

Heterogeneity of fresh-water Patagonian ecosystems

Beatriz E. Modenutti, Esteban Balseiro, Maria del Carmen Diéguez, Claudia Queimaliños and Ricardo Albariño

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

Abstract. *The wide diversity of Patagonian freshwater ecosystems may be classified into three groups: glacial Andean lakes, Extra-andine closed depressions, and rivers and man-made lakes. We here analysed the biotic structure of Patagonian lentic and lotic ecosystems. We focus on the effect of both abiotic (climate, water composition, etc.) and biotic factors (competition, predation) on species diversity and composition of these communities. Zooplankton (rotifers and copepods) and macrobenthic insects (Plecoptera) were chosen as examples of the distribution patterns observed in lakes and rivers respectively. Rotifer species richness was explained by altitude, while species composition was related with conductivity. Three different rotifer assemblages were identified and associated with particular ranges of conductivity. In addition, the distribution of two rotifer genera, Keratella and Asplanchna, was related with biotic interactions (competition and predation). Crustacean size spectrum depended on visual fish predation. Plecoptera species richness decreased as a function of the stream order. Low stream order covered by Nothofagus forest showed the highest species number.*

Introduction

Patagonia includes two geomorphological regions: the Andine-Patagonian Cordillera and the Extra-Andine Patagonia (Iriondo 1989, Drago and Quirós 1996). These two regions have different conditions for lake development, since their climate and geology differ markedly. The lacustrine environments of these extended areas can therefore be divided in glacial lakes of the southern Cordillera, and Patagonian closed depressions (Iriondo 1989). The most important watersheds are located at the Andes with a precipitation up to 3000 mm per annum. The main rivers fed with these Andean waters cross the plateau steppe and outflow to the Atlantic Ocean, but there are also shorter rivers that cross the Andes flowing towards the Pacific Ocean. In the last years, a series of reservoirs were built on the main rivers (Limay, Neuquén, and Chubut). Consequently, a number of man-made lakes were established on this plateau, where natural lentic environments are scarce.

The geological history, geomorphologic features, climate, and human activities bring out clear differences in the freshwater systems. Consequently, these different patterns also produce a particular distribution of the biota. Distinctive food web structures, such as the presence or absence of top predators (e.g. fishes), contribute to the final expression of a given species assemblage. Moreover, during the last century human activities have produced changes in the trophic levels of rivers and lakes, together with species translocation (mainly due to fish introductions) which contributed to modify the original distribution pattern.

All these factors interactively affect species distribution. In this contribution, we attempt to explain the structure of the biota in Patagonian freshwaters. We focus on the interpretation of patterns and their relationship with both species interactions (competition and predation) and abiotic controls such as geographic and limnological features of Patagonian freshwater ecosystems. For this purpose, we have selected some representative groups of freshwater organisms that are abundant and also important because of their role in ecosystem dynamics.

Main characteristics of the freshwater environments of Patagonia

Patagonian freshwaters comprise both lentic (lakes) and lotic (rivers) environments. In particular the lentic systems can be divided according to their origin: glacial, tectonic with aeolian erosion, and man made lakes. For these reasons, we classified the systems in three groups: Glacial lakes of the southern Cordillera (Andean Lakes); Patagonian closed depressions (Patagonian Plateau lakes) and Rivers and Man made lakes. The differences between them cause the primary basis of heterogeneity in Patagonia freshwaters. We include a brief description of the most outstanding features of each one.

Glacial lakes of the southern Cordillera (Andean Lakes)

A series of deep lakes of glacial origin is located between 39°S and 54°S in the Andean valleys (Figure 1). The northern most lake is Aluminé in Neuquén Province and the southern most is Lake Fagnano in Tierra del Fuego. These lakes belong to two different large watersheds, one Atlantic and the other Pacific (Table 1). Their depth is frequently greater than 100 m, and the Nahuel Huapi lake surpasses 400 m depth. The climate of the area is temperate cool with precipitation of up to 3000 mm per annum. Vegetation corresponds to the *Nothofagus* forest. The thermal regime of the lakes is almost warm monomictic with direct thermal stratification in summer and the thermocline is frequently very deep, reaching 30-40 meters (Quirós and Drago 1985). A mixture of crystalline igneous volcanic and plutonic rocks dominates the region, therefore the waters are very diluted solutions dominated by calcium, bicarbonate and dissolved silica (Pedrozo et al. 1993, Drago and Quirós 1996). These lakes are extremely transparent due to their oligotrophic condition and have an extended euphotic zone up to 50 meters (Morris et al. 1995). However, some of these lakes (e.g. Mascardi, Frías, and Argentino) receive glacial clays, which reduce the depth of the euphotic zone because of the increase of their light extinction coefficients.

As it was mentioned, the trophic level of these lakes is oligotrophic or ultraoligotrophic. Phytoplankton assemblages reflect this condition (Izaguirre et al. 1990), with a clear dominance of small flagellate cells in the community.

Patagonian closed depressions (Patagonian Plateau lakes)

Along the Extra-Andine Patagonia, there is a number of shallow and extended waterbodies (Figure 1). The climate is dry and cold with a severe aeolian erosion and the vegetation corresponds to a steppe (Paruelo et al. 1998). Two types of closed depressions are characteristic of the area: comparatively small depressions in deflation hollows and larger depressions in tectonically sunken blocks (Iriondo 1989). The lakes are located in the lowest part of the depressions and only few of them constitute permanent lacustrine environments (Iriondo 1989). In the central region of Río Negro Province, the Carrilufquen Grande, Carrilufquen Chica, and Ñe Luan lakes are the most important. South from these systems, in Chubut Province, large depressions contain the largest plateau lakes: Musters and Colhué Huapi (Figure 1, Table 1).

The waters are alkaline with moderate dissolved solids. The presence of waters alternatively rich in calcium or sodium indicates that rock dominance or evaporation-precipitation balance controls the water chemistry (Drago and Quirós 1996), adding complexity to the area. The lakes are turbid, due to presence of inorganic suspended particles. In addition, the trophic level is rather high with frequent cyanophyte blooms.

Rivers and Man made lakes

Lotic systems itself show a marked spatial heterogeneity along the course. The most important rivers that cross the Patagonian steppe have their headwaters in the Andes (Figure 1). River waters have similar ionic relation to those of the lakes with calcium and bicarbonate as dominants (Pedrozo et al. 1993). Headwaters are densely covered by *Nothofagus* forests, and therefore primary

Table 1. Some Limnological and Geographical Features of selected Freshwater Ecosystems (from Quirós and Drago 1985, and Calcagno et al. 1995). References: Z_{\max} : maximum depth. Z_{eu} : depth of the euphotic zone. n.a.: data not available.

	Area (Km ²)	Z_{\max} (m)	Z_{eu} (m)	Latitude	Altitude (m)
NATURAL GLACIAL LAKES OF THE SOUTHERN CORDILLERA					
<i>Atlantic Watershed</i>					
Aluminé	57.0	165.0	31.0	39° 15'S	1125
Quillén	23.0	155.0	38.8	39° 25'S	975
Huechulafquen	78.2	255.0	17.6	39° 46'S	875
Nahuel Huapi	557.0	464.0	59.0	40° 50'S	764
Argentino	1466.0	n.a.	n.a.	50° 20'S	187
Yehuin	43.5	42.7	n.a.	54° 24'S	241
<i>Pacific Watershed</i>					
Lácar	49.0	277.0	34.1	40° 14'S	600
Mascardi	39.2	218.0	23.5	41° 20'S	750
Puelo	44.0	180.0	15.3	42° 10'S	150
Rivadavia	21.7	147.2	27.0	42° 36'S	527
Futalafquen	44.6	168.0	32.9	42° 49'S	518
Fagnano	580.0	80.7	n.a.	54° 35'S	140
NATURAL PATAGONIAN CLOSED DEPRESSIONS					
Musters	414.0	38.5	2.8	45° 22'S	275
Colhué Huapi	810.0	5.5	0.3	45° 30'S	265
Cardiel	460.0	49.1	n.a.	48° 57'S	300
MAN-MADE LAKES					
Mari Menuco	174.0	130.0	20.0	38° 36'S	422
Los Barreales	411.0	120.0	4.9	38° 35'S	426
Arroyito	38.6	15.0	n.a.	39° 14'S	315
Ramos Mexía	816.0	60.0	9.4	39° 30'S	381
Alicura	67.5	110.0	n.a.	40° 40'S	705
Ameghino	65.0	61.5	5.4	43° 42'S	169
Amutui-Quimei	86.7	300.0	24.7	43° 03'S	502

production is limited by light, among other factors. These low order streams receive leaf litter from the forests and the cycling of this organic matter becomes an important factor for stream dynamics. Although man-made lakes are fed with Cordillera waters their chemical and thermal conditions differ considerably from those of the rivers that enter to the reservoir. Mariazzi et al. (1991) pointed out that salinity in a reservoir was about 20% higher than that of the river.

Two studied examples

The knowledge of the biota of Patagonian freshwaters is still fragmentary. However, recent studies provide evidence of how trophic structure can add to the heterogeneity determined by abiotic features. We include two examples, one of lentic zooplankton and the other one of lotic benthos. These examples are selected because they are important in determining lake and river dynamics. In addition, we have achieved experimental evidences of the interactions that may occur within these



Figure 1. Hydrological map of Patagonia. Dashed line shows the limit between Glacial lakes of the Southern Cordillera and Patagonian closed depressions (from Iriondo 1989 and Drago and Quirós 1996).

fractions (for an extensive revision of experimental evidences see Modenutti et al. 1998 and references therein).

Example 1. Lacustrine Zooplankton Composition and Structure

There are two large groups of factors to which zooplankton composition and structure can be related. First, factors that can be referred as abiotic, and second a group that includes the trophic state of the systems and the amount of competition and predation. These factors interactively shape the community. This has been well illustrated by the seminal work of Brooks and Dodson (1965).

During an examination of the distribution of the cladoceran *Daphnia* in the lakes of southern New England (USA), it was noted that large *Daphnia* could not be found in the plankton of several lakes. All of these lakes lacking large zooplankters had fish populations. On this basis, these authors formulated the Size-Efficiency Hypothesis that became a paradigm in aquatic ecology. This hypothesis stresses that the final composition of a given zooplankton assemblage is the result of competition and predation. Fish are responsible for the elimination of the large zooplankton species and large zooplankton themselves suppress the small species in the absence of fish by competitive interactions. Although there are some aspects of the competition side of the hypothesis that remain less clear, there are no doubts about its general trends (Lampert and Sommer 1997).

We will analyse two examples of zooplankter (rotifers and calanoid copepods) distributions showing how the geographic, abiotic heterogeneity and the interacting biota influence the final species assemblages.

Rotifer Distribution. Rotifer assemblages recorded in Patagonia correspond to the biogeographic Andean Patagonian Subregion with species typical of cold waters (José de Paggi 1990). In this Subregion are included both, Andean deep lakes and Patagonian plateau freshwater environments. However, at a more detailed scale, rotifers have been used as limnological indicators (Kuczynski 1987), showing that particular features of Patagonian waters correspond to different rotifer composition.

Recently, Modenutti (1998) studied a longitudinal and altitude gradient in the Río Negro Province and showed that altitude explained a significant amount of variation in rotifer species richness, while chlorophyll a, conductivity, and pH did not. On the other hand, conductivity affected species composition. Thus, three species assemblages were observed. One corresponded to Andean glacial lakes with conductivity values lower than $67 \mu\text{S cm}^2$, another one was observed in Patagonian Plateau lakes with higher concentration of total dissolved solids, and the third group included species with apparently wide distribution.

In particular, the genus *Brachionus* offers an interesting pattern of distribution in Patagonian waters. Species richness of this genus decreased towards the South, from nine species at 35°S to five at 41°S , and to only two at 45°S (Jose de Paggi 1990, Modenutti and Balseiro 1994). Although, *Brachionus* has a Gondwanian origin (Dumont 1983), the greatest number of species was recorded in the tropics, showing preference for shallow alkaline and warm waters (Ruttner-Kolisko 1974). Therefore the latter may be considered as a limiting factor for species distribution, since the lakes of the Patagonian Plateau are shallow and alkaline, but temperatures fall down to 0°C during winter. The slightly acid waters of the Andean lakes and their thermal features can be considered as restrictive for *Brachionus* and may be a suitable explanation for the absence of the genus in these lakes. The particular increase in salinity and temperature observed in man-made lakes may have allowed *B. calyciflorus* to colonize them, extending the distribution of the genus towards the west (Modenutti 1998).

Besides chemical and physical characteristics, biotic interactions can also play an important role in rotifer species distribution. 'The Size Efficiency Hypothesis predicts that large zooplankton dominates fishless lakes, while smaller zooplankters can coexist in lakes under strong visual predation pressure. Transparency benefits planktonic rotifers by reducing their visibility to fish. This situation was observed in Carrilauquén Chica lake (Modenutti and Balseiro 1994) where sizes over 0.5 mm are monopolised by the rotifer *Asplanchna* (Figure 2a). This rotifer possesses a clear translucent body that may reduce its visibility to visually feeding fish. The registered size spectrum of zooplankton (and therefore species composition) can be related with the strong fish predation pressure exerted by autochthonous and introduced fishes (rainbow trout and argentine silverside).

Rotifers share their habitat with cladocerans and copepods, interacting with them through exploitative and interference competition, and predation (Nogrady et al. 1993). The genus *Keratella* is widely distributed in Patagonia. *K. tropica* has a distributional pattern similar to that of the genus *Brachionus* (Diéguez and Modenutti 1996). On the other hand, *K. cochlearis* extends its distribution to Andean low conductivity lakes, but shows morphological variations in body size and the posterior spine (spined, spineless) in different environments (Diéguez and Modenutti 1996). These variations

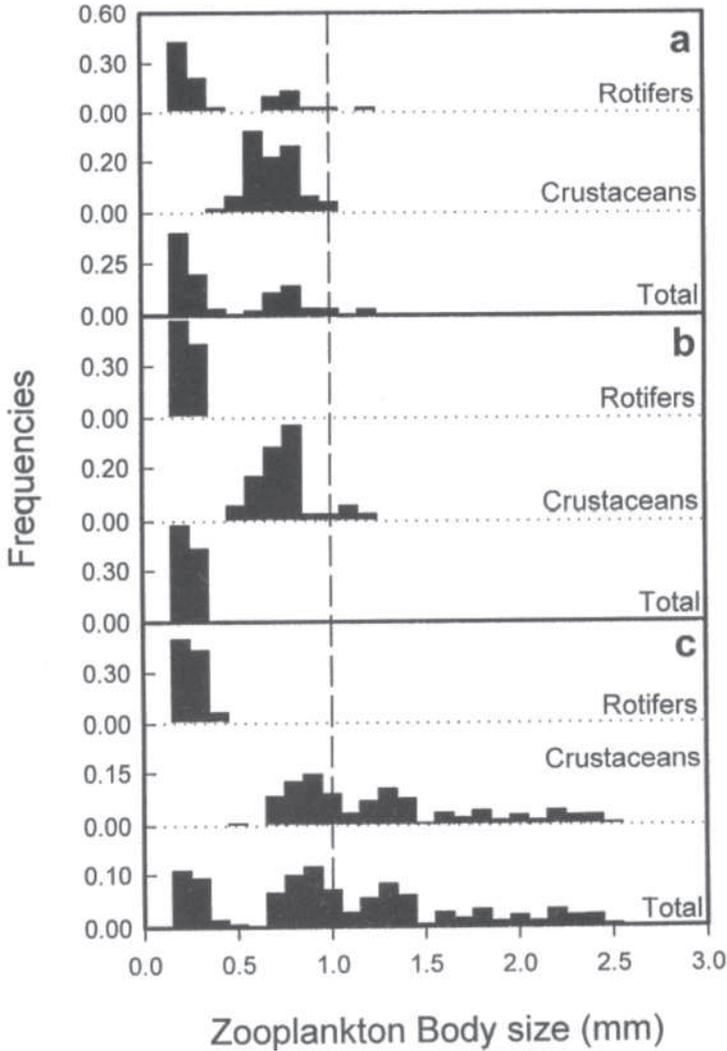


Figure 2. Zooplankton size spectrum in three lakes of Patagonian Plateau. a: Lake Carrilauquen Chica; b: Lake Carrilauquen Grande and c: an unnamed fishless lake. Note that in a and b total distribution resembles that of rotifers, as crustaceans are very scarce in the whole zooplankton assemblage (redrawn from Modenutti and Balseiro 1994).

are related to biotic interactions such as competition for resources and predation, since the largest spined forms are present in invertebrate predator-prone environments, while spineless forms appeared in higher trophic status Patagonian Plateau lakes. *Keratella cochlearis* is a clear example of distinctive morphology under different zooplankton assemblages and trophic level of Patagonian lakes. In this sense, different morphs were observed in Andean lakes, Patagonian Plateau lakes and a Patagonian reservoir (Diéguez and Modenutti 1996). Besides, several endemic species of *Keratella* were recorded in Tierra del Fuego bogs and in Cardiel and Colhué Huapi (José de Paggi 1990).

Boeckellids Distribution (Crustacea, Copepoda, Calanoida, Centropagidae). The boeckellids are restricted to the Southern Hemisphere with two exceptions, one in Mongolia and the other in

northern Italy (Bayly 1992a). Their importance as biogeographical indicators has been longly recognised (Brehm 1936, Ringuet 1958). The present distribution can be related with the progressive fragmentation of Gondwana during the latter Mesozoic (Bayly 1992b). In South America, boeckellids occur even as far north as Ecuador and Colombia at altitudes of about 4000 m (Löffler 1963). It has been proposed that the distribution of this group is related to the availability of a thermal refuge (cold waters), as they have colonised lower latitudes through the high altitude Andean corridor (Bayly 1992b).

In Patagonia, centropagids are the only calanoids and they are distributed both in Andean and Patagonian Plateau lakes. There are still open questions in the taxonomy of this group and in its environmental requirements (Menu-Marque and Zúñiga 1994). If we consider the existence of the two old genera *Boeckella* and *Pseudoboeckella* (they have been fused in an unique *Boeckella* genus by Bayly (1992a)) then, a particular habitat partition can be proposed. The old *Boeckella* species generally inhabit the pelagial of lakes, feeding on the small sized fraction of phytoplankton (less than 20 μm) (Haney and Trout 1985, Menu-Marque and Zúñiga 1994, Queimaliños et al. 1998). On the other hand, *Pseudoboeckella* species preferentially dominate ponds and shallow lakes, most of them fishless lakes (Menu-Marque and Zúñiga 1994, Modenutti and Balseiro personal observation). These species are unspecialised filter feeders with a tendency to macrophagy including large algae (benthic diatoms and filaments of cyanobacteria) as well as smaller preys like rotifers (Weller 1977, Jarvis 1988, Modenutti 1993).

Visual predation pressure exerted by fishes can be also considered a factor that affects boeckellids distribution. Some species of this group (mainly *Pseudoboeckella* species) are densely pigmented with colours that go from bright red to black, causing a different vulnerability to fish predation. Therefore, these species are restricted to fishless lakes (Modenutti and Balseiro personal observation) or they never dominate the pelagic community (Menu-Marque and Marinone 1986, Menu-Marque and Zúñiga 1994). Besides, large body sizes of some species offer also high susceptibility to fish predation pressure. In several Patagonian Plateau lakes it was observed that only small boeckellids (less than 1.2 mm) might be able to persist in fish lakes (Modenutti and Balseiro 1994) (Figure 2b), while a broader zooplankton size spectrum was found in fishless ponds (Figure 2c). Moreover, Menu-Marque and Marinone (1986) pointed out that the large centropagid *Parabroteas sarsi* (Daday) occurs in the pelagial only in turbid waters (e.g. Colhué Huapi) where the suspended matter diminishes their vulnerability to fish predation. The introduction of fishes in lakes will therefore affect greatly the zooplankton constitution, changing the predation pressure and driving the outcome of intrazooplankton interactions. These examples point out the importance of the changes in natural zooplankton assemblages that have been produced by the combined introduction of rainbow trout and argentinian silverside as a traditional practice in South America (Hurlbert et al. 1986).

Example 2. Benthic Plecoptera of Patagonian rivers

The Andean region contains rithronic streams. These lotic environments constitute the headwaters of the main rivers that cross Patagonia (Figure 1). The *Nothofagus* forest densely covers the headwaters and provides allochthonous organic matter. This condition is drastically modified as rivers enter into the Patagonian steppe and change their order and magnitude. From headwaters to the mouth, heterotrophic systems gradually turn into autotrophic systems and the composition of benthic macroinvertebrates reflects this change (Vannote et al. 1980). The cycling or spiralling of the organic matter is produced by the action of the river biota, in which benthic insects are an important fraction. Therefore, river invertebrates have been classified in the following functional feeding groups: shredders, collectors, grazers and predators (Cummins 1973). There is a downstream decrease in the size of organic particles resulting in an increasing importance of collectors, the species that utilise fine particles most effectively.

This general scheme proposed for the Northern Hemisphere may also represent Patagonian river dynamics. In headwaters, where *Nothofagus* forest cover the low order streams, a co-dominance of shredders and collectors can be predicted, while collectors and grazers would tend to prevail in intermediate to high order rivers. However, additional complexities can occur because

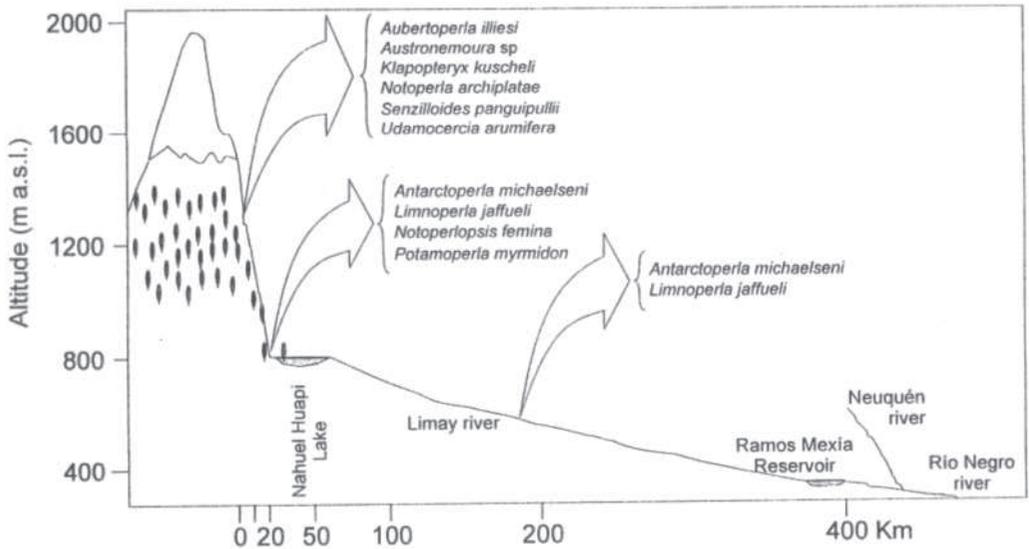


Figure 3. Schematic cross section of Patagonia from Andes to Rio Negro river, showing the Plecopteran species distribution along the Ñireco-Limay river. (Data from Wais 1990 and Albariño 1997)

rivers run through lakes before crossing Patagonian steppe. For example, headwaters as Ñireco, Casa de Piedra, Castilla and López among other streams run through Nahuel Huapi lake which then drains to the Limay river.

In Andean streams, benthic invertebrate communities have been poorly studied. However, Plecoptera have received special attention because of their endemic and relictual zoogeographic distribution (Illies 1963, 1964, Wais 1984, 1987). Andean low order streams have cold and well-oxygenated waters, which are the most suitable environments for Plecoptera. Six families are known in South America, and three of them (Austroperlidae, Diamphipnoidae and Eustheniidae) have a restrictive distribution to Andean Cordillera (Benedetto 1974).

Wais (1990) reported 22 species of Plecoptera from the Limay Basin and more recently, Albariño (1997) studied the spatial distribution of this group in the Ñireco stream, a low order stream of the same system. Considering both contributions, an interesting pattern can be pointed out in relation to river conditions (low order and major river) (Figure 3).

In the upper section of a low order stream, seven Plecopteran species were found. From these: *Klapopteryx kuscheli*, *Senzilloides panguipullii*, *Austronemoura sp.*, *Notoperla archiplatae* and *Udamocercia arumifera* were exclusive of this stream section (Figure 3). These species showed preferences for cold stenothermal conditions and a habitat densely covered by deciduous *Nothofagus* forest. *Klapopteryx kuscheli* belongs to the functional feeding group of shredders and dominates the biomass of the macroinvertebrate fraction. The numerical importance of this species is due both to physical condition of this mountain rithronic environment and the presence of deciduous *Nothofagus* surrounding forest.

The lower section of this stream, just before Nahuel Huapi lake, can be considered a piedmont rithronic environment. Plecoptera species richness decreased and only four species were found: *Antarctoperla michaelseni*, *Limnoperla jaffueli*, *Notoperlopsis femina*, and *Potamoperla myrmidon*, being *P. myrmidon* and *N. femina* restricted to this section of the stream (Figure 3). The decrease in species number can be related to the change in riparian vegetation, since there is no *Nothofagus*

forest covering the stream. The other two species found in this stream section, *A. michaelsoni* and *L. jaffueli*, extend their distribution to major rivers since they have been recorded along the Limay river (Wais 1984).

This example shows the spatial heterogeneity of a Patagonian river and the importance of both the characteristics of the stream and the riparian vegetation. Riparian vegetation is susceptible to change because of human activities through deforestation or reforestation with exotic tree species. Therefore stream conditions, heterotrophic or autotrophic, may be modified and consequently, their benthic fauna will be remodelled.

The future

The increase of human activity in Patagonia will have an important effect on distribution and interactions of species. We attempted, through these selected examples, to point out the probable changes that man could produce in natural communities. As was examined before, species introductions in freshwater ecosystems will greatly affect biotic assemblages through changes in species interactions such as predation and competition. The present man-made lakes have modified the natural condition of a region with scarcity of permanent lentic environments. Furthermore, the sustained construction of new reservoirs will enhance the alterations in species distribution.

An increment in nutrient input to freshwater ecosystems can be also expected since human settlements increase soil erosion, sewage discharges and alterations in the land-water interface. Consequently, aquatic communities would result deeply altered. Land use becomes crucial for river dynamics since it modifies river channel, erosion, sediment transport and riparian vegetation. Therefore, natural stream heterogeneity would be adjusted, resulting in a different pattern of biota distribution and energy transfer within the ecosystem.

Finally, climate change adds to and interacts with substantial ongoing anthropogenic changes in ecosystems (Carpenter et al. 1992). Therefore, global changes, land use and direct human use of freshwaters, must be taken into account for future research. In this sense, it will be necessary to develop new models accounting for the effect of precipitation, plant responses to carbon dioxide, runoff and vegetation changes.

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

References

- Albariño, R. 1997. Spatial distribution of Plecoptera from an Andean-Patagonic lotic environment in Argentina. *Rev. Brasil. Biol.* 57:629-636.
- Bayly, I.A.E. 1992a. Fusion of the genera *Boeckella* and *Pseudoboeckella* (Copepoda) and revision of their species from South America and sub-Antarctic islands. *Rev. Chil. Hist. Nat.* 65:17-63.
- Bayly, I.A.E. 1992b. The non-marine Centropagidae (Copepoda, Calanoida) of the World. SPB Academic Publishing bv, The Hague, 30 pp.
- Benedetto, L. 1974. Clave para la determinación de los Plecópteros sudamericanos. *Stud. Neotrop. Fauna* 9:141-170.
- Brehm, V. 1936. Ober die Tiergeographischen Verhältnisse der Circumantarktischen Süßwasserfauna. *Biol. Rev.* 11:477-493.
- Brooks, S.L. and S.I. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150:28-35.
- Calcagno, A., M.A. Fioriti, F. Pedrozo, P. Vigliano, H. Lopez, C. Rey, M.E. Razquin and R. Quirós (eds.). 1995. Catálogo de lagos y embalses de la Argentina. Min. Econ. Obr. Serv. Públ., Seer. Obr. Públ., Subs. Rec. Hidr., Buenos Aires.
- Carpenter, S.R., S.G. Fisher, N.B. Grimm and J.F. Kitchell. 1992. Global change and freshwater ecosystems. *Annu. Rev. Ecol. Syst.* 23:119-139.
- Cummins, K.W. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.* 18:183-206.

- Diéguez, M.C. and B.E. Modenutti. 1996. *Keratella* distribution in North Patagonian lakes (Argentina). *Hydrobiologia* 321:1-6.
- Drago, E. and R. Quirós. 1996. The hydrochemistry of the inland waters of Argentina: a review. *Int. J. Salt Lake Res.* 4:315-325.
- Dumont, H.J. 1983. Biogeography of Rotifers. *Hydrobiologia* 104:19-30.
- Haney, J.F. and M.A. Trout. 1985. Size selective grazing by zooplankton in Lake Titicaca. *Arch. Hydrobiol. Beih.* 21:147-160.
- Hurlbert, S.H., L. Washington and T. Moreno. 1986. Fish-flamingo-plankton interactions in the Peruvian Andes. *Limnol. Oceanogr.* 31:457-468.
- Illies, J. 1963. Revision der südamerikanischen Gripopterygiden (Plecoptera). *Mitt. Schweiz. Ent. Ges.* 36:145-248.
- Illies, J. 1964. Südamerikanischen Perlidae (Plecoptera), besonders aus Chile and Argentinien. *Beit. Neotrop. Fauna* 3:207-233.
- Iriondo, M. 1989. Quaternary lakes of Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 70:81-88.
- Izaguirre, I., P. del Giorgio, I. O'Farrell and G. Tell. 1990. Clasificación de 20 cuerpos de agua Andino-Patagónicos (Argentina) en base a la estructura del fitoplancton estival. *Cryptogamie (Algologie)* 11:31-46.
- Jarvis, A.C. 1988. Diel zooplankton community feeding activity and filtration rates of *Pseudoboeckella volucris* and *Daphnidiopsis studeri* on sub-antarctic Marion Island. *Hydrobiologia* 164:13-21.
- José de Paggi, S. 1990. Ecological and biogeographical remarks on the rotifer fauna of Argentina. *Rev. Hydrobiol. trop.* 23:297-311.
- Kuczynski, D. 1987. The rotifer fauna of Argentine Patagonia as a potential limnological indicator. *Hydrobiologia* 150:3-10.
- Lampert, W. and U. Sommer. 1997. *Limnoecology. The Ecology of lakes and streams.* Oxford Univ. Press, New York, 382 pp.
- Löffler, H. 1963. Zur Ostrakoden and Copepodenfauna Ekuadors (mit Beschreibung 6 neuer Arten and 3 neuer Unterarten). *Arch. Hydrobiol.* 59:196-234.
- Mariuzzi, A., V. Conzonno, R. Echenique and H. Labollita. 1991. Physical and chemical characters, phytoplankton and primary production of Ezequiel Ramos Mexía Reservoir (Argentina). *Hydrobiologia* 209:107-116.
- Menu-Marque, S. and M.C. Marinone. 1986. El zooplankton de seis lagos del Chubut (Argentina) y sus probables relaciones con la ictiofauna y algunos factores ambientales. *FAO* 4:90-114.
- Menu-Marque, S.A. and L.R. Zúñiga. 1994. *Boeckella diamantina* n.sp. (Calanoida, Centropagidae), from a high Andean lake in Mendoza, Argentina. *Hydrobiologia* 292/293:81-87.
- Modenutti, B.E. 1993. Summer population of *Hexarthra bulgarica* in a high altitude lake of South Andes. *Hydrobiologia* 259:33-37.
- Modenutti, B.E. 1998. Distribution of planktonic rotifers in North Patagonian lakes (Argentina). *Verh. Internat. Verein. Limnol.* 26:1968-1972.
- Modenutti, B.E. and E.G. Balseiro. 1994. Zooplankton size spectrum in four lakes of the Patagonian Plateau. *Limnologica* 24:51-56.
- Modenutti, B.E., E.G. Balseiro, C.P. Queimaliños, D.Añon Suárez, M.C. Diéguez and R.J. Albariño. 1998. Structure and dynamics of food web in Andean lakes. *Lakes and Reservoirs Res. and Managements* 3:179-186.
- Morris, D., H. Zagarese, C. Williamson, E. Balseiro, B. Hargreaves, B. Modenutti, R. Moeller and C. Queimaliños 1995. The attenuation of UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.* 40:1381-1391.
- Nogrady, T., R.L. Wallace and T.W. Snell. 1993. *Rotifera: Biology, Ecology and Systematics.* S.P.V. Academic Publishing bv, The Hague 142 pp.
- Paruelo, J.M., A. Beltrán, E. Jobbágy, O.E. Sala and R. Golluscio. 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecologia Austral* 8:85-101.
- Pedrozo, F.L., S. Chillrud, P. Temporetti and M.M. Diaz. 1993. Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39° 5'-42° S; 71° W) (Rep. Argentina). *Verh. Internat. Verein. Limnol.* 25:207-214.
- 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. *Freshwater Biol.* 40:41-49.
- Quirós, R. and E. Drago. 1985. Relaciones entre variables físicas, morfométricas y climáticas en lagos patagónicos. *Rev. Asoc. Cienc. Nat. Litoral* 16:181-199.

- Ringuelet, R.A. 1958. Los crustáceos copépodos de las aguas continentales de la República Argentina. Cont. Cient. Fac. Cienc. Exact. Fís. Nat., UBA, Zool.1:35-126.
- Runner-Kolisko, A. 1974. Plankton Rotifers: Biology and Taxonomy. Binnengewässer 26: 1-146.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, R. Sedell and C. E. Cushing. 1980. The river continuum concept. J. Fish. Aq. Sci.37:130-137.
- Wais, I.R. 1984. Two Patagonian basins - Negro (Argentina) and Valdivia (Chile) - as habitats for Plecoptera. Anns. Limnol. 20:115-122.
- Wais, I.R. 1987. Macrozoobenthos of Negro River Basin, Argentine Patagonia. Stud. Neotrop. Fauna and Environ. 22:73-91.
- Wais, I.R. 1990. A checklist of the benthic macroinvertebrates of the Negro River Basin, Patagonia, Argentina, including an approach to their functional feeding groups. Acta Limnol. Brasil. 3:829-845.
- Weller, D.L.M. 1977. Observations on the diet and development of *Pseudoboeckella poppei* (Calanoida, Centropagidae) from an Antarctic Lake. Br. Antarct. Surv. Bull. 45:77-92.

Received: May 11, 1998

Accepted: December 16, 1998