of aquatic food webs, since a top-down effect, such as fish predation, has also bottom-up consequences, such as changes in available nutrient for producers.

Acknowledgements. This work was supported by UNC Grant B701 to BEM and ANPCyT Grant PICT 01-00000-01194 to EGB.

References

- Andersen, T. and D.O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.* 36:807-814.
- Azam, F., T. Fenchel, J.E. Field, J.S. Gray, L.A. Meyer-Riehl and F. Thingstad. 1983. The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10:257-263.
- Balseiro, E.G. 1992. The role of pelagic watermites in the control of cladoceran population in a temperate lake of the Southern Andes. *J. Plankton Res.* 14:1267-1277.
- Balseiro, E.G. and B.E. Modenutti. 1990. Zooplankton dynamics of Lake Escondido (Rio Negro, Argentina) with special reference to a population of *Boeckella gracilipes* (Copepoda, Calanoida). *Int. Revue ges. Hydrobiol.* 75:475-491.
- Balseiro, E.G. and M. Vega. 1994. Vulnerability of *Daphnia middendorffiana* to *Parabroteas sarsi* predation: the role of the tail spine. *J. Plankton Res.* 19: 783-793.
- Balseiro, E.G., B.E. Modenutti, and C.P. Queimaliños. 1992. The coexistence of *Bosmina* and *Ceriodaphnia* in a South Andes lake: an analysis of demographic responses. *Freshwat. Biol.* 28: 93-101.
- Balseiro, E.G., B.E. Modenutti and C.P. Queimaliños. 1997. Nutrient recycling and shifts in N:P ratio by different zooplankton structures in a South Andes lake. *J. Plankton Res.* 19: 805-817.
- Brooks, J.L. and S.L. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.
- Capblancq, J. 1990. Nutrient dynamics and pelagic food web interactions in oligotrophic and eutrophic environments: an overview. *Hydrobiologia.* 207:1-14.
- Carpenter, S.R., J.F. Kitchell and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-638.
- Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He, and C.N. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863-1876.
- Cervellini, P.V., M. Battini and V. Cussac. 1993. Ontogenetic shifts in the diet of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae). *Environ. Biol. Fishes* 36:283-290.
- Diaz, M. and F. Pedrozo. 1993. Seasonal succession of phytoplankton in a small andean Patagonian lake (Argentina) and some considerations about the PEG model. *Arch. Hydrobiol.* 127:167-184.
- Elser, J.J., M.M. Elser, N.A. MacKay and S.R. Carpenter. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. *Limnol. Oceanogr.* 33:1-14.
- Foissner, W. and S. Wölf. 1994. Revision of the genus *Stentor* Oken (Protozoa, Ciliophora) and description of *S. araucanus* nov. spec. from South American Lakes. *J. Plankton Res.* 16:255-289.
- Gulati, R.D., E.H.R.R. Lammens, M.L. Meijer and E. Van Donk (eds). 1990. Biomaniplulation- Tool for water management. *Hydrobiologia* 200/201:1-628
- Hall, D.J., S.T. Threlkeld, C.W. Burns and P.H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7:177-208.
- Hessen, D.O. 1990. Carbon, nitrogen, and phosphorus status in *Daphnia* at varying food conditions. *J. Plankton Res.* 12:1239-1249.
- Hessen, D.O. 1997. Stoichiometry in food webs - Lotka revisited. *Oikos* 79:195-200.
- Hessen, D.O. and T. Andersen. 1992. The algae-grazer interface: feedback mechanisms linked to elemental ratios and nutrient cycling. *Arch. Hydrobiol. Beih.* 35:111-120.
- Hessen, D.O. and A. Lyche. 1991. Inter- and intraspecific variations in zooplankton elemental composition. *Arch. Hydrobiol.* 121:343-353.
- Lampert, W. and U. Sommer. 1997. *Limnoecology: The ecology of lakes and streams.* Oxford University Press. Oxford. 382 pp.
- Lehman, J.T. 1984. Grazing, nutrient release, and their impacts on the structure of phytoplankton communities. Pp. 49-72. In: Meyers, D.G. and J.R. Strickler (eds.) *Trophic interactions within aquatic ecosystems.* American Assoc. Adv. Sci. Select. Symp. 85. Westview Press, Boulder.
- Lotka, A.J. 1925. *Elements of physical biology.* Williams and Wilkins, Baltimore. 460 pp.
- Matveev, V. and E.G. Balseiro. 1990. Contrasting responses of two cladocerans to changes in the nutritional value of nanoplankton. *Freshwat. Biol.* 23: 197-204.
- Mc Queen, D.J., M.R.S. Johannes, J.R. Post, T.J. Stewart and D.R.S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* 59:289-309.

- Modenutti, B.E. 1988. Presencia de *Ophrydium naumanni* Pejler (Ciliophora, Peritricha) en lagos andinos rionegrinos. *Neotropica* 36:99-103
- Modenutti, B.E. 1993. Summer population of *Hexarthra bulgarica* in a high altitude lake of South Andes. *Hydrobiologia* 259. 33-37.
- Modenutti, B.E. 1997. Distribución de los Ciliados Planctónicos *Ophrydium naumanni* y *Stentor araucanus* en Lagos Oligotróficos Andinos. *Rev. Soc. Mex. Hist. Nat.* 47:79-83.
- Modenutti, B.E., E.G. Balseiro and P.M. Cervellini. 1993. Effect of selective feeding of *Galaxias maculatus* (Salmoniforme, Galaxiidae) on zooplankton of a South Andes lake. *Aquatic Sciences*. 55:65-75.
- Modenutti, B.E., E.G. Balseiro and R. Moeller. 1997. Vertical distribution and resistance to ultraviolet radiation of a planktonic ciliate, *Stentor araucanus*. *Verh. int. Verein. Limnol.* 26 (in press).
- Modenutti, B.E., E.G. Balseiro, M.C. Diéguez, C.P. Queimaliños and R.J. Albariño. 1998. Heterogeneity of fresh-water Patagonian ecosystems. *Ecología Austral* 8:155-165.
- Peters, R.H. 1975. Phosphorus regeneration by natural populations of limnetic zooplankton. *Verh. int. Ver. Limnol.* 19:273-279.
- Queimaliños, C.P. 1997. Some physical and biological factors affecting a spring-summer phytoplankton dynamics in a shallow, temperate lake of south Andes (Argentina). *Internat. Revue ges. Hydrobiol.* 82:147-160.
- Queimaliños, C.P., B.E. Modenutti and E.G. Balseiro. 1998. Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake. *Freshwat. Biol.* 40:41-49.
- Queimaliños, C.P., B.E. Modenutti and E.G. Balseiro. 1999. Symbiotic consortium of the ciliate *Ophrydium naumanni* with *Chlorella* causing deep Chlorophyll-a maximum in an oligotrophic South Andes lake. *J. Plankton Res.* 21:167-178
- Quirós, R. 1998. Fish effects on trophic relationship in the pelagic zone of lakes. *Hydrobiologia* 361:101-111.
- Sternér, R.W. 1989. The role of grazers in phytoplankton succession. Pp. 107-170. In: Sommer, U. (ed.). *Plankton ecology: succession in plankton communities*. Springer-Verlag, Berlin.
- Sternér, R.W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. *Am. Nat.* 136:209-229.
- Sternér, R.W. and D.O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.* 25:1-29.
- Sternér, R.W., J.J. Elser and D.O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry* 17:49-67.
- Urabe, J., M. Nakanishi and K. Kawabata. 1995. Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in lake Biwa. *Limnol. Oceanogr.* 40:232-241.
- Vega A.P.M. 1995. Morphology and defensive structures in the predator-prey interaction: an experimental study of *Parabroteas sarsi* (Copepoda, Calanoida) with different cladoceran prey. *Hydrobiologia* 299: 139-145.

Received: May 11, 1998

Accepted: January 10, 1999